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SYNTHESIS

Palaearctic biogeography revisited: evidence for the existence of a North African refugium for Western Palaearctic biota

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ABSTRACT

Aim In contrast to the attention given to southern Europe both as a centre of speciation and differentiation and as a Pleistocene refugium of Western Palaearctic taxa, North Africa has been relatively neglected. In this paper, we set out to address this shortfall.

Location North-West Africa and the Mediterranean.

Methods We reviewed the existing literature on the biogeography of North Africa, and carried out analyses of species distribution data using parsimony, nestedness and co-occurrence methods.

Results In many cases, distribution patterns of non-flying mammals, bats, amphibians, reptiles, butterflies, zygaenid moths and odonates demonstrated important biogeographical affinities between Europe and North Africa at the species level. On the other hand, species co-occurrence, nestedness and parsimony analysis also revealed some deep splits between the Maghreb and Europe; yet even in these cases the closest affinities were found between the Iberian Peninsula and the Maghreb. Furthermore, North Africa harbours the highest proportion of endemic taxa (13.7%) across all groups analysed. Many molecular studies demonstrated a strong genetic cohesiveness between North Africa and Europe despite the potential barrier effect of the Mediterranean Sea. In other taxa, however, remarkable splits were detected. In addition, southern European genetic lineages were often nested within North African clades, and many taxa showed exceptionally high genetic variability and differentiation in this region.

Main conclusions The Maghreb was an important differentiation and speciation centre for thermophilic organisms during the Pliocene and Pleistocene with high relevance as a colonization source for Europe. The regions around the sea straits of Gibraltar and Sicily have acted as important biogeographical links between North Africa and Europe at different times.

Keywords

Biodiversity hotspot, climatic oscillations, differentiation centre, genetic structure, North Africa, phylogeography, Quaternary, refugia, sea straits, species assemblages.

> In effect, researchers commonly neglect the fact that Europe is not a biogeographic zone in its own right, but constitutes the northern and western part of the Palaearctic.
>
> (Vila & Ödeen, 2004, p. 55)

INTRODUCTION

As early as the mid-19th century, Nilsson (1847) hypothesized that warm-adapted (thermophilic) organisms followed suitable climatic conditions during the glacial stages of the

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Pleistocene and therefore shifted their distributions to lower latitudes and lower elevations, and those that did were thus able to outlast the cold periods. At the end of the 19th century, this postulate led to the hypothesis of an alternation between southward retractions during glacial phases and northward expansions in the wake of post-glacial warming (Geikie, 1881; Reid, 1899). However, analytical tools to test these ideas were limited and were mostly based on shared species distribution patterns (so-called 'Formenkreise') and patterns of intraspecific morphological variation (Holdhaus, 1904, 1954; Reinig, 1937, 1938, 1950; Holdhaus & Lindroth, 1939). By that time, many scientists agreed on the existence of three major refugia located in the southern European peninsulas: Iberia, Italy and the Balkans. De Lattin (1949) refined this biogeographical viewpoint and postulated the existence of nine refugial subcentres in the Mediterranean region, each harbouring characteristic and partly endemic biota. These subcentres were named according to their geographical locations: Atlanto-Mediterranean, Adriato-Mediterranean, Ponto-Mediterranean, Tyrrhenian, Canarian, Mauritanian, Cyrenian, Cretian, and Cyprian refugium (Fig. 1). De Lattin (1949) emphasized the importance of North Africa and assigned two distinct biogeographical centres to this region: the southern part of the Atlanto-Mediterranean and the Mauritanian subcentres, located north and south of the Atlas Mountains. He postulated two different biogeographical patterns: (1) an affinity between North Africa and Europe by including Iberia and the northern part of the Maghreb in the Atlanto-Mediterranean subcentre; and (2) a high degree of endemism in the Maghreb triggered by the orographic barrier effects found in this area.

The molecular revolution, starting in the 1970s, and especially the development of polymerase chain reaction (PCR) and Sanger sequencing, provided new tools to test biogeographical hypotheses. Subsequently, the southern European refugia were intensively analysed using these methods in combination with pollen and fossil records (Hewitt, 2000). Consequently, we now have detailed information about the location of these refugia and post-glacial re-colonization routes. These refugia were crucial as retreats for many temperate and thermophilic animal and plant species, which would have gone extinct in the tundra and cold steppe ecosystems of central Europe during glacial phases (Willis & Whittaker, 2000; but see Stewart & Lister, 2001; Stewart *et al.*, 2010; Schmitt & Varga, 2012). While many of the organisms trapped in just one refugium were endemic to that particular region, the ranges of other taxa were separated into allopatric populations in different refugial areas. Since these retreats were not interconnected geographically, isolated populations had their own evolutionary trajectories and became differentiated from each other. In some cases, especially after longer periods of allopatry, speciation occurred as a result of adaptive (selection) and non-adaptive (genetic drift) processes (Hewitt, 1989, 1996).

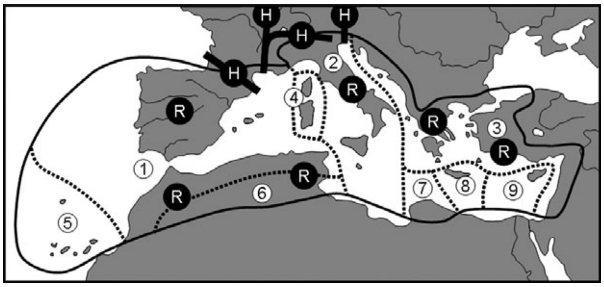

Figure 1 Overview of glacial refugia, biogeographical subcentres and hybrid zones of the south-western Palaearctic region. Refugia (R) postulated by Reinig (1937) and De Lattin (1949, 1967), hybrid zones (H) according to Hewitt (1999) and Schmitt (2007) and the nine Mediterranean subcentres *sensu* De Lattin (1967): 1, Atlanto-Mediterranean; 2, Adriato-Mediterranean; 3, Ponto-Mediterranean; 4, Tyrrhenian; 5, Canarian; 6, Mauritanian; 7, Cyrenian; 8, Cretian; 9, Cyprian.

At the beginning of the post-glacial period, the environmental conditions in central and northern Europe became more favourable for warm-adapted species again, leading to the re-colonization of these areas. The barrier effect of the European high mountain systems (in particular the Alps and the Pyrenees) varied for different taxa, resulting in the four paradigms of terrestrial post-glacial range expansions (Hewitt, 1999; Habel *et al.*, 2005). As a consequence of these large-scale range expansions, contact and hybrid zones between the formerly isolated genetic lineages are detectable throughout Europe (Comes & Kadereit, 1998; Taberlet *et al.*, 1998; Hewitt, 1999, 2004) (Fig. 1).

While the general biogeographical patterns are understood for Europe, far less is known about the importance of North Africa as a refugium and differentiation centre for Western Palaearctic thermophilic species. Most biogeographical analyses (even on species with typical European–North African distributions) only marginally refer to or entirely neglect the North African populations so that the relevance of this region is often overlooked (Dobson, 1998; Vila & Ödeen, 2004). Those studies that have focused on the biogeography within North Africa have tended not to discuss the relationships between North Africa and Europe (e.g. Boursot *et al.*, 1985; Franck *et al.*, 2001; Griswold & Baker, 2002; Lumaret *et al.*, 2002; Gantenbein & Largiadèr, 2003; Ödeen & Björklund, 2003; Harris *et al.*, 2004a,b; Perera & Harris, 2010; Habel *et al.*, 2012; Husemann *et al.*, 2012; Sousa *et al.*, 2012), or highlight the biogeographical relationships between North Africa and Europe (e.g. Harris & Sá-Sousa, 2002; Harris *et al.*, 2002; Carranza *et al.*, 2004, 2006a; Cosson *et al.*, 2005; Fritz *et al.*, 2006; Stöck *et al.*, 2006, 2008a,b, 2012; Weingartner *et al.*, 2006; Busack & Lawson, 2008; Habel *et al.*, 2008, 2009, 2010, 2011a; Guiller & Madec, 2010). In this synthesis, we summarize existing knowledge about the post-glacial biogeography of North Africa and its affinity to Europe. We focus on post-glacial colonization routes of well-studied vertebrates and invertebrates and on molecular genetic studies of a variety of taxa.

PALAEOCLIMATIC HISTORY OF NORTH AFRICA: CLIMATIC SHIFTS, OROGRAPHIC STRUCTURES AND SHARED BIOTA

Abiotic similarities and biotic connections of Europe and North Africa

While the climatic conditions during glacial phases were rather unfavourable for thermophilic species across major parts of central Europe, these organisms found suitable conditions in parts of the southern European peninsulas and the Maghreb region. As a consequence, species characteristic of tundra and cold steppe habitats expanded their distributions as far south-west as the northern parts of Spain and Portugal, as documented by fossil remains of mammoth (*Mammuthus primigenius*), bison (*Bison priscus*), reindeer (*Rangifer tarandus*) and woolly rhinoceros (*Coelodonta antiquitatis*) (García & Arsuaga, 2003; López González, 2003). Furthermore, the Sahara desert retracted significantly to the south during the Last Glacial Maximum (LGM, 25,000–18,000 years ago; Glennie & Singhvi, 2002), and relatively humid and moist climatic conditions transformed the vegetation of the lower elevations of North Africa into warm mixed forests at the onset of the post-glacial stages (Jolly *et al.*, 1998a; Jedoui *et al.*, 2002). About 6000 years ago, in both southern Europe and North Africa, warm mixed forests were common at intermediate elevations, whereas temperate xerothermic wood and shrublands were found at low elevations (Jolly *et al.*, 1998b). The persistence of moist ecosystems in parts of southern Iberia and the western Maghreb region throughout the Quaternary and parts of the Tertiary is documented by the extant, but very localized relicts of (otherwise Macaronesian) *laurisilva* (laurel) vegetation found in both regions (Galán de Mera *et al.*, 2003). These ecological similarities in the south of Europe and parts of North Africa confirm the availability of similar habitats for temperate species in both regions.

Sea straits – migration pathways or barriers?

Europe and North Africa are separated by the Mediterranean Sea, a strong geographical barrier for most terrestrial, non-flying and salt-water-intolerant (semi-)aquatic taxa. However, parts of south-eastern Iberia (i.e. the Baetic Cordillera) geologically belong to the North African continent, but have been separated from it since the Miocene (Carranza *et al.*, 2006a). Today, both continents are in close geographical proximity in two regions: the Straits of Gibraltar (between Iberia and Morocco) and Sicily (between Sicily and Tunisia). Both sea straits linked the continents as land bridges (or nearly so in the case of the Strait of Sicily) during the Messinian Salinity Crisis, 5.96 to 5.33 Ma (Krijgsman *et al.*, 1999; Duggen *et al.*, 2003). Several studies of the marine fauna support this closure of the Strait of Gibraltar by showing strong genetic differentiation between the Atlantic and the Mediterranean, with distinct marine lineages on either side of this strait (Roldán *et al.*, 1998; Lundy *et al.*, 1999; Pérez-Losada *et al.*, 2002). However, other studies have revealed a second biogeographical breakpoint at the Almeria-Oran Front east of the Strait of Gibraltar (reviewed in Patarnello *et al.*, 2007). The front represents the contact zone of two different currents; the associated high water current speed, temperature and salinity steps constitute a strong barrier for marine organisms (Patarnello *et al.*, 2007). Isolated lineages of marine organisms can also be found on either side of the Strait of Sicily (Debes *et al.*, 2008; Mejri *et al.*, 2009).

During the Messinian Salinity Crisis, the Strait of Gibraltar and, to a lesser degree, the Strait of Sicily, served as important migration corridors for terrestrial organisms, even for strictly salt-water-intolerant species (e.g. most amphibians, Stöck *et al.*, 2006, 2008a,b, 2012). The flooding of the Strait of Gibraltar and the associated refilling of the Mediterranean Sea *c.* 5.3 Ma renewed the isolation of terrestrial biota on either side. Thus, the straits of Gibraltar and Sicily were categorized as insurmountable barriers to gene flow for many terrestrial species after the Messinian Salinity Crisis when the Mediterranean became permanently connected with the Atlantic (Cheylan, 1991; Schüle, 1993; Dobson, 1998; Dobson & Wright, 2000). This assumption is well supported by genetic studies for many salt-water-intolerant taxa such as amphibians (e.g. Steinfartz *et al.*, 2000; Fromhage *et al.*, 2004; Veith *et al.*, 2004, 2009) and sedentary taxa such as scorpions (e.g. Sousa *et al.*, 2010, 2012; Habel *et al.*, 2012), but also for some salt-water-tolerant organisms such as reptiles (e.g. Carranza *et al.*, 2006a; Velo-Antón *et al.*, 2012). On the other hand, no significant differentiation between populations on both sides of the Strait of Gibraltar was detected for anemochorous and zoochorous plants by Lavergne *et al.* (2013).

Similarly, strong affinities between Europe and North Africa are detectable for the Strait of Sicily, despite the overseas distance of 140 km. Some species show strong genetic cohesiveness between Sicily and Tunisia (Cosson *et al.*, 2005; Habel *et al.*, 2009, 2010, 2011b). This might have been fostered by the lower sea level during the glacial phases, reducing the distance between the two continents and causing the emergence of potential stepping-stone islands. A study on the toad genus *Bufo* showed a sister group relationship between Sicilian and North African taxa, with divergence time estimates placing the split at the Pliocene–Pleistocene boundary (Stöck *et al.*, 2008b) and providing additional evidence for post-Messinian connections via the Strait of Sicily. However, the prevalent differences between the faunas of Italy and North Africa indicate a stronger isolating effect of the Strait of Sicily compared with the Strait of Gibraltar (below). The distribution of many endemic species is restricted to the Maghreb and Iberia as well as the Maghreb and Italy (Table 1) and 3.3% of all species analysed are restricted to the Atlanto-Mediterranean range (Maghreb and Iberia) occurring on both sides of the Strait of Gibraltar. In contrast, Italian–North African endemics shared across the

Table 1 Total species numbers of seven groups of animals native to the four study regions of Maghreb, Iberia, Italy and the Balkans, percentage of these species native in each of these regions and percentage of these species endemic to one of these regions and the two-region combinations Maghreb + Iberia and Maghreb + Italy. Occurrence data were taken from Tolman & Lewington (1998), Naumann *et al.* (1999), Mitchell-Jones *et al.* (1999a,b), Dijkstra & Lewington (2006), Dietz *et al.* (2007), Boudot *et al.* (2009), Heiser & Schmitt (2010), Kudrna *et al.* (2011) and Tshikolovets (2012). Data on the distribution of amphibians and reptiles were taken from the *Gridded Species Distribution* database (http://sedac.ciesin.columbia.edu/species/, accessed 19 November 2012). An overview of all species and species-specific distributions is given in Appendix S1.

	Total species numbers	Maghreb		Iberia		Italy		Balkans		Maghreb + Iberia	Maghreb + Italy
Taxon		native	endemic	native	endemic	native	endemic	native	endemic	endemic	endemic
Mammals (excl. bats)	135	47.4	9.5	37.2	5.1	35.0	4.4	45.9	3.6	3.6	0.0
Bats	39	65.0	0.0	67.5	0.0	65.0	0.0	77.5	7.5	2.5	0.0
Amphibians	51	21.5	10.8	33.8	16.9	12.3	0.0	32.3	6.2	3.1	1.5
Reptiles	120	53.2	29.0	17.7	8.1	7.3	0.0	16.9	0.0	4.8	1.0
Butterflies	316	39.5	7.5	51.4	5.3	45.5	1.3	68.0	4.1	6.6	1.3
Zygaenid moths	79	37.9	32.9	37.9	13.9	32.9	6.3	37.9	0.0	1.3	0.0
Odonates	115	38.9	5.6	41.9	0.0	41.9	1.2	49.4	2.5	1.2	0.0
Overall	855	43.3	13.6	41.1	7.0	34.4	1.9	46.8	3.4	3.3	0.5

Strait of Sicily (0.5% of all species analysed) are much rarer (Table 1).

Distribution and endemism of species in North Africa and southern Europe

The palaeoecological similarities of North Africa and southern Europe in combination with the geographical connection via sea straits have led to a circum-Mediterranean distribution of many taxa. Mammal species in particular are distributed across both Europe and North Africa (Auboire & Gillon, 1995; Hamdine *et al.*, 1998; Straus, 2001), although, at least in some cases, translocations through humans (including inadvertent ones) cannot be excluded.

In this context, we analysed the distribution patterns of numerous species from seven well-studied animal groups: mammals (excluding bats, which were analysed as a separate group because they strongly diverge from other mammals in their dispersal capacity), bats, amphibians, reptiles, butterflies, zygaenid moths and odonates. Distribution data compiled from the literature (Table 1, Appendix S1 in Supporting Information) underpin the general pattern of high similarity of North Africa and southern Europe. However, the highest rates of endemism (here defined as species restricted to exclusively one of the four Mediterranean regions – Maghreb, Iberia, Italy and the Balkans – in relation to all species native to our study area) exist for the Maghreb: 9.5% of mammals (excluding bats), 0% of bats, 10.8% of amphibians, 29.0% of reptiles, 7.5% of butterflies, 32.9% of zygaenid moths, and 5.6% of odonates; overall: 13.6%. These rates of endemism are considerably higher than in the southern European peninsulas (Iberia: 7.0%; Italy: 1.9% and the Balkans: 3.4%; Table 1). High rates of endemism in combination with relatively moderate species numbers are typical of a refugial region only functioning as a source of colonization, but not as a receptor from other areas. These data indicate that many taxa may have evolved or survived in the Maghreb and later expanded to Europe, whereas the reverse appears to be rare. Consequently, the fauna of the Maghreb is mostly of Atlanto-Mediterranean and Saharan origin with only a few additional Macaronesian elements and mostly does not represent a mixture of different faunal elements, as for example observed in the Balkan Peninsula, which represents a biogeographical melting pot influenced from multiple directions.

To assess patterns of species co-occurrence among the Maghreb, Iberia, Italy and the Balkans, we performed parsimony, co-occurrence and nestedness analyses based on an ordinary species × region presence–absence matrix of the above-mentioned seven animal groups. We estimated patterns of negative species associations using the common *C*-score metric (Stone & Roberts, 1990; Ulrich & Gotelli, 2013). High values of the *C*-score point to a segregated pattern of species co-occurrence among sites. To assess spatial turnover of species among regions, we sorted rows and columns according to the first axis of correspondence analysis and quantified the spatial turnover of species by the squared coefficient of correlation r^2 between the row and column numbers of the ordinated matrix (Ulrich & Gotelli, 2013). We estimated the degree of range size coherence by the number of embedded absences within the first and last occurrence of each species in the ordinated matrix (Leibold & Mikkelson, 2002). A low embedded absences score points to a coherent range size. We used the NODF metric (nestedness by overlap and decreasing fill; Almeida-Neto *et al.*, 2008) to assess the degree of nested species co-occurrences and the respective degree of idiosyncrasy of sites. Nestedness refers to the ordered loss of species richness along a predefined environmental or geographical gradient (Ulrich *et al.*, 2009). NODF values range from zero (maximal scatter) to 1 (perfect nested pattern). Idiosyncrasy (Atmar & Patterson, 1993) refers to the deviation of sites or species from this ordered pattern of species loss and is quantified by the number of unexpected absences or occurrences with respect to a perfectly nested pattern of species occurrence. To test for statistical significance of the observed scores, we used a null model approach (Gotelli & Ulrich, 2012) and compared observed metrics with the distribution of metrics obtained from 200 randomized matrices. Because there is no a priori reason that constraints potential occurrences across sites, we used the equiprobable null model *ee* that controls only for the total number of species across all sites but does not fix total numbers of species occurrences among and total species richness within sites (Gotelli, 2000). All calculations were carried out using the software applications NODF (Almeida-Neto & Ulrich, 2011) and TURNOVER (Ulrich & Gotelli, 2013). We used standard parsimony analysis as implemented in PAST 2.0 (Hammer *et al.*, 2001) to assess the relationships in species composition between our four faunistic regions (Kitching *et al.*, 1998). We applied Wagner optimization and provide the strict consensus tree with respective branch lengths. Dolly and Fitch optimizations gave identical results (not shown).

The strict parsimony consensus tree first applied to all taxa joined Italy and the Balkan region; North Africa appeared to be most basal (Fig. 2). Co-occurrence analyses revealed a strong species turnover for most taxa (except the highly mobile Odonata and Chiroptera) and therefore the existence of regionally distinct faunas among the four regions (Iberia, Italy, Balkans and the Maghreb). We did not detect a tendency for scattered occurrences that would indicate post-glacial regional extinctions (Table 2). Our nestedness analysis revealed significant positive degrees of nested subset patterns (the ordered loss of species along presumed colonization trajectories, reviewed in Ulrich *et al.*, 2009) in mammals (except bats) and butterflies, while amphibians and reptiles were less nested than expected by chance [overall degree of nestedness standardized effect sizes (SES) = 5.1, $P < 0.0001$]. These findings supported a general trend of an ordered species loss along the colonization pathways from the Maghreb to Europe (particularly into south-eastern Europe) (Table 2); similar patterns of nestedness have been found in previous studies for darkling beetles (Fattorini & Ulrich, 2012) and springtails (Fiera & Ulrich, 2012).

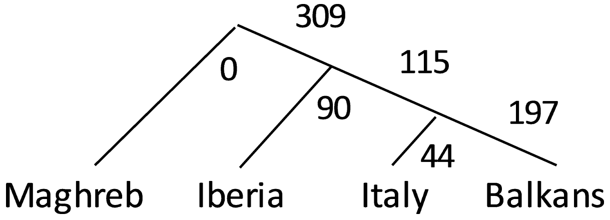

Figure 2 Parsimony strict consensus tree (Wagner strict consensus) with branch lengths based on all species of seven groups native to the four biogeographical regions considered (species lists are given in Appendix S1).

Table 2 Standardized effect sizes (SES) on the degree of range size coherence according to Leibold & Mikkelson (2002), species turnover according to Ulrich & Gotelli (2013), and nestedness according to Almeida-Neto *et al.* (2008) for seven groups of animals native to the four study regions of Maghreb, Iberia, Italy and the Balkans. Calculations of coherence were performed using 200 null model randomizations based on the equiprobable reshuffling of species occurrences holding total richness values per region constant (Ulrich *et al.*, 2009). Negative nestedness scores point to higher numbers of unexpected species occurrences or absences with respect to a fully nested subset pattern.

Taxon	Coherence	Turnover	Nestedness
Mammals (excl. bats)	−5.5	5.1	2.5
Bats	−4.2	0.1	−0.1
Ambibians	−1.7	3.0	−4.1
Reptiles	−2.2	4.7	−4.7
Butterflies	−5.1	7.4	5.7
Zygaenid moths	−5.7	4.9	−2.4
Odonates	−6.8	−2.0	−4.3
Overall	−8.9	6.6	5.1

OUT OF NORTH AFRICA – THE ORIGIN OF WESTERN PALAEARCTIC DIVERSITY

While the distribution of species can inform about a region's biogeographical history, the distribution of genetic variation provides higher resolution and can be used to test specific hypotheses. The question of the direction of colonization, for example, has been studied in a variety of organisms. In general, two criteria, especially if applied in combination, may help to detect refugial areas using molecular tools: (1) the level and structure of genetic differentiation between populations; and (2) a comparison of the genetic diversity (alleles and haplotypes) among respective regions (Hewitt, 2004; Habel *et al.*, 2013a). Constant climatic conditions not only support a long-lasting persistence of a species in an area, but also reduce the risk of population bottlenecks and consequently foster the maintenance of high genetic variability (Hewitt, 1996). Furthermore, high levels of genetic diversity can enhance strong differentiation patterns over limited spatial scales (reviewed in Gómez & Lunt, 2007). Finally, the structures of gene trees often help resolve the question of source and receptor regions. For instance, if taxon B is phylogenetically nested within taxon A, the colonization occurred from location A to B, as A represents the older and B the younger (nested) genetic lineage.

Genetic differentiation and coherence between North Africa and Europe differs among taxa

Genetic analyses of taxa distributed on both sides of the Mediterranean Sea mostly support a North African origin and expansions to southern Europe at different time horizons (e.g. Boursot *et al.*, 1985; Franck *et al.*, 2001; Griswold & Baker, 2002; Ödeen & Björklund, 2003; Harris *et al.*, 2004a,b;

Busack *et al.*, 2005; Fritz *et al.*, 2006; Recuero *et al.*, 2007; Paulo *et al.*, 2008; Guiller & Madec, 2010; Habel *et al.*, 2012; Santos *et al.*, 2012; Sousa *et al.*, 2012). Franck *et al.* (1998, 2001) were among the first to present a case study displaying a colonization of Europe from North Africa using molecular tools. In their study on the phylogeography of the honey bee, *Apis mellifera*, the authors suggested that North Africa was an important glacial refugium for the species and served as the source for the later colonization of Europe.

In some cases of dispersal from North Africa and subsequent allopatric differentiation, the lineages are very old, and different species have evolved on either side of the Strait of Gibraltar, as exemplified by lizards of the genus *Timon* (Paulo *et al.*, 2008); another example for such an ancient colonization is the scorpion genus *Buthus* (Habel *et al.*, 2012). Other expansions are more recent, dating back to the Pliocene or early Pleistocene, and have not yet led to allopatric species (Harris *et al.*, 2004a,b; Veith *et al.*, 2004). In butterflies of the *Pararge* species group, the persistence of the taxon in North Africa was dated back to the early Pliocene, when *Pararge xiphia* from Madeira separated from the ancestors of North African *Pararge aegeria*. The colonization of Europe most likely did not occur earlier than 900,000 years ago, but nevertheless populations from both continents are significantly differentiated (Weingartner *et al.*, 2006; Habel *et al.*, 2013b). Similarly, the butterfly *Melitaea cinxia* might have its origin in North Africa, from where it colonized Europe and subsequently split into several independent lineages (Wahlberg & Saccheri, 2007). Other species, although considerably differentiated within North Africa, arrived rather recently (in the late Pleistocene or even the post-glacial period) in Europe. Examples for such taxa are the pond turtle *Mauremys leprosa* (Fritz *et al.*, 2006) and the shrew *Crocidura russula* (Cosson *et al.*, 2005). Similar results were presented for chameleons and tortoises whose European populations seem to have multiple origins; the divergence between the continents is very young in both cases, and anthropogenic introduction has been inferred (Paulo *et al.*, 2002; Fritz *et al.*, 2009). However, at least in the case of the tortoise genus *Testudo,* the divergence pre-dates historical times so that an anthropogenic origin can be excluded and Europe must have been colonized from a Northern African source (Graciá *et al.*, 2013). The snake species *Macroprotodon brevis*, *Malpolon monspessulanus* and *Hemorrhois hippocrepis* lack genetic differentiation between Iberian and North African populations, and molecular clock estimates suggested that Iberia was colonized less than 200,000 years ago and possibly even in historical times (Carranza *et al.*, 2004, 2006b). However, it is generally difficult to date very recent divergences, and therefore, it can be complicated to distinguish late Pleistocene colonizations from anthropogenic introductions (Graciá *et al.*, 2013).

Many fewer cases are known in which colonizations occurred from Europe to North Africa. Most documented cases come from reptiles and amphibians, for example from midwife toads (genus *Alytes*) during the Messinian Salinity Crisis (Fromhage *et al.*, 2004; Martínez-Solano *et al.*, 2004; Gonçalves *et al.*, 2007). Similarly, salamanders colonized North Africa during the same time period, with the Maghreb endemic *Salamandra algira* evolving in allopatry (Steinfartz *et al.*, 2000). This species is the sister species of the European fire salamander, *Salamandra salamandra*. Both species represent a monophylic group within *Salamandra*, which becomes paraphyletic if excluding the North African *S. algira* (Steinfartz *et al.*, 2000). The lizard *Psammodromus algirus* is paraphyletic in Iberia and monophyletic in North Africa but nevertheless well differentiated from the Iberian lineages, and its arrival in North Africa was dated to the early or middle Pleistocene (Carranza *et al.*, 2006a). The butterfly *Maniola jurtina* is not differentiated between Italy and North Africa, but the Italian populations are genetically more diverse and more differentiated from each other than the North African ones, supporting a very recent, most probably even post-glacial, colonization of the Maghreb region via the Strait of Sicily (Habel *et al.*, 2009). The pond turtle *Emys orbicularis* most likely reached the Maghreb recently from Iberia (Lenk *et al.*, 1999), but has a more complex colonization history, with a subsequent re-invasion of Europe from North Africa (Fritz *et al.*, 2007).

In some cases, species became separated north and south of the Mediterranean Sea, but the origin of their ancestors is unknown. Many such taxa evolved into different species in Iberia and the Maghreb, as exemplified for the butterflies *Melanargia galathea* and *Melanargia lachesis; M. galathea* subsequently colonized Europe via the Strait of Sicily and later recolonized Tunisia from Sicily (Habel *et al.*, 2011b). In *Podarcis* wall lizards, the relationships are even more complicated (Harris *et al.*, 2002; Pinho *et al.*, 2007a,b). First, a European origin of the genus was inferred (Oliverio *et al.*, 2000). This was confirmed by Harris *et al.* (2002), who suggested that North Africa was colonized at least twice after the Strait of Gibraltar had formed. Busack *et al.* (2005) suggested a vicariant divergence between Iberian *Podarcis hispanica* and *Podarcis vaucheri* in the Betic-Rif Massif and mainland North Africa driven by geographical changes at the Miocene–Pliocene boundary and associated habitat transformations (Busack *et al.*, 2005). The most recent studies suggest that North Africa was colonized by Iberian *Podarcis* twice, once before and once after the Messinian Salinity Crisis (Kaliontzopoulou *et al.*, 2011). This suggests that the opening of the Strait of Gibraltar had less effect on the diversification of the group than the geological history of the Betic-Rif massif and the climatic fluctuations during the Pleistocene (Kaliontzopoulou *et al.*, 2011).

In other taxa, colonization was very recent and/or gene flow still persists, but the direction is unclear; examples include the three butterfly species *Lycaena phlaeas*, *Polyommatus icarus* and *Pyronia cecilia*, which lack genetic differentiation between Tunisia and Sicily (Habel *et al.*, 2010). A similar pattern is seen in the butterfly *Melanargia ines* in Iberia, Morocco and Tunisia (Habel *et al.*, 2011a). Such absence of genetic differentiation between North Africa and Europe further indicates that exchange between the two continents was possible for many taxa even after the end of the Messinian Salinity Crisis, most likely during glacial advances when the overseas distances between North Africa and southern Europe across the sea straits were considerably reduced (Brandt *et al.*, 1996; Pérez-Losada *et al.*, 2002; Carranza *et al.*, 2006b; Santos *et al.*, 2012).

Refugia within a refugium: North Africa, a hotspot of intraspecific diversity

Most molecular biogeographical studies performed in North Africa yielded high estimates of genetic diversity, and the majority of taxa exhibited multiple endemic genetic lineages. Divergence estimates for many clades date back to the Pliocene or even longer, and splits between North African lineages are often deeper than among the European ones: such deep divergences have been found, for example in the ivy genus *Hedera* (Grivet & Petit, 2002), lizards of the genera *Podarcis* (Oliverio *et al.*, 2000; Harris & Sá-Sousa, 2002; Pinho *et al.*, 2007a,b, 2008; Kaliontzopoulou *et al.*, 2011) and *Timon* (Paulo *et al.*, 2008; Perera & Harris, 2010), vipers (Brito *et al.*, 2011), *Quedenfeldtia* geckos (Barata *et al.*, 2012), *Calopteryx* damselflies (Weekers *et al.*, 2001), *Meladema* beetles (Ribera *et al.*, 2003), the butterfly *Melanargia galathea* (Habel *et al.*, 2011b), *Buthus* scorpions (Gantenbein, 2004; Sousa *et al.*, 2010, 2012; Habel *et al.*, 2012; Husemann *et al.*, 2012) and the shrew *Crocidura russula* (Cosson *et al.*, 2005).

The high genetic diversity and strong structuring detectable in North African populations of many species might be the result of (1) long-lasting persistence of these species in the Maghreb, but also of (2) the strong topographic heterogeneity found across major parts of North Africa (Pleguezuelos *et al.*, 2010). The Atlas Mountains comprise the highest elevations of North Africa and provide strong orographic barriers that rendered large range shifts impossible or even unnecessary. Instead of latitudinal shifts, species expanded their distributions to lower elevations during cooler phases and shifted to higher elevations during the drier and hotter interglacial phases. Comparable shifts within a restricted geographical area can be observed for taxa in the Alps (Schmitt, 2009) and the Pyrenees (Mouret *et al.*, 2011). These elevational range shifts might have fostered the long-term persistence of many species in North Africa. However, while providing prolonged habitat stability, the strong barriers represented by high mountain ranges also played a pivotal role in separating local populations of species, leading to strong genetic divergence among North African populations and high rates of micro-endemism (Habel *et al.*, 2012). Various structures and processes (e.g. main chains of the different mountain blocks of the Atlas massif, large river valleys, sometimes in combination with temporary sea transgressions) might have acted as strong south–north and west–east barriers. Thus, distinct genetic lineages are often found north and south of the Atlas Mountains, confirming the barrier effect of this mountain system (Fritz *et al.*, 2006; Gonçalves *et al.*, 2012). Another common pattern is a split between the western and the eastern Maghreb, mostly triggered by river valleys temporarily transgressed by the sea (Veith *et al.*, 2004; Cosson *et al.*, 2005; Paulo *et al.*, 2008). Other taxa have allopatric lineages following more subtle, fine-scaled orographic structures of the Atlas Mountains within the region (Harris *et al.*, 2004a,b; Fonseca *et al.*, 2008; Habel *et al.*, 2012; Husemann *et al.*, 2012; Sousa *et al.*, 2012).

Natural versus human-mediated dispersal between Europe and North Africa: confounding anthropogenic impacts

As demonstrated above, there are strong natural biogeographical connections between North Africa and southern Europe. However, human interference through translocations has also occurred repeatedly, confounding natural patterns in a variety of species, particularly (although by no means exclusively) in mammals. In some cases where typically African species also occur in southern Europe, the question of natural or anthropogenic origin has not been resolved with certainty. Examples for such cases include the common genet (*Genetta genetta*) and the Egyptian mongoose (*Herpestes ichneumon*) in Iberia and the crested porcupine (*Hystrix cristata*) in Italy (including Sicily). While the genet was probably introduced (Gaubert *et al.*, 2011), the porcupine, long believed to have been introduced in Roman times, may well be native to Europe (based on fossil data; Mitchell-Jones *et al.*, 1999a,b). The frog *Hyla meridionalis* is thought to have been translocated very recently from Northern Africa to Iberia (Recuero *et al.*, 2007). Another study, however, suggests a natural post-Messinian colonization of Europe (Stöck *et al.*, 2008a,b). If the divergence of lineages is very recent, it can be difficult to obtain robust age estimates, and therefore testing the alternative hypotheses of anthropogenic translocation and natural colonization may not be feasible (Graciá *et al.*, 2013). Similar cases are represented by chameleons and tortoises, where originally an anthropogenic origin of European populations was invoked (Paulo *et al.*, 2002; Fritz *et al.*, 2009). Yet, at least in the case of the tortoises, a natural origin has been demonstrated (Graciá *et al.*, 2013). The genetic uniformity and lack of fossils suggest that the circum-Mediterranean distribution of *Hemidactylus turcicus* is the result of anthropogenic translocations (Carranza & Arnold, 2006). The introduction of the North African *Discoglossus pictus* in Spain has led to the spread of that species across parts of Spain and France and has negatively altered amphibian communities (Richter-Boix *et al.*, 2013). Molecular evidence also convincingly suggests a natural origin for the Egyptian mongoose in Europe. The data indicate that the species crossed the Mediterranean Sea across the Strait of Gibraltar before the earliest human impact, which would constitute the first such case for a larger mammal (Gaubert *et al.*, 2011). North African wild boars (*Sus scrofa*) also show close genetic affinities with their European conspecifics, but their distribution history so far remains unclear. There are, however, Pleistocene fossil records for North Africa suggesting that the distribution across the two continents may be natural (Dobson, 1998; Hajji & Zachos, 2011), although later translocations cannot be ruled out.

The Tyrrhenian Islands (Sardinia and Corsica) have been the focus of many biogeographical studies using palaeontological, archaeozoological and genetic data. Human impacts were particularly important on these islands: the entire autochthonous fauna of large mammals became extinct in the wake of human colonization, while more than 25 taxa of mammals were subsequently introduced (Vigne, 1992).

CONCLUSIONS

Palaeoecological evidence suggests that the climatic and ecological conditions were quite similar over major parts of southern Europe and North Africa during the Pliocene and Pleistocene, leading to similarities in species composition of both regions. During the late Miocene, the Messinian Salinity Crisis led to the desiccation of the Mediterranean Basin and resulted in the connection of North Africa and Europe at two locations: Gibraltar and the Strait of Sicily. These connections facilitated the migration between North Africa and Iberia and between Italy and North Africa and homogenized the early Pliocene faunas and floras on both sides of the western Mediterranean. The end of the Messinian Salinity Crisis and the refilling of the Mediterranean Sea, resulting in the eventual separation of Europe and North Africa in the western Mediterranean, was an important trigger for many differentiation processes between European and North African populations. The Pleistocene was characterized by strong glacial–interglacial cycles and fluctuating distances between the European and North African coastlines, partly allowing overseas gene flow between the two continents. As a consequence of the late Neogene and Quaternary history, the biota of southern Europe and North Africa are still closely related, while at the same time, the geographical isolation facilitated differentiation and speciation in many taxa. The degree of differentiation between North African and European populations strongly depends on the age of separation, the life history of the respective taxon, and, more recently, anthropogenic translocations. Phylogeographical studies have more often revealed European lineages to be nested within African clades, indicating that a northward colonization from North Africa to Europe was more common than the reverse, and suggesting an important role of North Africa as a glacial refugium during the Pleistocene and as a source for the post-glacial colonization of Europe. The high genetic diversity and differentiation at the intraspecific level as well as the high rates of endemism within North Africa indicate the importance of the region as an evolutionary hotspot. The intricate phylogeographical relationships of species on both sides of the Mediterranean highlight the need to include North African populations in phylogeographical studies, even if the taxon in question is mainly distributed in Europe. If North African populations are neglected, as is frequently the case, patterns important for the understanding of the biogeography of the Western Palaearctic will remain enigmatic.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Overview of all species used in analyses of species distribution patterns.

BIOSKETCH

Martin Husemann is currently a PhD candidate in the Biology Department at Baylor University in Waco, Texas. His main interests are the evolution of species-rich animal groups, especially Malawian cichlids and band-winged grasshoppers. All the authors are interested in the distribution of biodiversity and the understanding of the underlying processes, with a special focus on the biogeography of the Palaearctic region.

Author contributions: M.H., J.C.H., T.S. and F.Z. conceived the ideas and collected the data from previous publications; W.U. analysed the data. All authors contributed equally to the text.

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