Endemism in Sardinia: Evolution, ecology, and conservation in the butterfly Maniola nurag
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Citation for published version (APA):
Amsterdam: IBED, Universiteit van Amsterdam

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Summary

Evolution means 'change'. For population geneticists evolution more specifically means 'change in the allele frequencies of a population in time'. These changes can result in species' differentiation and are the source of biological diversity. An understanding of the evolutionary processes creating diversity is therefore not only of theoretical interest, but may also lead to a better understanding of the reasons why species go extinct, and could in the end have a practical use in nature conservation.

In this thesis I focus on the evolution and ecology of species, that are restricted to the Mediterranean island of Sardinia, *i.e.*, are endemic to Sardinia. Besides providing natural laboratories to study evolution, differentiation and speciation in particular, endemic species are also a major focus in conservation biology, as their disappearance from the small area they occupy would signify their total extinction. Sardinia belongs to an archipelago called the Tyrrhenian islands. These islands are one of the ten Mediterranean hotspots of diversity and endemism. In Sardinia, for example, 12% of all plants are endemic, and 14 of the 56 butterfly species occurring on the island are Tyrrhenian endemics.

I start with a general overview of endemic species in Sardinia (Part 1), zoom in on butterflies (Part 2), and finally concentrate on the Sardinian satyrid *Maniola nurag* (Part 3 and 4).

Quite a few early evolutionary biologists have been inspired by the great diversity in pattern and colour found on the wings of butterflies. Butterflies of the genus *Maniola* are highly polymorphic. Variation includes intra- as well as interspecific differences. Notably, three of the seven species in the genus are island endemics (*M. nurag, M. chia, M. cypricola*). Usually, endemics are distributionally separated from their widespread relatives. However, in Sardinia, an endemic (*M. nurag*) and a widespread *Maniola* species (*M. jurtina*) occur sympatrically, which might indicate a sympatric speciation event (speciation without an extrinsic barrier to gene-flow) as an alternative to an allopatric speciation event (speciation without gene-flow) to explain the origin of *M. nurag*.

The first part of this thesis deals with the question - "Which are the endemics and where do they live?" It starts with a review of recent literature describing patterns of endemity in different groups of organisms (plants, butterflies, beetles, amphibians, and lizards) endemic to Sardinia (Chapter II). I shortly summarize the geological history of the Mediterranean basin and try to relate dated geophysical events to molecular-based estimates of species' divergence times. Areas of endemism generally coincide with mountain areas. Most endemics appear to have originated through vicariance or are relics (palaeo-endemics) from pre-glaciation periods. Some came to the island by active dispersal, or passively by human transportation. Mediterranean shrubland communities are identified as an important habitat for endemic Sardinian species, particularly butterflies (Chapter III). Further, I compare butterfly (hebivore) species richness in different habitat types with...
spider (predator) species richness, and find no significant relationship between these two groups. In the areas studied in Sardinia, butterflies are thus not such straightforward indicators of overall species diversity as they are often supposed to be. On the other hand, the number of butterfly species present in an area was positively related to overall plant species richness and elevation above sea level.

Part two deals with the conservation of Sardinian endemics. - "How to protect endemics?" Legal tools for setting nature conservation priorities are addressed as well as landscape management. The threat status of Sardinian butterflies is assessed by applying the IUCN criteria (Chapter IV). This chapter also shows how the quantitative information, as formulated in the IUCN criteria, can be combined with a qualitative assessment of human induced threat factors. This method allows an objective standardised assessment of threat, even when data are scarce. Two butterfly species, *Pseudophilotes barbagiae* and *Lysandra coridon gennargenti*, were identified as globally 'vulnerable', and their inclusion in the European Habitat Directive and the Bern Convention is strongly recommended. A mark-recapture study showed that populations of the endemic butterfly *M. nurag* form metapopulation networks whose long-term persistence requires connectivity between local populations (Chapter V). It also became apparent that areas to protect *nurag*-type species should cover at least 200 ha. I recommend traditional land-use practises as an important tool to combine nature-conservation interests with the interests of regional economy.

The third part continues questioning the origin of *M. nurag*. The two chapters in this part of the thesis take the butterfly *M. nurag* as a model to trace the evolutionary history of an island endemic, and connect present theoretical advances in evolutionary biology with population genetic data on the endemic butterfly (Chapter VI and VII). This part combines ecological field data (mark-release-recapture) with molecular genetic data (allozyme markers). Patterns of genetic diversity and population structure of Sardinian populations of *M. nurag* and *M. jurtina* are compared to mainland populations of *M. jurtina*. Results are used to determine whether allopatric or sympatric speciation best explains the origin of *M. nurag*. The small genetic distance between *M. jurtina* and *M. nurag* indicates that they are closely related. Divergence-time was estimated at 1.8 - 3 ma ago.

*M. nurag* is a mountain species, whereas *M. jurtina* also occurs at sea-level. At intermediate altitudes they meet and occasionally seem to produce hybrids. Geographic patterns in allele frequency patterns indeed hint at the presence of hybrids in areas where *M. nurag* and *M. jurtina* fly together, and also morphologically these individuals are intermediate between *M. nurag* and *M. jurtina*. From genetic and ecological data, it is concluded that *M. nurag* might not be the result of vicariance but originated under sympatric or parapatric circumstances, as a consequence of adaptation along an environmental gradient. The results underline the importance of environmental gradients in generating biodiversity. Disjunct distributions of closely related species do not
necessarily have to be the result of passive (allopatric) splitting of populations in the past, but can also follow genetic splitting within the population itself.

Part four provides a description of the genitalia structure of three endemic Maniola species, *M. nurag*, *M. chia*, and *M. cypricola* (Chapter VIII). It gives the first detailed description and illustration of the genitalia of *M. nurag*, and is extended to an overview of morphologic variation in the genus Maniola. Given the overlap in wing patterns and geographic distribution in this genus, genitalia morphology is occasional the only feature to tell species apart. Further, I describe two Sardinian individuals with intermediate characteristics between *M. nurag* and *M. jurtina*. These two specimen also appeared genetically as 'intermediates' (as explained in chapter VII). I describe a number of diagnostic characters to distinguish various Maniola species by means of genitalia morphology, and shortly discuss the justification of the species status for *M. chia* and *M. cypricola*. Chapter IX describes an aberration (two bursae copulatrices) in the female genitalia of an individual of *M. jurtina* found in Amsterdam during the collection of material for the present thesis.