Relict Species: From Past to Future

Jan C. Habel, Thorsten Assmann, Thomas Schmitt, and John C. Avise

1 What Are Relicts?

Dictionaries define a "relict" as something that has survived, usually as a trace, from the past. In biology, relicts are distinctive populations or species that typically are small in size or severely restricted in geographic range. Biologists distinguish between taxonomic and biogeographic relicts. Taxonomic relicts are a few or sole survivors of a once diverse taxonomic assemblage, whereas biogeographic relicts are descendants of once widespread taxa (or populations) that now have a narrow geographic distribution (Lomolino et al. 2006). Both categories sometimes coincide, as for example in the case of "living fossils" (such as ginko, lungfishes, crossopterygians, or marsupials) that closely resemble their ancient ancestors in overall phenotype (Futuyma 2005; Lomolino et al. 2006; Beierkuhnlein 2007). In the following, we focus on biogeographic relicts.

Climatic and other large-scale environmental changes can have fundamental impact on the distributional patterns of species and alter the composition of communities and ecosystems (e.g. Hewitt 1999; Schweiger et al. 2009). Species react by range shifts, or by local or regional extinctions when their *adaptive capacity* is exceeded (Agarwal 2001). The origins and distributions of modern-day relicts can often be related to environmental changes of the past. Glacial periods and warm interglacial periods of the Quaternary, in particular, often help us to understand how relict species and

J.C. Habel (\boxtimes)

Musée national d'histoire naturelle, Section Zoologie des Invertébrés, L-2160 Luxembourg, Luxembourg e-mail: Janchristianhabel@gmx.de

J.C. Habel and T. Schmitt Department of Biogeography, Trier University, D-54286 Trier, Germany

T. Assmann Institute of Ecology and Environmental Chemistry, Leuphana University Lüneburg, D-21335 Lüneburg, Germany

J.C. Avise University of California, CA 92697 Irvine, USA populations arise and sometimes have served as important sources for re-colonizing much larger areas (de Lattin 1967). For example, many thermophilic species survived the last ice age in relatively small refugia on Europe's Southern peninsulas. During interglacial periods, these species often colonized large areas. Thus, many temperate species that are widespread today existed as small relict populations just a few thousand years ago (cf. Schmitt 2007). Conversely, many cold-adapted species show evidence of formerly wide distributions, followed by severe range restrictions during postglacial warming. Prominent examples of the latter are the butterflies Proclossiana eunomia pictured on this book (front side) and Lycaena helle (small picture on the back side), which currently resides only in high-elevation mountain enclaves and at more Northern latitudes that have been shown to coincide with distinctive genetic clusters in this species (Habel et al. 2009). Although such species today (and during the other warm periods between glacial periods) are restricted to small areas, they may have the potential to recolonize larger areas if and when the climate cools again. In general, the assumption that relict species inevitably are on their way to extinction may be erroneous; at least some relict populations undoubtedly retain the potential to adapt to a broad spectrum of environmental conditions (Hampe and Petit 2005).

Range restrictions and expansions are also known to result from human-mediated landscape changes. For example, woodlands covered large areas of Central Europe prior to anthropogenic deforestation. Especially during the Middle Ages and early modern times, these extensive woodlands were degraded to a few small remnants. After the establishment of modern forestry and changes in land use, woodland coverage again increased enormously. The former woodland remnants preserved forest-inhabiting plants and animals, some of which still show relict-like distributions but others of which were able to re-colonize large areas (e.g. Assmann 1999; Drees et al. 2008). Comparable changes are known for numerous habitat types and regions. These alternating scenarios of range expansions and restrictions remind us that species with relict-like versus wide distributions are *not* necessarily contradictory indicators of past environmental changes.

2 Conservation of Relict Species and Populations

Why focus special conservation attention on relict as opposed to non-relict taxa? One explanation may reside in the connotation for relict that appears from the word "trace" in the dictionary definition. Typically, little remains of any relict, implying in the current biological context that extant populations of a relict species are few in number or small in size. Thus, populations of a relict taxon might occupy disjunct mountain peaks or perhaps a few isolated lakes, for example. Rarity and restricted distributions obviously place relict species in special demographic jeopardy of extinction, especially in the face of ongoing climatic changes and other ecological perturbations.

Another more subtle connotation in the dictionary definition is that relicts are unchanged or "left behind" relative to their non-relict counterparts. It seems doubtful, however, that evolutionary genetic change has ceased or even slowed substantially in relict species. Indeed, if genetic drift is a potent evolutionary force (as expected for small populations), then the genetic differences of extant relicts from their ancestors or from their modern sister taxa might even be greater than the genetic differences of non-relict species from their respective ancestors or extant relatives. One of the most robust discoveries from the field of molecular evolution is that genetic change proceeds inexorably through time, in essentially all species, and sometimes at surprisingly steady mean rates. An interesting scientific question is whether relict species (as defined by small population size or restricted geographic distribution) tend to evolve at the genotypic or phenotypic levels at rates that differ consistently from those of their non-relict counterparts (García-Ramos and Kirkpatrick 1997).

Another set of scientifically interesting questions stems from the fact that various relict species and populations can have strikingly different ages, thus making them excellent objects for comparative evolutionary and ecological studies (Lesica and Allendorf 1995). In particular, phylogeographic surveys can give great insights into historical, ecological and evolutionary processes related to past shifts (restrictions and expansions) in the distributions of species (Avise 2000; Hewitt 2000, 2004; Schmitt 2007). Moreover, by helping to identify evolutionarily significant units (ESUs) and management units (MUs), phylogeographic and population genetic analyses can help to identify relict populations of special importance for conservation and management (cf. Moritz 1994; Avise and Hamrick 1996; Pérez-Tris et al. 2004; De Guia and Saitoh 2006). Finally, there is a huge scientific interest in stochastic processes as well as inbreeding in relict species that consist either of single populations or structured metapopulations (cf. Melbourne and Hastings 2008). These processes can reduce genetic variability (Petit et al. 2003; Chang et al. 2004) and diminish genetic fitness (cf. Berger 1990; Reed and Frankham 2003) within relict populations of both plants (Oostermeijer et al. 1996) and animals (Wynhoff et al. 1996; Madsen et al. 1999).

Many relict species are already endangered and referenced in *Red Lists*. Conservation must not ignore relicts, as they form an essential component of overall biodiversity. Relict populations and species are, almost by definition, "survivors". Thus, it is both sad and ironic that conservation biologists must now be concerned about the survival into the future of relict species that, by definition, are proven survivors from the evolutionary past. Nonetheless, such conservation concern is merited, because human actions are precipitating global climatic and other environmental changes that may fall outside the adaptive scope of many relict (and other) living species.

3 The Scope of This Book

This book focuses on relict species and describes their history, current status, and future trends. It presents a compilation of case studies representing different methodological approaches and different temporal and spatial scales, all meant to

illustrate evolutionary processes and ecological traits of isolated remnant populations. The book is structured into five sections. Section 1 deals with the basics of climate change and the responses of species and ecosystems. Sections 2 and 3 deal with the effects of pre-glacial and glacial phenomena, and postglacial range expansions, on relict species. Section 4 includes conservation approaches to protect and preserve relict species. Finally, in Section 5, future trends of relict species and their projected distributional patterns are discussed. The book also includes four mini-reviews that highlight molecular techniques, the biogeography of Europe, cave species, and ecological niche modelling.

References

- Agarwal AA (2001) Phenotypic plasticity in the interactions and evolution of species. Science 294:321–326
- Assmann T (1999) The ground beetle fauna of ancient and recent woodlands in the lowlands of North-West Germany (Coleoptera, Carabidae). Biodivers Conserv 8:1499–1517
- Avise JC (2000) Phylogeography. The history and formation of species. Harvard University Press, Cambridge
- Avise JC, Hamrick JL (eds) (1996) Conservation genetics: case histories from nature. Chapman & Hall, New York
- Beierkuhnlein C (2007) Biogeographie Die räumliche Organisation des Lebens in einer sich verändernden Welt. UTB Ulmer, 397
- Berger J (1990) Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. Conserv Biol 4:91–98
- Chang CS, Kim H, Park TY, Maunder M (2004) Low levels of genetic variation among Southern peripheral populations of the threatened herb, *Leontice microrhyncha* (Berberidaceae) in Korea. Biol Conserv 119:387–396
- De Guia APO, Saitoh T (2006) The gap between the concept and definitions in the Evolutionarily Significant Unit: the need to integrate neutral genetic variation and adaptive variation. Ecol Res 22:1440–1703
- Drees C, Matern A, Rasplus J-Y, Terlutter H, Assmann T, Weber F (2008) Microsatellites and allozymes as the genetic memory of habitat fragmentation and defragmentation in populations of the ground beetle *Carabus auronitens* (Col., Carabidae). J Biogeogr 35:1937–1949
- Futuyma DJ (2005) Eolution. Sinauer Associates, Sunderland, MA
- García-Ramos G, Kirkpatrick M (1997) Genetic models of adaptation and geneflow in peripheral populations. Evolution 51:21–28
- Habel JC, Augenstein B, Nève G, Rödder D, Assmann T (2009) Population genetics and ecological niche modelling reveal high fragmentation and potential future extinction of the endangered relict butterfly *Lycaena helle* in. In: Habel JC, Assmann T (eds) Relict species, phylogeography and conservation biology. Springer, Heidelberg
- Hampe A, Petit RJ (2005) Conserving biodiversity under climate change: the rear edge matters. Ecol Lett 8:461–467
- Hewitt GM (2000) The genetic legacy of the ice ages. Nature 405:907-913
- Hewitt GM (2004) Genetic consequences of climatic oscillations in the Quaternary. Philos Trans R Soc Lond B 359:183–195
- Hewitt GM (1999) Postglacial re-colonization of European biota. Biol J Linn Soc 68:87-112
- de Lattin G (1967) Grundriß der Zoogeographie. Verlag Gustav Fischer, Jena
- Lesica P, Allendorf FW (1995) When peripheral populations are valuable for conservation. Cons Biol 9:753–760

Lomolino MV, Riddle BR, Brown JH (2006) Biogeography. Sinauer, Sunderland, MA

- Madsen T, Shine R, Olsson M, Wittzell H (1999) Restoration of an inbred adder population. Nature 402:34–35
- Melbourne BA, Hastings A (2008) Extinction risk depends strongly on factors contributing to stochasticity. Nature 454:100–103
- Moritz C (1994) Defining evolutionarily significant units for conservation. Trends Ecol Evol 9:373–375
- Oostermeijer JGB, Brugman ML, De Boer ER, Den Nijs HCM (1996) Temporal and spatial variation in the demography of *Gentiana pneumonanthe*, a rare perennial herb. J Ecol 84:166–174
- Pérez-Tris J, Bensch S, Carbonell R, Helbig AJ, Tellería JL (2004) Historical diversification of migration patterns in a passerine bird. Evolution 58:1819–1832
- Petit RJ, Aguinagalde I, de Beaulieu JL, Bittkau C, Brewe S, Cheddadi R (2003a) Glacial refugia: hotspots but not melting pots of genetic diversity Science 300:1563–1655
- Petit RJ, Aguinagalde I, de Beaulieu JL, Bittkau C, Brewe S, Cheddadi R (2003b) Glacial refugia: hotspots but not melting pots of genetic diversity. Science 300:1563–1655
- Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conserv Biol 17:230–237
- Schmitt T (2007) Molecular biogeography of Europe: pleistocene cycles and postglacial trends. Front Zool 4:11
- Schweiger O, Stettele J, Kudrna O, Klotz S, Kühn I (2009) Climate change can cause spatial mismatch of trophically interacting species. Ecology 89:3472–3479
- Wynhoff I, Oostermeijer JGB, Scheper M, Van der Made JG (1996) Effects of habitat fragmentation on the butterfly *Maculinea alcon* in the Netherlands. In: Settele J, Margules C, Poschlod P, Henle K (eds) Species survival in fragmented landscapes. Geo J Libr 35:15–23