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RESEARCH PAPER

Do biological traits drive geographical patterns in European amphibians?

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ABSTRACT

Aims The present-day biogeography of European amphibians has been hypothesized to have arisen from range expansion and recolonization of the northern part of the continent from southern late Pleistocene refugia, such that northern species generally possess large ranges while southerly species are mostly small-ranged. Here we test the hypothesis that these patterns are likely to be underpinned by biological traits associated with dispersal ability. We do this by analysing data for anurans and urodeles, the two main groups of European amphibians.

Location Europe.

Methods We built a database of biological traits (body size, fecundity, life span, habitat specialization) of European amphibians, excluding island endemics. We mapped the basic macroecological patterns of range size and position, and analysed the causal pathways for range size using structural equation models (SEMs).

Results Amphibian species with a small range size are largely restricted to areas in southern Europe associated with putative Pleistocene refugia. Those present in northern Europe are exclusively large-ranged species whose distributions extend all the way from southern Europe. SEMs explained 54% of range size variation for anurans, with long life span and high fecundity being influential explanatory variables, and explained 61% of range size variation within urodeles, with measures of species fecundity being influential.

Main conclusions Species that have successfully recolonized the north following deglaciation have the largest ranges for both groups of amphibians. These large-ranged species generally possess traits that indicate the potential for rapid range expansion, with differences apparent in the balance of traits between anurans and urodeles. The traits linked to northern distributions (and large range size) appear to be a mix of *r* and *K* traits, indicating that intermediate life-history strategies have proved to be optimal for range expansion into northern regions. These results integrate species biology with geographical history in explaining present-day patterns of species distribution, range size and diversity.

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Amphibian biogeography, body size, clutch size, developmental biology, Europe, geographical range size, habitat specialization, macroecology, structural equation models, trait biogeography.

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INTRODUCTION

Variation in the geographical range size of species underpins coarse-scale patterns of species richness and is linked to both extinction risk and sensitivity to environmental change (Brown, 1995; Gaston & Blackburn, 2000). More specifically, small range size has been shown to be a strong predictor of extinction risk in frogs (Murray & Hose, 2005a; Cooper *et al.*, 2008). Knowledge of range sizes may thus be particularly important in the conservation of amphibians, which in recent years have suffered serious declines (Houlahan *et al.*, 2000). Amphibians might also be particularly susceptible to range contractions due to climate change (Araújo *et al.*, 2006), because many species have a low dispersal ability and respond slowly to environmental change.

It has been hypothesized that macroecological patterns in European amphibian diversity reflect the effect of Pleistocene glaciations (Zeisset & Beebee, 2008), which forced Europe's amphibians to retreat to southern refugia. This conjecture is supported by phylogeographical studies (e.g. Rowe *et al.*, 2006; Wielstra *et al.*, 2013). In addition, we note that (1) historical climate stability has been found to be a better predictor of amphibian distribution than current climate (Araújo *et al.*, 2008), and (2) whereas the northern fauna is composed of species with larger ranges, almost all small-ranging amphibians are distributed in the south of the continent, reflecting limited dispersal out of Pleistocene refugia (Sillero *et al.*, 2014).

Despite their relatively poor dispersal ability (Smith & Green, 2005), amphibians are widely distributed on a global scale. Recently, van Bocxlaer *et al.* (2010) suggested that the cosmopolitan distribution of toads is the result of highly dispersive phenotypes that have evolved multiple times in the history of amphibians. These phenotypes are characterized by traits that allow individuals to move rapidly and tolerate adverse climatic conditions. In bufonids these traits include the presence of parotoid glands, large body size and an aquatic–opportunistic oviposition strategy (van Bocxlaer *et al.*, 2010). The same set of biological traits may also be linked to survival in multiple refugia (see Dufresnes & Perrin, 2015) and the ability to disperse out of Pleistocene refugia and to cross dispersal barriers (López-Villalta, 2012).

Taken together, these observations indicate that species-specific traits, in combination with the geographical and climatic history of the region, may have acted to shape macroecological patterns in Europe: patterns such as the spatial distribution of species richness and of geographical range size, and the trait distribution of the regional species pool in northern latitudes. The basic question, i.e. whether large-scale properties of regional species pools are influenced mainly by historical contingency or current environmental limitations, remains a major challenge in ecology and biogeography.

Although various species traits may potentially affect the geographical range size of animal species, only a few have been thoroughly studied, including body size, local abundance and dietary niche breadth – and then only for particular taxa. In a meta-analysis of 64 studies across taxa, Slatyer *et al.* (2013) recently found a significant positive relationship between range size and measures of niche breadth, including environmental tolerance, habitat breadth and dietary breadth. In addition, range size seems to be positively correlated with body size and local abundance in many species of animals, although the relationships are seldom strong (reviewed in Gaston & Blackburn, 1996; Borregaard & Rahbek, 2010). In addition to these general studies, a few studies of amphibians have also related variation in geographical range size to reproductive traits. Clutch size has been found to be positively correlated with geographical range size in frogs (Cooper *et al.*, 2008), and so has body size (Murray et al., 1998). A negative correlation between egg size and range size (Murray & Hose, 2005b) have been reported for Australian frogs. Here, we tested the prediction that European amphibian species differing in geographical range size would also differ in those biological traits associated with dispersal ability.

Owing to inherent differences in the body plan, reproductive mode and main mode of locomotion, the importance of specific traits is predicted to differ between the two main groups of European amphibians, anurans (frogs and toads) and urodeles (newts and salamanders). Generally, European urodeles can be regarded as *K*-reproductive strategists that produce a relatively small number of eggs (tens to hundreds) and frequently show parental care, such as wrapping individual eggs into the leaves of aquatic vegetation (e.g. species of *Triturus* and *Lissotriton*) or guarding the eggs (e.g. *Speleomantes*). European anurans, on the other hand, are typical opportunists (*r*-strategists) that produce thousands of eggs with little parental care (see Arnold & Ovenden, 2002). Hence, although anurans are usually very fecund, they tend to produce relatively small juveniles and suffer greater juvenile mortality than urodeles.

Additional complications include the possibility that certain traits may interact to influence geographical range size simultaneously (Brown *et al.*, 1996), and that the same trait can have both positive and negative indirect effects (e.g. as shown for body size in European passerines by Laube *et al.*, 2013). Thus, to understand the relationships between geographical range and traits it is important to consider multiple traits and their interactions. We used structural equation modelling to test the hypothesis that specific trait combinations may explain which species of European anurans and urodeles were able to disperse into and colonize northern areas after the end of the Last Glacial Maximum (LGM).

MATERIALS AND METHODS

Data set

We used global range polygons (IUCN, 2012) to define geographical ranges (in km^2) for all amphibian species occurring within the geographical boundaries of Europe (defined as the part of the Eurasian continent located west of the Ural Mountains). The recent taxonomic revision of Speybroeck *et al.*

(2010) was used to recognize species status and for nomenclature. Range maps of species that deviated from this taxonomy were modified accordingly. Taxa that occurred only in eastern Europe and were not covered by the taxonomy of Speybroeck *et al.* (2010) were recognized according to IUCN (2012). Range extensions by means of recent reintroductions and ranges of exotic, recently introduced species (e.g. *Lithobates catesbeianus*) were excluded. We also excluded 14 species strictly confined to islands, resulting in a list of 65 amphibian species. For the trait analysis we excluded 11 species with insufficient data and two klepton species, resulting in 52 amphibian species (*c.* 66% of the indigenous species list).

Species traits

We gathered information on species biological traits from scientific papers, species descriptions, field guides, the IUCN global amphibian assessment (GAA) and Amphibiaweb (Appendix 1 and Table S1 in Supporting Information). Priority was given to the primary sources (i.e. scientific papers). We identified four biological traits that a priori were expected to affect range expansion ability: body size, fecundity, life span and adult habitat specialization. Three of the measured traits (body size, clutch size, adult habitat) have previously been shown to promote range expansion of toads (van Bocxlaer *et al.*, 2010). We linked these traits to range size in a hypothesized causal diagram (see Fig. S1), which was used to specify structural equation models (SEMs). We provide detailed justification for each variable below.

Body size

Amphibians with larger bodies have a higher relative water storage ability (e.g. Schmid, 1965) and greater locomotor performance (e.g. Emerson, 1978), allowing them to move actively over longer distances. Also, body size may affect range size via an indirect effect on fecundity (e.g. Lüddecke, 2002) and intrinsic development rate (see Morrison & Hero, 2003). A positive correlation of body size with maximum longevity has also been reported in amphibians (Blanco & Sherman, 2005); we modelled this relationship as a covariance in our SEM (Fig. S1). We measured body size as the maximum snout–vent length (SVL), which is the most commonly used proxy for body weight in amphibians. For urodeles there are two methods of measuring SVL; we used the length from the tip of the snout to the posterior angle of the cloaca (sometimes referred to as the standard length, STL; e.g. Malmgren & Thollesson, 1999) whenever possible.

Fecundity

In general, species with high fecundity (e.g. large clutch sizes) may be more likely to undergo passive dispersal of eggs and larvae, and may also have a colonization advantage because of the possibility of rapid population growth (Begon *et al.*, 1996). It is also possible that fecund species may be under stronger selection for juvenile dispersal to reduce the effect of competition among siblings. It has also been suggested that high fecundity in frogs should predispose species for high local abundances, which can have an indirect effect on range size via metapopulation dynamics (Murray & Hose, 2005b). There may be a trade-off between clutch size and the rate of juvenile development (e.g. Lüddecke, 2002), because species with large clutches tend to have smaller eggs (e.g. Parichy & Kaplan, 1995). We used maximum (annual) clutch size of eggs (or number of live young in cases of viviparity) as a measure of fecundity for each species. Excluding strictly viviparous species (*Salamandra atra* and *Salamandra lanzai*) from the SEM analysis decreased model fit, but did not qualitatively alter the presented results (see Fig. S2). The analyses in the main paper therefore include these species.

Life span

Species with longer individual life spans may be able to disperse further in the adult stage. Long-lived amphibians exhibit negligible senescence, with modestly indeterminate growth and undiminished reproductive capacity (Kara, 1994). Life span may also indirectly affect range sizes via an effect on fecundity, as long-lived species may allocate fewer resources to yearly reproduction and have more attempts at reproduction during their lifetime. We used a measure of maximum age observed in the wild or in captivity, as estimated from skeletochronological studies or by direct observation.

Habitat specialization

Species with specialized habitat associations are likely to have smaller geographical ranges (Brown, 1984). We used data on adult habitat preference from the GAA data (IUCN, 2012), which are categorized according to the degree of habitat specialization outside the breeding season. Aquatic, semi-aquatic and terrestrial amphibian species were categorized into: (1) opportunistic (eurytopic) species that use a wide range of terrestrial and aquatic habitats and (2) specialized (stenotopic) species with a narrow range of environmental tolerance that depends on a specific habitat with constant availability of water.

Statistical analyses

We conducted all analyses separately for anurans and urodeles. Trait variables were $\log_{10}$-transformed to improve normality (with the exception of habitat specialization, which is defined on a nominal scale).

Structural equation models

We represented our a priori hypothesized causal relationships between species traits and geographical range size as a causal graph (Fig. S1) that then formed the basis for the SEMs. We used the protocol described in Grace *et al.* (2012) to simplify the SEM diagram to produce the final models. We examined the available data, considered the focus of the analysis, sample size, appropriate model complexity and the need to including latent variables. Due to the small sample size (anurans $n = 28$, urodeles $n = 24$), we kept models simple, with

five SEM parameters and no latent variables. We included the direct effects of life span, fecundity and body size on geographical range size, as well as the direct effects of life span and body size on fecundity. Associations between life span and body size were considered as co-variation. The same SEM design was used for anurans and urodeles.

We evaluated the fit of the SEMs using several diagnostic metrics: chi-square tests, the root mean square error of approximation (RMSEA), the goodness-of-fit index (GFI) and the comparative fit index (CFI). The RMSEA ranges from 0 to 1, with lower values indicating a better fit. GFI and CFI range from 0 to 1, with higher values indicating a better fit. A good model fit was inferred when the chi-square *P*-value was > 0.05, the RMSEA value was < 0.1, and the CFI and GFI indices were > 0.90. Standardized path coefficients and model fit index values were calculated using SPSS AMOS (Arbuckle, 2008).

Phylogenetic relatedness

Because functional traits evolve gradually over evolutionary time, the traits of related species are not independent (e.g. Felsenstein, 1985), hence standard regression analyses have been suggested to overestimate the degrees of freedom. This issue arises if the dependent and independent variables in a regression share the same autocorrelation structure. Sophisticated tools exist for implementing phylogenetic structure directly into regression analyses (e.g. Martins & Hansen, 1997) and SEMs (von Hardenberg & Gonzalez-Voyer, 2013; Olalla-Tárraga *et al.*, 2015). However, these tools require branch lengths to be estimated robustly and trait definitions to be defined for the entire (global) tree; thus it was not feasible to implement these methods in a robust and transparent manner in the current study. As a crude test of whether phylogenetic relatedness was an issue for our analysis, we followed the protocol of Laube *et al.* (2013) in testing for phylogenetic signal in the residuals of multiple regressions of traits against range size. For this we used the Abouheif test (Abouheif, 1999) implemented in the R package ADEPHYLO (Jombart *et al.*, 2010), using 999 randomizations of the structure of a regional amphibian phylogeny extracted from the global species-level phylogeny by Pyron & Wiens (2011) (all species were present in this phylogeny). No phylogenetic signal existed in the residuals, which gives some indication that the results were robust to phylogenetic autocorrelation.

Nonetheless, SEM models are based on multiple correlations between specified traits, and thus there is a potential for phylogenetic autocorrelation to affect the deeper relationships in our SEM models, for example relationships between body size and fecundity, even if the overall residuals are free from autocorrelation. This means that the causal relationship among these traits should be interpreted with caution. However, phylogenetic autocorrelation is not expected to be a problem for the correlations between range size and the various biological traits. Range size generally has very little phylogenetic autocorrelation (e.g. Brown, 1995), and for European amphibians the majority of the species range extents have formed within the last 10,000 years, and thus under a much faster time-scale than that of trait evolution. The situation where, for example, two closely related species have similar body sizes, allowing them to attain a larger range, is not a statistical problem in the context of phylogenetic autocorrelation. In our SEM analyses, the direct relationships between biological traits and range size are generally stronger than relationships among biological traits.

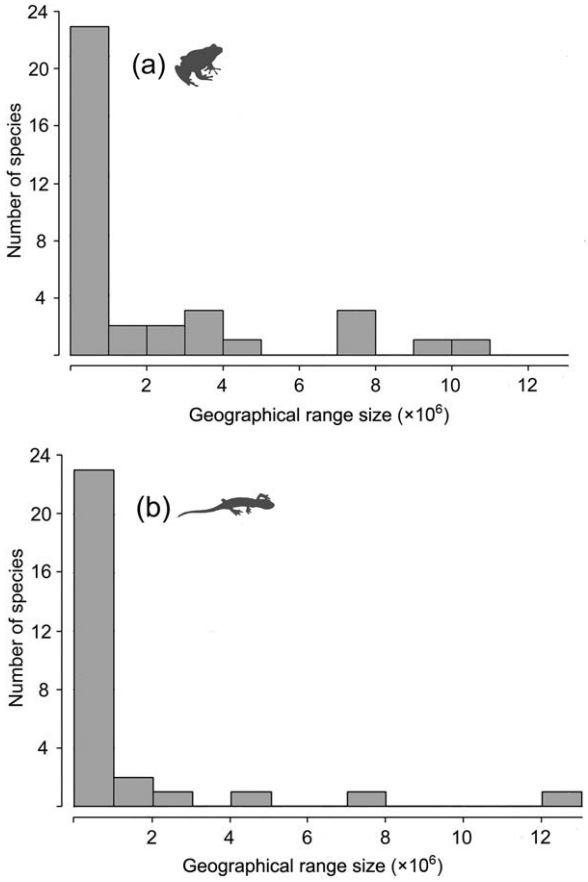

Figure 1 Frequency distributions of geographical range size (in 1,000,000-km^2 bins) for (a) 36 species of anurans and (b) 29 species of urodeles in Europe.

RESULTS

Range size frequency distributions

The range size distributions of European amphibians were strongly right-skewed (Fig. 1), with mean range sizes (2.016×10^6 km^2 for anurans and 1.109×10^6 km^2 for urodeles) markedly larger than the medians (0.554×10^6 km^2 and 0.164×10^6 km^2, respectively). On average, anurans had significantly larger geographical ranges than urodeles (*t*-test on $\log_{10}$-transformed ranges, $P = 0.03$). More than a quarter of anuran species (27.8%) and more than a third of the urodeles (41.4%) had geographical ranges $< 120{,}000$ km^2 (smaller than the area of England or Greece). (Note that had we included the insular species, the proportion of small-

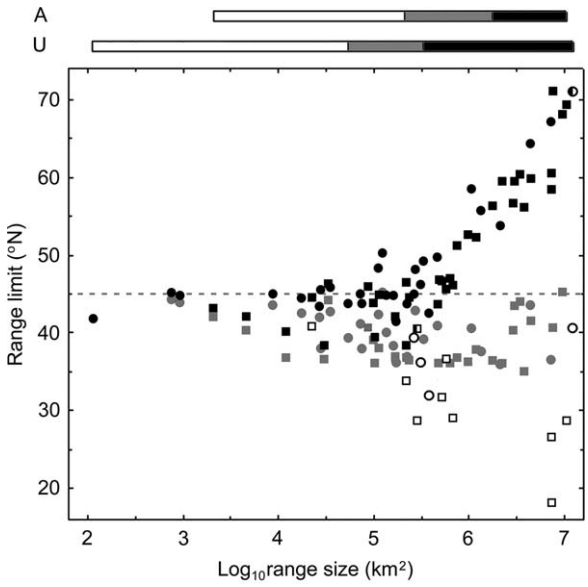

Figure 2 Range limit–range size plot for European amphibians ($n = 65$, island endemics excluded). Squares represent anurans, circles represent urodeles; black-closed and grey-closed symbols show the northern and southern limit of the species ranges, respectively. Half-open and open symbols, respectively, show northern and southern range limits that are outside Europe. The dashed horizontal line represents the approximate southern limit of the 0 °C isotherm of annual mean surface air temperature (Kim *et al.*, 2008) during the Last Glacial Maximum. Strips above the graph indicate the extent of range sizes for the third of species with the smallest ranges (open), the third with intermediate-sized ranges (grey) and the third with the largest ranges (black) of European anurans (A) and urodeles (U).

ranged species would have increased to 36.6% and 55.3% for anurans and urodeles, respectively.)

The position of latitudinal range margins

We found a tight link between the range position (i.e. the position of the range margins) and the range size of European amphibians: species with small ranges were located in a narrow latitudinal band around (mostly just south of) 45° N (Fig. 2), close to the southern limit of the 0 °C annual mean temperature isotherm during the LGM (Kim *et al.*, 2008). This latitudinal band includes areas implicated as climatic refugia during the LGM, such as the Balkans, northern Iberia and north Italy (Zeisset & Beebee, 2008). Amongst the most widespread species, the distance from their northern range margin to the latitude of Ice Age refugia increased approximately linearly with range size (Pearson correlation coefficient of $\log_{10}$-transformed > 500,000 km^2 geographical ranges versus northern range limits: $r = 0.92$, $P < 0.001$, $n = 25$).

Range extents of widespread anurans were more symmetrical around the latitude of 45° N in comparison with the urodeles, as many large-ranged anurans have southern range limits in North Africa, outside the study region.

Table 1 The standardized structural equation modelling effects of biological traits on ($\log_{10}$-transformed) range sizes of European amphibians (anurans $n = 28$, urodeles $n = 24$).

Biological traits	Total effect	Direct effect	Indirect effect
Anurans			
Body size*	0.239	0.101	0.138
Life span†	0.600	0.590	0.010
Fecundity‡	0.177	0.177	–
Habitat specialization	−0.153	−0.153	–
Urodeles			
Body size*	0.033	0.143	−0.110
Life span†	0.277	0.157	0.120
Fecundity‡	0.669	0.669	–
Habitat specialization	−0.284	−0.284	–

*Body size = $\log_{10}$ SVL (snout–vent length).
†Life span = $\log_{10}$ life span.
‡Fecundity = $\log_{10}$ clutch size.
Significance (P) values of direct effects are shown in Fig. 3 and Table S2.

Structural equation models

Amphibian species with a longer life span, higher fecundity, larger bodies (only in anurans) and less specialized habitat associations had larger geographical ranges. The SEM fit was considered good for anurans (chi-square $P = 0.715$, RMSEA < 0.001, GFI = 0.981, CFI = 1; $n = 28$) and marginal for urodeles (chi-square $P = 0.076$, RMSEA = 0.237, GFI = 0.906, CFI = 0.881; $n = 24$). The SEMs explained $R^2 = 0.54$ and $R^2 = 0.61$ of the variation in geographical ranges size of European anurans and urodeles, respectively. The SEM results were not influenced by the phylogenetic relatedness as there were no phylogenetic signals in the multiple regression residuals (Abouheif's test, $P = 0.993$ and $P = 0.991$ for anurans and urodeles, respectively).

In the anuran SEM, life span (maximum longevity) had the highest positive total effect on geographical range size, followed by smaller positive effects of body size and fecundity, while habitat specialization had a small negative effect (Table 1). Life span also had the highest direct positive effect on range size ($P < 0.001$, based on the critical ratio between the unstandardized regression weights and the maximum likelihood estimate of the approximate standard error; see Table S2) followed by the body size, fecundity and habitat specialization (negative effect). The indirect effect of body size on range size in anurans was greater than the direct effect. Life span had a small indirect effect (Table 1, Fig. 3a).

In the urodele SEM, the same order of traits (ranked from highest to lowest effects) was found for both the total and direct effects on geographical range size (Table 1). Fecundity had the highest positive effect ($P < 0.001$) on geographical range size of urodeles, followed by smaller negative effects of habitat specialization ($P < 0.05$) and by positive effects of life span (Table 1, Fig. 3b). Body size of urodeles had opposing direct (positive) and indirect (negative) effects on range size,

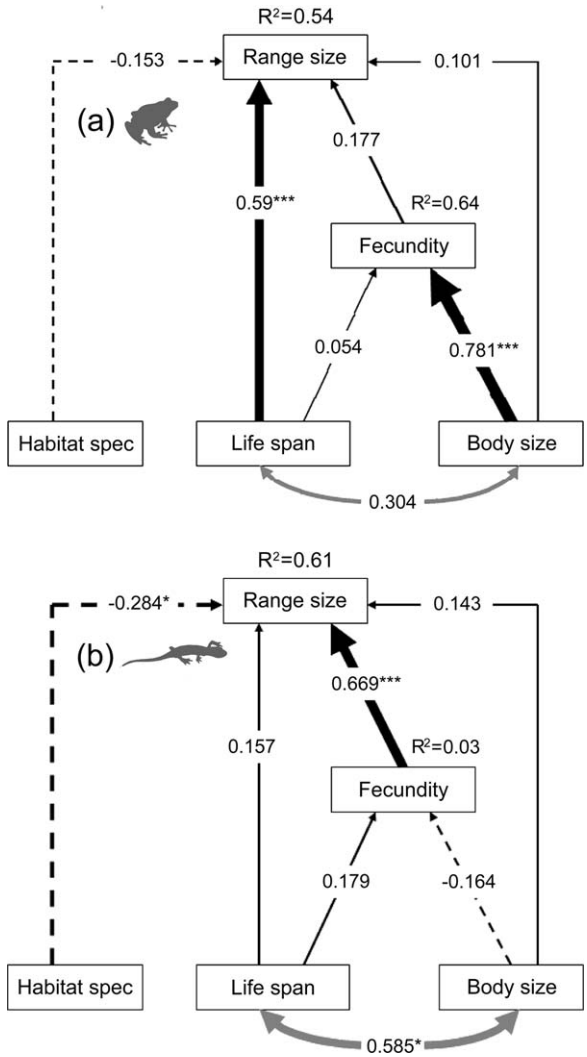

Figure 3 Structural equation models representing direct and indirect effects (standardized regression coefficients) of (a) anuran ($n = 28$) and (b) urodele ($n = 24$) species traits on range size: range size = $\log_{10}$ geographical range area; body size = $\log_{10}$ SVL (snout–vent length); fecundity = $\log_{10}$ clutch size; life span = $\log_{10}$ life span; habitat spec., habitat specialization. Solid arrows indicate positive relationships, dashed arrows negative relationships; curved arrows are co-variances between exogenous variables. The thickness of the arrows is proportional to the coefficient strength for coefficients > 0.1 (*$P < 0.05$; ***$P < 0.001$).

resulting in little total effect. For urodeles, we found a strong covariance between body size and life span in urodeles ($P < 0.05$), whereas this was non-significant in anurans. For anurans we found a strong relationship between body size and fecundity ($P < 0.001$) (Fig. 3).

DISCUSSION

Our results support the idea that species-specific traits promoting dispersal ability are important determinants of species range size in European amphibians. The range size frequency distribution is strongly right-skewed, as is common in large-scale analyses. For European amphibians, this may indicate that only a small number of species had the specific combination of traits necessary for range expansion and colonization after glaciation. The strong link between species range size and the geographical location of range limits further implies that species traits may indirectly determine the spatial distribution of species richness and thus play a major role in structuring the macroecological patterns of European amphibians. Our data showed that for the *c.* 75% most widespread amphibians, the distance from the northern range margin to the latitude of Ice Age refugia increased approximately linearly with range size (Fig. 2). This is consistent with the conjecture that species have acquired large ranges by range expansion out of relatively restricted glacial refugia over the last *c.* 10,000 years. This interpretation is supported by the observed asymmetry of the north–south distributional extent in widespread urodeles. Some work has been done for individual species of European amphibians to establish the major post-glacial colonization routes (Zeisset & Beebee, 2008), and further investigation along these lines would be fruitful for testing this hypothesis.

Our interpretation ties together species traits, geographical history and spatial distributions into a coherent and parsimonious framework, and posits a strong alternative to widely cited hypotheses based on the effect on contemporary abiotic factors for the large-scale richness patterns in European amphibians. Specifically, these hypotheses have generally explained the positive association between range size and range position (essentially Rapoport's rule; Stevens, 1989) as an effect of range position on species traits (i.e. northern species should be adapted to more variable climatic conditions), which in turn affect species range size. One of the key traits highlighted by our analysis, body size, is one of the traits generally assumed to be affected by range position (as per Bergmann's rule; Bergmann, 1847), on the rationale that larger-bodied populations of a species should retain body heat more easily than small-bodied populations (an interspecific form of the rule has also been the subject of discussion) and should also be able to retain fat reserves for survival throughout the cold season (Ashton, 2002).

Because of the strong association between range position and range size, it is very difficult to unequivocally disentangle the direction of causality. Although we cannot use our results to refute the classic hypotheses, we regard our interpretation, based on regional history and considerations of species ecology, to be a parsimonious explanation of the observed patterns. We do not see any a priori reason to assume a certain relationship between species fecundity and range position (though they are likely to be linked in some way), and with regard to body size, evidence is lacking to suggest that Bergmann's rule generally applies to amphibians (e.g. Adams & Church, 2008). It has even been argued that the opposite relationship from Bergmann's rule should be expected for ectotherms, as they do not generate heat and small-bodied species can warm up more quickly during short periods of sunlight (Pincheira-Donoso *et al.*, 2008). Olalla-Tárraga & Rodríguez (2007) reported contrasting latitudinal patterns of

body size between anurans and urodeles in North America and Europe (Bergmann's rule was supported for anurans), and suggested that the thermoregulatory abilities of anurans should allow them to reach larger body sizes in colder climates, whereas urodeles, which have limited thermoregulation, should be smaller in cooler areas. Araújo *et al.* (2008) also questioned whether contemporary climate is a driver of macroecological patterns (in their case, species richness) of European amphibians by showing that palaeoclimatic stability explained at least as much variation in amphibian species richness as contemporary climate did.

Nevertheless, we did not test the niche breadth hypothesis explicitly here, and it is likely to play a contributory role in the observed patterns (Quintero & Wiens, 2013). Overall, our findings support the idea that species of urodeles and anurans tolerant of a wide range of conditions (i.e. eurytopic species) also have particular combinations of traits that underpin their ability to (1) survive in multiple glacial refugia, (2) disperse successfully out of these refugia, and (3) thereby colonize larger territories. These suggestions are supported by observations that broad-ranged European amphibians: (1) can survive in harsh environments, e.g. *Rana temporaria* (Muir *et al.*, 2014); and (2) persisted in multiple glacial refugia, e.g. *Rana arvalis*, (Babik *et al.*, 2004) and *Lissotriton vulgaris* (Pabijan *et al.*, 2015).

Our SEM analysis revealed that the traits that were most important for range expansion differed between anurans (frogs and toads) and urodeles (newts and salamanders). For anurans, the strongest determinant of range size was adult life span, whereas fecundity was the most important trait for urodeles (Fig. 3). This may reflect a difference in mechanisms for range expansion, related to different life-history strategies for the two groups. Although many field studies, for both anurans and urodeles, have shown that most dispersal in amphibians happens in the juvenile stage (i.e. in the first months after metamorphosis; Berven & Grudzien, 1990; Kupfer & Kneitz, 2000), it is possible that adult-stage dispersal plays a relatively larger role in range expansion in anurans than it does for urodeles. Also, there is need to note that the sample size of anurans and urodeles employed in the analysis is relatively small, thus the differences between the two models might also be influenced by stochasticity. Our SEM results were not affected by the phylogenetic signals; thus, the effect sizes of the influence of traits on geographic ranges of European amphibians were not affected by the relatedness of the species. In addition, geographical range size may be a very labile trait, and indeed very little phylogenetic autocorrelation is generally found in species range size (e.g. Freckleton & Jetz, 2009).

These results also demonstrate that range expansion ability in European amphibians is controlled by some *r*-strategy and some *K*-strategy life-history traits, indicating that a trade-off between these two strategies characterizes the most widespread species. Large-ranged species were more fecund (an *r*-selected trait) than small-ranged species for both anurans and urodeles, consistent with the findings of van Bocxlaer *et al.* (2010) for toads. High fecundity may increase geographical range size via an effect on local abundance (Murray & Hose, 2005b), which has been hypothesized to stimulate range expansion via metapopulation dynamics and rescue effects in small populations (reviewed in Borregaard & Rahbek, 2010). High fecundity might also be advantageous because the larger number of eggs and larvae increases the chances of passive long-distance dispersal in the juvenile stage. There is some evidence for the role of passive long-distance dispersal of larval or adult amphibians by passive drift, floating in water currents (e.g. Johnson & Goldberg, 1975; Smith & Green, 2006), or amphibian eggs transported on the feet and plumage of water birds, as speculated by Darwin (1859) to occur for snails.

Anurans and urodeles with larger range sizes had longer life spans (enhanced *K*-strategy) than did the small-ranged species. A long life span may enhance a species' range expansion capability, as it gives more time for active dispersal in the adult stage and allows for more attempts at reproduction. This possible effect of longevity on geographical range size remains largely unexplored in the literature (but see Strona *et al.*, 2012). Body size would also be predicted to play a role in range expansion, as species with larger bodies have greater locomotor performance (Emerson, 1978; Marvin, 2003) and can move longer distances. The second strongest total effect in the SEM models was the weak (0.24) effect of body size on geographical range in anurans, although the direct effect (0.1) was weaker than the indirect effect (0.14), and the overall effect was insignificant. This trait well illustrates the complexity of the relationship between traits of individual species and geographical range. A positive relationship between body size and geographical range has been reported in many taxa (reviewed in Gaston & Blackburn, 1996), but in our analysis, the correlations were non-significant (see Table S2) (as also reported by Murray & Hose, 2005b). However, body size is correlated with other species traits that were important for geographical range. Such complexity of the drivers of geographical range was also shown recently for European passerines (Laube *et al.*, 2013), and may be a general rule.

There are other traits that could be important for determining the range expansion ability of species that have not been considered here. One of these is the ability of some amphibians to adapt their life history to varying environmental conditions. In urodeles, paedomorphs (adults that retain some larval characteristics and remain in a water habitat) are likely to occur when aquatic conditions are favourable and terrestrial conditions poor (Denoel & Ficetola, 2014). Thus, the potential for developmental plasticity in variable environments could play an important role in colonization success of spatially distant and environmentally heterogeneous areas. Another potentially important trait is behavioural site fidelity in adult individuals. The adult site fidelity of amphibians varies from species that are highly faithful (e.g. *Ichthyosaura alpestris*) to very vagile species such as the large-ranged species *Bufo calamita*, which usually breeds in open, temporary ponds (Semlitsch, 2008). For anurans, the traits that are associated with large range size are traits that would enhance active dispersal by adult

individuals. A longer life span allows for a longer period of active dispersal in the adult stage and possibly more successful reproductive events, enhancing lifetime fecundity.

In short, our results have clarified that biological traits of amphibians may have interacted with each other and with the long-term environmental history of Europe to generate the currently observed patterns of species distribution and richness. The actual causal pathways are complex, and likely to differ among groups with different ecologies and life-history strategies. However, should clear patterns emerge from extending such analyses to other groups, this endeavour may pave the way for a macroecological synthesis that integrates species ecology, history, and geography into a coherent understanding.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Table S1 Amphibian trait data.
Table S2 Results of structural equation modelling for the models of Fig. 3.
Figure S1 Hypothesized initial causal diagram for development of structural equation models.
Figure S2 Structural equation models of urodeles excluding strictly viviparous species.

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Giedrius Trakimas is a lecturer at Vilnius University. He has research interests in mechanisms that drive variation of amphibian life-history traits at large spatial scales and determine geographical range sizes.

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Author contributions: data were assembled by G.T.; analyses were conducted by G.T. and M.K.B.; framing of analysis, interpretation of the results and writing were done by all authors.

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APPENDIX 1 DATA SOURCES USED IN THIS STUDY

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