The biogeography of the western Mediterranean: elucidating contradictory distribution patterns of differentiation in *Maniola jurtina* (Lepidoptera: Nymphalidae)

LEONARDO DAPPORTO[1], JAN CRISTIAN HABEL[2]*, ROGER L. H. DENNIS[3,4] and THOMAS SCHMITT[5]

[1]*Istituto Convenevole da Prato, Via Primo Maggio 40, 59100 Prato, Italy*
[2]*Musée National d'Histoire Naturelle Luxembourg, Section Zoologie des Invertébrés, L-2160, Luxembourg*
[3]*Institute for Environment, Sustainability and Regeneration, Room S122, Mellor Building, Staffordshire University, College Road, Stoke on Trent ST4 2DE, UK*
[4]*School of Life Sciences, Oxford Brookes University, Headington, Oxford OX3 0BP, UK*
[5]*Trier University, Department of Biogeography, D-54296 Trier, Germany*

In the western Palaearctic, the Mediterranean zone is an important region where taxa and genes of thermophilous organisms are preserved during glacial stages and new clades are generated. This is achieved through the existence of refugia over Mediterranean Europe and North Africa, where organisms persisted and continued to evolve during the cold phases. However, it is not clear in detail how these refugia function for the maintenance of ancestral taxa, the evolution of new taxa, and as launching pads during postglacial colonizations of northern Europe. One outstanding issue is the incongruence of findings from different marker systems. For the butterfly *Maniola jurtina*, morphometry and allozyme data analyzed for populations scattered over Europe and North Africa show congruent patterns for Sicily and the Maghreb but produce discrepant results for the Italian mainland. This discrepancy between allozyme and morphological data can be explained by recent gene flow in the wake of postglacial range expansions and shifts. It is evident that colonization histories are far more complex than originally considered. We highlight different aspects of colonization and evolutionary history emerging from the joint use of different marker systems and advocate multiple uses of different markers in paleobiogeographic reconstructions to explore evolutionary events and colonization pathways. © 2011 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2011, **103**, 571–577.

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INTRODUCTION

The biogeographical effects of extinctions and (re)colonizations from the main southern European refugia have been explored intensively during the last few decades (Reinig, 1937; de Lattin, 1967; Dennis, Williams & Shreeve, 1991, 1998; Dennis, Shreeve &

Williams, 1995; Taberlet *et al.*, 1998; Hewitt, 1999, 2000). Hewitt (1999, 2000) discriminated amongst these complex range shifts over Europe by distinguishing three model patterns of southern refugia with different recolonization tracks; subsequently, a further model pattern has been identified (Habel, Schmitt & Müller, 2005). In detail these are: (1) the hedgehog paradigm with postglacial northwards expansion from all southern European refugia; (2) the grasshopper paradigm with postglacial expansion from Iberia and southeast Europe; (3) the bear

*Corresponding author. E-mail: janchristianhabel@gmx.de

paradigm with postglacial range expansion from Iberia and the Balkans (note that the refuge area of Ursus arctos was more to the north than in the bear paradigm); and (4) the butterfly paradigm with expansion out of Italy and the Balkans. These paradigms are mostly triggered by the different barrier functions of the mountain ranges of the Alps and Pyrenees and thus varying degrees of isolation of the Iberian and Italian lineages.

The theoretical number of colonization pathways after relaxation of glacial climatic conditions depends on the number of refugial blocks on which populations of a taxon may have survived at Mediterranean latitudes (Fig. 1). Two types of pathways need to be distinguished because a taxon can spread both latitudinally (north–south) and longitudinally (east–west) (Hewitt, 1999, 2000; Schmitt, 2007; Dapporto *et al*., 2009; Dapporto, 2010a). With three Mediterranean refugial blocks (Iberia, Italy, Balkans), there are seven possible northward pathways and, independently, a maximum of two lateral movements out of a set of four based on the occurrence of lateral interactions (Fig. 1). Potential for interactions between longitudinal and latitudinal movements suggests that a large number of different recolonization tracks may have occurred in different taxa. Moreover, it is well known that multiple refugia within major refugial land blocks have often occurred, further complicating the picture (Schmitt *et al*., 2006). This large spectrum warns against assuming undue simplicity
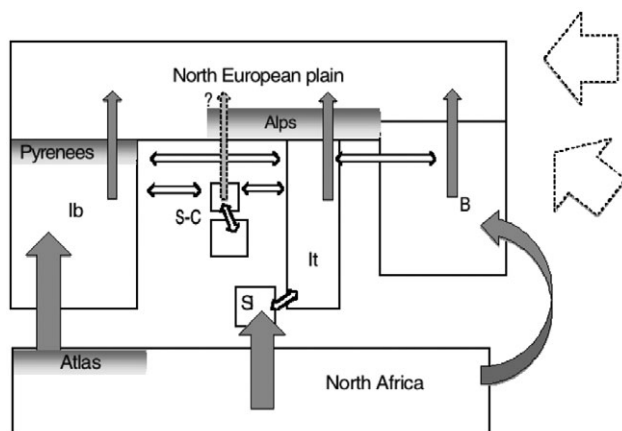
and suggests the need for indepth multidisciplinary assessments before any conclusion is drawn.

Recently, two studies have advocated the existence of completely different biogeographical and evolutionary patterns for the same butterfly species. Dapporto *et al*. (2009) examined male genitalia of the meadow brown *Maniola jurtina* and revealed that populations from North Africa are very similar to those inhabiting Spain and the West Mediterranean islands, although they differ substantially from those populations found on the Italian mainland. Habel *et al*. (2009) analyzed the pattern of allozyme variation for the same species over the same geographical region; they revealed the same close similarity not only between populations in North Africa and Sicily, but also between populations in these areas and others on the Italian Peninsula. Different results from allozymes and morphology in analyzing the same biogeographical question illustrate the need for caution in the interpretation of biogeographical patterns, which not only may be more complex than usually considered, but also provide tools for disclosing complex histories.

THE ENIGMATIC *M. JURTINA*

The case of *M. jurtina* is a model example demonstrating contradictory and concordant biogeographical patterns for species displaying similar clade distinctions and geographical ranges: specimens from mainland Italy, Sicily, and North Africa share the same allozyme set which comes into contact with an Iberian and a Balkan lineage in southern Central Europe (Alps, northernmost Italy) (Habel, Dieker & Schmitt, 2009). By contrast, specimens from mainland Italy share a shape of genitalia with specimens from the Balkan Peninsula and most of East and Central Europe (Thomson, 2011; Dapporto *et al*., 2009); however, populations in Sicily, Sardinia, Malta, and the Balearic islands have the Spanish–North African shape of genitalia, whereas populations from Corsica and the Italian islets (Elba, Pianosa, Giglio, Ischia, and Capri) have intermediate morphotypes (Thomson, 2011; Dapporto *et al*., 2009; L. Dapporto, unpubl. data for Ischia). Thus, based on morphometric measurements, populations on the circum-Italian islands differ markedly from those on the adjacent Italian mainland, although the same is not the case for islands off Spain and the Balkans (Balearics, Crete, and Zakynthos; Thomson, 2011; Dapporto *et al*., 2009; L. Dapporto, unpubl. data for Zakynthos) (Fig. 2A).

The evolution of these differences in patterns between genetic and morphological characters is still in need of interpretation. The discrepancy may be explained by different evolutionary pressures on the two distinct genetic and phenotypic traits. This may result in dissimilar dynamics of gene flow occurring

Figure 1. Refugial blocks for thermophilous organisms during glaciations in the Mediterranean with potential postglacial colonization pathways. Grey arrows, northward tracks; white arrows, longitudinal tracks within the Mediterranean Basin; large pecked outline arrows (right), inputs from east and south east; ?, uncertain north track from Sardinia–Corsica (S-C). Ib, Iberia; It, Italian peninsula; B, Balkans; Si, Sicily. Grey bands are major mountain barriers to dispersal for thermophilous organisms.
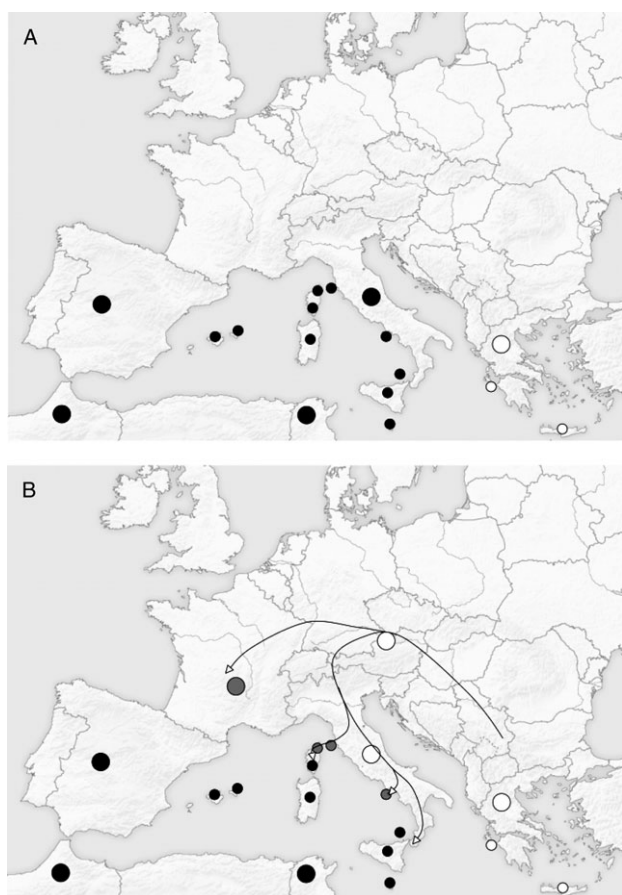
Figure 2. Hypothetical glacial distribution of the western (black circles) and eastern (white circles) genitalia lineages of *Maniola jurtina* (A) and successive invasion on Italian Peninsula by the eastern lineage (B). Small dots, islands; large dots, analyzed mainlands.

during range expansion. Such differential dynamics in gene distribution has been demonstrated for several organisms (Currat *et al.*, 2008; Excoffier, Hofer & Foll, 2009). Simulation and empirical studies have shown that the genomes of the invading taxa are largely replaced by those of the local populations (Currat *et al.*, 2008; Excoffier *et al.*, 2009). In particular, Currat *et al.* (2008) revealed that, in more than 80% of reviewed studies, gene flow is directed from resident to invasive taxa. These studies revised and modelled genetic introgression between different species. However, there is no reason to hypothesize that the same mechanisms also operate among putative conpecific lineages in *M. jurtina*. We therefore postulate that when individuals of *M. jurtina* from the Balkans colonized mainland Italy, they were more efficient competitors, driving the resident population to extinction. However, before this happened, the foreign population was able to capture (by gene flow) some adaptive genes from the resident population.

There is substantial evidence that phenotypic traits in butterflies may be under strong evolutionary and ecological pressures and may evolve as a rapid response to environmental conditions (Dennis & Shreeve, 1989; Shreeve, Van Dyck & Konvicka, 2009; Otaki *et al.*, 2010). However, this applies mainly to traits linked to external morphology (wing shape, size, coloration), whereas the same phenomenon is not expected to occur for genes controlling genitalia shape, which is probably not under strong environmental selection (Mutanen *et al.*, 2007; Gilligan & Wenzel, 2008). By contrast, when a comparative analysis was conducted on butterflies, genitalia have shown a high correlation with genetic characteristics not evident for wing shape (Cesaroni *et al.*, 1994). Moreover, Dapporto *et al.* (2009, 2011) demonstrated large differences in genitalia between the Tuscan islands and the nearest (<10 km) fossil islands connected to the mainland. Because islands and fossil islands in Tuscany are virtually identical with respect to ecology, geology, and geography, they should have the same genitalia shape if this trait has been influenced by ecological conditions. For this reason, we consider that genitalia shape is a neutral genetic marker with respect to ecological influences (Dapporto *et al.*, 2011).

The great variability of allozymes in butterflies often furnishes impressive results comparable to those obtained with microsatellite analyses (Habel *et al.*, 2011). Such evidence suggests evolutionary neutrality of most allozymes (Schmitt, 2007, 2009), although some loci were repeatedly observed as being under environmental selection, as reported in butterflies for the PGI, PGM, and G6PDH loci (Watt, 1977, 1983; Watt, Donohue & Cater, 1996; Karl, Schmitt & Fischer, 2009), including *M. jurtina* (Goulson, 1993). Of the two loci most clearly separating lineages in *M. jurtina*, one (G6PDH) belongs to the group frequently being found under selective pressure, whereas the other is not known as a selective marker (PEP); on the other hand, the two loci most often observed as being selected (PGI, PGM) show no major differences among lineages or gradients within lineages. Thus, allozymes not only represent neutral markers, but also markers undergoing environmental selection (Van Oosterhout, Van Heuven & Brakefield, 2004). The emergence of a new set of allozymes therefore could spread rapidly over large areas occupied by different genetic lineages, which could maintain other specific characteristics. However, an opposite phenomenon can occur in which resident genes selected in particular environments are expected to be assimilated into the invading population. During a hypothetical invasion from the Balkans, foreign allozymes (selected because advantageous in another context) might have been selected against, whereas

individuals into which allozymes of the resident population have been introgressed received an advantage. Thus, a situation can be envisaged where an immigrant population with the Balkan genitalia shape might well have accumulated Italian allozymes in its genome.

THE BIOGEOGRAPHICAL ANOMALY OF ISLANDS

In the context of major environmental changes, islands have generally been considered as areas where species are likely to have relatively short life-spans owing to the combined effects of higher extinction rates and higher speciation rates compared to mainland areas (Whittaker, 1998; Losos & Ricklefs, 2010). On the other hand, islands are also well known to present conservative faunas and biotopes. Many, once widespread, taxa only survived on islands after mainland areas were invaded by more successful competitors; these island taxa thus persist as paleoendemics (Whittaker, 1998; Karanth *et al*., 2005; Jones *et al*., 2009). However, the persistence of such paleoendemics is inevitably a phenomenon limited by time, owing to extinction, speciation, and invading competitors, although the process may be delayed (Myers & De Grave 2000). Such a delay has been directly demonstrated for the fossil vertebrate fauna of West Mediterranean islands by Masini *et al*. (2008). In their study, the authors show that no exchanges have occurred between islands and the mainland, that the environment has not been adversely affected by climate changes, and that many organisms (e.g. mammals) have persisted considerably longer on Sardinia than on the Italian mainland. Masini *et al*. (2008) thus demonstrated that large and isolated islands may represent more stable refugia than the neighbouring mainland.

Hewitt (1999, 2000) emphasized the importance of the three main peninsulas (Iberian, Italian, and Balkan) as refugia during cold periods; in addition, we suggest that inertia in both glacial and interglacial periods is one of the most important phenomena shaping the distribution of butterflies in the Mediterranean area, especially on the large Mediterranean islands and in North Africa. Where island populations are characterized by such strong inertia, there is a vital corollary: populations from such islands may be considered to be, in effect, living fossils, ancestral indicators of which species and genetic lineages occupied neighbouring mainland areas in the more or less recent past.

Dapporto *et al*. (2009, 2011) also suggested that the inertia of an island taxon should correlate directly with its geographical area and indirectly with its

isolation; distant islands are predicted to receive a smaller number of immigrants and large islands host larger populations that are predicted to take a longer time to be replaced (MacArthur & Wilson, 1967). This hypothesis is supported by the fact that hybrid populations of *M. jurtina* occur on small islands that are located close to the Italian mainland (Capri, Ischia, Elba, Pianosa, Giglio) and, only partially, on Corsica, although not on Sardinia (see above) (Fig. 2B).

THE REPETITIVENESS OF THE *M. JURTINA* PATTERN

Altogether, the different patterns of *M. jurtina* morphology and allozymes suggest: (1) the existence of ancient widespread populations in the western Mediterranean areas and islands (Fig. 2A) subsequently replaced in Italy by an invading group from the Balkans; (2) the resistance of an ancestral set of allozymes against the invading population; and (3) the persistence of both an ancestral allozyme set and morphology in island populations not accessed by massive invasions of foreign individuals (Fig. 2B). Finally, concordance between morphology in Greece as well as Zakynthos and Crete, suggests that the eastern lineage of *M. jurtina* did not enter Europe from Russia and/or Asia Minor but already occupied the Balkan area during the last Würm glacial advance, as suggested by Schmitt, Röber & Seitz (2005). In this model case of a recent replacement of the Balkan populations, similar discordances as in the case of Italy and its islands would be observed and not homogeneous structures.

The question arises as to whether these results reflect a more general biogeographical scenario. Habel *et al*. (2008) demonstrated a close genetic similarity between Europe and Morocco for the butterfly *Melanargia galathea* supporting a relatively recent connection. However, these North African populations have a higher genetic variability compared to those in Europe, thus making the former region the most likely centre of origin for this species. However, sequencing of mitochondrial (mt)DNA shows remarkable differentiation between north-west Africa and all other European provinces (Nazari, Ten Hagen & Bozano, 2010). Similar differentiation at the mtDNA level was also observed for *Parage aegeria* (Weingartner, Wahlberg & Nylin, 2006) and Lycaenid butterflies (Wiemers, Stradomsky & Vodolazhsky, 2010). From the allozyme pattern of *M. galathea* and the absence of the species from most parts of Iberia (where it is replaced by *Melanargia lachesis*; García-Barros *et al*., 2004), a scenario of immigration of *M. galathea* from the Maghreb via Italy to Europe is suggested. Furthermore, similarities in allozyme patterns between

Italy, Sicily, and North Africa have been confirmed in other Satyrinae and Lycaenidae butterflies (Habel *et al*., 2010); thus, that Italy, Sicily, and Northern Africa were probably linked by gene flow in butterflies and other similarly mobile taxa during Pleistocene glacial maxima. On the other hand, Dapporto (2010a) and Dapporto *et al*. (2011) have demonstrated that a number of Satyrinae butterflies show a similar intraspecific morphological pattern to *M. jurtina* across the Strait of Sicily and concluded that this is a common pattern in genital morphology linking most western Mediterranean islands with North Africa, Spain, and France. In this context, it would be helpful to know the allozyme patterns of populations from islands other than Sicily.

In view of these observations, an ancillary problem requiring explanation is why the Italian Peninsula has been so often invaded compared to Iberia, France, and North Africa. It has to be noted that the Italian Peninsula has a relatively small land area compared to France and Iberia and is located close to the large Balkan area. If the Dapporto *et al*. (2009, 2011) hypothesis is correct and populations on large land areas require more time to be replaced, then Italy is predicted to maintain its ancestral populations for a shorter period. The narrow Italian peninsula is more susceptible to incursions and less able to maintain its ancestral populations than Iberia and the Balkans. From this perspective, Satyrinae and Lycaenidae butterflies not only appear to have the dispersal capacity to facilitate spread throughout mainland areas, during both cold and warm periods, but also sufficient potential to persist on islands, even in the face of invasion, the basis for the inertia phenomenon. The end product is discordant populations among islands, even neighbouring ones, in addition to discordance with those on the nearest mainlands.

The dynamics of distributions hypothesized in the present study suggests that sufficient gene flow occurred across sea straits to ensure cohesiveness during glacial stages among populations of butterfly species on the southern European mainland and islands, as well as in North Africa (Fig. 1). It is noteworthy that a higher rate of sea crossing between Italy and North Africa and between mainland and islands is expected during Pleistocene cold stages than during the current warm stage, owing to the lowered sea level and therefore the reduced distances between land masses. For example Elba, Pianosa, Ischia, and Capri were connected to the Italian mainland during glacial maximum advances. The distance between Sicily and North Africa was reduced from the current 140 km to approximately 50 km, with the crossing interspersed with island stepping stones. Corsica was connected to Sardinia and both were less than 40 km from Italy rather than the current dis-

tance of approximately 60 km. Moreover, the ancestral lineages could have survived in the south of Italy and on many islands (e.g. Corsica and Tuscan Archipelago). Re-colonization of vacated islands by the ancestral lineages could have occurred in the immediate postglacial when climatic conditions were already favourable and sea levels were still low (Dennis, 1977; Thiede, 1978; Giraudi, 2004). Colonization of empty areas is likely to be more rapid and successful than the process of replacement by introgressive hybridization (Hewitt, 2000). Indeed, growth of invader genes in an island population could be impeded not only by rarity of immigrants across sea straits, but also by the potential lower vitality of hybrids as demonstrated between French and British populations of the Satyrinae *Lasiommata megera* (Olivier, 1972). This phenomenon would bolster island inertia. The problem of a lower vitality of hybrids is not expected for a phalanx-like spread of lineages over mainland regions (as proposed for *M. jurtina* by Schmitt *et al*., 2005).

Finally, climate change is a major factor in generating changes in species' geographical ranges; for thermophilous organisms, typically, expansions occur during warm phases and contractions during cold phases (Dennis *et al*., 1991). Although not the only factor influencing range changes, climate change influences key biotic and abiotic environmental regimes through the availability of heat and water, underpinning, for example, the invasion of more competitive taxa into new ecological settings. For a temperate species such as *M. jurtina*, the glacial stage conditions could have led to the contraction in its distribution in North Europe, although likely facilitated expansion of populations at the southern range margins (North Africa, Sicily, and Southern Italy). Although both temperature and precipitation decline over Europe, in the Mediterranean, the lower temperatures resulted in lower evapotranspiration rates, whereas summer temperatures (in these high insolation level environments) would have remained suitable for adult butterfly activity. Such conditions could have favoured a particularly rapid dispersal of the species among these areas and the formation of a unique highly similar population. Allozyme variation and genitalic pattern on islands actually suggests the persistence of such an interconnected common refugium for several butterfly species in Southern Italy, North Africa, and Sicily.

CONCLUSIONS

In the western Palearctic, the Mediterranean zone holds a vital place where taxa and genes are preserved for thermophilous organisms during glacial phases and new clades are generated. It does this

through the existence of refugia, isolated large blocks of land on which organisms can persist and continue to evolve during the severe cold phases prevalent in Europe north of the Alps (Dennis *et al.*, 1991; Hewitt, 1999, 2000; Schmitt, 2007). However, it is clear that interactions among the populations from different refugial blocks also occur during postglacial range expansion; one outstanding issue is the incongruent findings from different genetic markers (Dapporto *et al.*, 2009; Habel *et al.*, 2009, 2010; Dapporto, 2010a, b). From their use, it is evident that colonization histories are far more complex than originally considered and it represents a complex combination of glacial, sudden postglacial, and recent dispersal events, which are more or less impeded by mountain chains and sea straits (Dapporto *et al.*, 2009; Habel *et al.*, 2009, 2010, 2011; Dapporto, 2010a, b). Different aspects of colonization and evolutionary history emerge from their joint use, and we advocate multiple application of different markers in paleobiogeography reconstructions that search for evolutionary events and colonization pathways. In particular, a distributional pattern, widespread among butterflies, appears to suggest a broad cohesiveness in the West Mediterranean during the last glacial phase and a rapid postglacial invasion of the Italian Peninsula, presumably from the Balkan area, during more recent times.

REFERENCES

Cesaroni D, Lucarelli M, Allori P, Russo F, Sbordoni V. 1994. Patterns of evolution and multidimensional systematics in graylings (Lepidoptera, *Hipparchia*). *Biological Journal of the Linnean Society* **52:** 101–111.

Currat M, Ruedi M, Petit RJ, Excoffier L. 2008. The hidden side of invasions: massive introgression by local genes. *Evolution* **62:** 1908–1920.

Dapporto L. 2010a. Satyrinae butterflies from Sardinia and Corsica show a kaleidoscopic intraspecific biogeography (Lepidotpera, Nymphalidae). *Biological Journal of the Linnean Society* **100:** 195–212.

Dapporto L. 2010b. Speciation in Mediterranean refugia and post-glacial expansion of *Zerynthia polyxena* (Lepidoptera, Papilionidae). *Journal of Zoological Systematics and Evolutionary Research* **48:** 229–237.

Dapporto L, Bruschini C, Baracchi D, Cini A, Gayubo F, Gonzàlez JA, Dennis RLH. 2009. Phylogeography and counter-intuitive inferences in island biogeography: evidence from morphometric markers in the mobile butterfly *Maniola jurtina* (Linnaeus) (Lepidoptera, Nymphalidae). *Biological Journal of the Linnean Society* **98:** 677–692.

Dapporto L, Schmitt T, Vila R, Scalercio S, Biermann H, Dincă V, Gayubo SF, González JA, Lo Cascio P, Dennis RLH. 2011. Phylogenetic island disequilibrium: evidence for ongoing long-term population dynamics in two Mediterranean butterflies. *Journal of Biogeography*, DOI: 10.1111/j.1365-2699.2010.02452.x.

Dennis RLH. 1977. *The British butterflies. Their origin and establishment*. EW Classey: Oxon.

Dennis RLH, Shreeve TG. 1989. Butterfly wing morphology variation in the British Isles: the influence of climate, behavioural posture and the hostplant-habitat. *Biological Journal of the Linnean Society* **38:** 323–348.

Dennis RLH, Williams WR, Shreeve TG. 1991. A multivariate approach to the determination of faunal units among European butterfly species (Lepidoptera: Papilionoidea, Hesperioidea). *Zoological Journal of the Linnean Society* **101:** 1–49.

Dennis RLH, Shreeve TG, Williams WR. 1995. Taxonomic differentiation in species diversity gradients among European butterflies: contribution of macroevolutionary dynamics. *Ecography* **18:** 27–40.

Dennis RLH, Williams WR, Shreeve TG. 1998. Faunal structures among European butterflies: evolutionary implications of bias for geography, endemism and taxonomic affiliations. *Ecography* **21:** 181–203.

Excoffier L, Hofer T, Foll M. 2009. Detecting loci under selection in a hierarchically structured population. *Heredity* **103:** 285–298.

García-Barros E, Munguira ML, Martín Cano J, Romo Benito H, Garcia-Pereira P, Maravalhas ES. 2004. *Atlas de las mariposas de la Península Ibérica e islas Baleares (Lepidoptera: Papilionoidea & Hesperioidea)*. Zaragosa: Monografias SEA Sociedad Entomológica Aragonesa.

Gilligan TM, Wenzel JW. 2008. Extreme intraspecific variation in *Hystrichophora* (Lepidoptera: Tortricidae) genitalia – questioning the lock-and-key hypothesis. *Annales Zoologici Fennici* **45:** 465–477.

Giraudi C. 2004. The Apennine glaciations in Italy. In: Ehlers J, Gibbard PL, eds. *Quarternary glaciations – extent and chronology*. Part I: Europe. Developments in quaternary science, Vol. 2a. Amsterdam: Elsevier Science, 215–224.

Goulson D. 1993. Allozyme variation in the butterfly, *Maniola jurtina* (Lepidoptera: Satyrinae) (L.): evidence for selection. *Heredity* **71:** 386–393.

Habel JC, Schmitt T, Müller P. 2005. The fourth paradigm pattern of postglacial range expansion of European terrestrial species: the phylogeography of the marbled white butterfly (Satyrinae, Lepidoptera). *Journal of Biogeography* **32:** 1489–1497.

Habel JC, Meyer M, El Mousadik A, Schmitt T. 2008. Africa goes Europa: the complete phylogeography of the marbled white butterfly species complex *Melanargia galathea / lachesis*. *Organisms, Diversity & Evolution* **8:** 121–129.

Habel JC, Dieker P, Schmitt T. 2009. Biogeographical connections between the Maghreb and the Mediterraenan peninsulas of southern Europe. *Biological Journal of the Linnean Society* **98:** 693–703.

Habel JC, Rödder D, Scalercio S, Meyer M, Schmitt T. 2010. Strong genetic cohesiveness between Italy and the Maghreb in four butterfly species. *Biological Journal of the Linnean Society* **99:** 818–830.

Habel JC, Rödder D, Schmitt T, Nève G. 2011.

Global warming will affect genetic diversity of *Lycaena helle* populations. *Global Change Biology* **17:** 194–205.

Hewitt GM. 1999. Post-glacial re-colonization of European biota. *Biological Journal of the Linnean Society* **68:** 87–112.

Hewitt GM. 2000. The genetic legacy of the Quaternary ice ages. *Nature* **405:** 907–913.

Jones MEH, Tennyson AJD, Worthy JP, Evans SE, Worthy TH. 2009. A sphenodontine (Rhynchocephalia) from the Miocene of New Zealand and palaeobiogeography of the tuatara (Sphenodon). *Proceedings of the Royal Society of London Series B, Biological Sciences* **276:** 1385–1390.

Karanth KP, Delefosse T, Rakotosamimanana B, Parsons TJ, Yoder AD. 2005. Ancient DNA from giant extinct lemurs confirms single origin of Malagasy primates. *Proceedings of the National Academy of Sciences of the United States of America* **102:** 5090–5095.

Karl I, Schmitt T, Fischer K. 2009. Genetic differentiation between alpine and lowland populations of a butterfly is related to PGI enzyme genotype. *Ecography* **32:** 488–496.

de Lattin G. 1967. *Grundriss der Zoogeographie*. Stuttgart: Fischer.

Losos JB, Ricklefs RE, eds. **2010.** *The theory of island biogeography revisited*. Princeton, NJ: Princeton University Press.

MacArthur RH, Wilson EO. 1967. *The theory of island biogeography*. Princeton, NJ: Princeton University Press.

Masini F, Petruso D, Bonfiglio L, Mangano G. 2008. Origination and extinction patterns of mammals in three central Western Mediterranean islands from the Late Miocene to Quaternary. *Quaternary International* **182:** 63–79.

Mutanen M, Rytkonen S, Linden J, Sinkkonen J. 2007. Male genital variation in a moth *Pammene luedersiana* (Lepidoptera: Tortricidae). *European Journal of Entomology* **104:** 259–265.

Myers AA, De Grave S. 2000. Endemism: origins and implications. *Vie et Milieu* **50:** 195–204.

Nazari V, Ten Hagen W, Bozano GC. 2010. Molecular systematics and phylogeny of the 'marbled whites' (Lepidoptera: Nymphalidae, Satyrinae, Melanargia Meigen). *Systematic Entomology* **35:** 132–147.

Olivier CG. 1972. Genetic differentiation between English and French populations of the satyrid butterfly *Pararge megera* L. *Heredity* **29:** 307–313.

Otaki JM, Hiyama A, Iwata M, Kudo T. 2010. Phenotypic plasticity in the range-margin population of the lycaenid butterfly *Zizeeria maha*. *BMC Evolutionary Biology* **19:** 252.

Reinig WF. 1937. *Die holarktis*. Jena: Fischer.

Schmitt T. 2007. Molecular biogeography of Europe: Pleistocene cycles and postglacial trends. *Frontiers in Zoology* **4:** 11.

Schmitt T. 2009. Biogeographical and evolutionary importance of the European high mountain systems. *Frontiers in Zoology* **6:** 9.

Schmitt T, Röber S, Seitz A. 2005. Is the last glaciation the only relevant event for the present genetic population structure of the meadow brown butterfly *Maniola jurtina* (Lepidoptera: Nymphalidae)? *Biological Journal of the Linnean Society* **85:** 419–431.

Schmitt T, Habel JC, Zimmermann M, Müller P. 2006. Genetic differentiation of the Marbled White butterfly, *Melanargia galathea*, accounts for glacial distribution patterns and postglacial range expansion in southeastern Europe. *Molecular Ecology* **15:** 1889–1901.

Shreeve TG, Van Dyck H, Konvicka M. 2009. The functional significance of butterfly wing morphology variation. In: Settele J, Shreeve TG, Konvicka M, Van Dyck H, eds. *The ecology of butterflies in Europe*. Cambridge: Cambridge University Press.

Taberlet P, Fumagalli L, Wust-Saucy AG, Cosson JF. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* **7:** 453–464.

Thiede J. 1978. A glacial Mediterranean. *Nature* **276:** 680–683.

Thomson G. 2011. The Meadow Brown butterflies – a study in genetics, morphology and evolution. ISBN 9780954089139.

Van Oosterhout C, Van Heuven MK, Brakefield PM. 2004. On the neutrality of molecular genetic markers: pedigree analysis of genetic variation in fragmented populations. *Molecular Ecology* **13:** 1025–1034.

Watt WB. 1977. Adaptation at specific loci. I. Natural selectionon on phosphoglucose isomerase of *Colias* butterflies: biochemical and population aspects. *Genetics* **87:** 177–194.

Watt WB. 1983. Adaptation at specific loci. II. Demographic and biochemical elements in the maintenance of the *Colias* PGI polymorphism. *Genetics* **103:** 691–724.

Watt WB, Donohue K, Cater PA. 1996. Adaptation at specific loci. IV. Divergence vs. parallelism of polymorphic allozymes in molecular function and fitness-component effects among *Colias* species (Lepidoptera, Pieridae). *Molecular Biology and Evolution* **13:** 699–709.

Weingartner E, Wahlberg N, Nylin S. 2006. Speciation in *Pararge* (Satyrinae: Nymphalidae) butterflies – North Africa is the source of ancestral populations of all *Pararge* species. *Systematic Entomology* **31:** 621–632.

Whittaker RJ. 1998. *Island biogeography: ecology, evolution, and conservation*. Oxford: Oxford University Press.

Wiemers M, Stradomsky BV, Vodolazhsky D. 2010. A molecular phylogeny of *Polyommatus* s. str. and *Plebicula* based on mitochondrial COI and nuclear ITS2 sequences (Lepidoptera: Lycaenidae). *European Journal of Entomology* **107:** 325–336.