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The role of chromosomal inversions in rough periwinkle snails (*Littorina saxatilis*)

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Akademisk avhandling för filosofie doktorsexamen i Naturvetenskap med inriktningen marina vetenskaper, som med tillstånd från Naturvetenskapliga fakulteten kommer att offentligt försvaras måndag den 3e, juni, 2024 kl. 10:00 i Hörsalen, Tjärnö marina laboratorium, Institutionen för marina vetenskaper, Laboratorievägen 10, 452 96 Strömstad

ISBN 978-91-8069-721-7 (PRINT)
ISBN 978-91-8069-722-4 (PDF)
Tillgänglig via: http://hdl.handle.net/2077/80417

Keywords: evolution | population genetics | molluscs | speciation | chromosomal inversions | local adaptation | ecotypes | hybrid zone | *Littorina saxatilis*

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Abstract

Chromosomal inversions are genomic rearrangements that may have a major role in local adaptation, facilitating ecotype formation and speciation. Recombination can hinder these processes as it breaks apart beneficial combinations of alleles, mixing them with alleles brought in by gene flow. Inversions suppress recombination, preventing the breakdown of beneficial allele combinations. Thus, they are expected to harbour loci influenced by habitat-driven selection. Sharp habitat transitions between boulder fields and rocky shores have been used to study the genetic basis of habitat-driven selection in the intertidal snail *Littorina saxatilis.* Snail populations are adapted to different environmental pressures on each side of these habitat transitions. A *Crab* ecotype that is resistant to predation in boulder fields, and a *Wave* ecotype that is present in rocky shores and has adapted to resist being swept away by strong waves. Hybrid zones join these ecotypes, where strong changes in phenotype and shifts in allele frequencies have been observed. Eighteen inversions have been found with shifts in arrangement frequencies across the *L. saxatilis* hybrid zones. Three of them have a strong association to *Crab-Wave* ecotype formation, two are related to shore height adaptation, and three are linked with sex determination. However, much of our understanding of *L. saxatilis* inversions comes from sampling across hybrid zones, from a handful of sites in Sweden. This sampling may not reflect the role of inversions across the species' range. I investigated the broader roles that these inversions have in adaptation across a range of Swedish habitats, and their broader role across the species range and in other *Littorina* species. I show that most inversions have links to local environmental variation, not just at the major habitat boundary between the *Crab* and *Wave* ecotypes (**Chapter 1**). Extensive local sampling showed that ecotypes are the extreme ends of a continuum of phenotypic diversity, and all inversions have roles in local adaptation across multiple environmental gradients (**Chapter 2**). At the broader taxonomic scale, I found the inversions are distributed across the species range and across species boundaries, suggesting they are ancient (**Chapter 3**). This suggests inversions contribute to the parallel evolution of ecotypes across European coasts. Inversions are, however, not linked to the different reproductive modes of *L. arcana* and *L. saxatilis*, demonstrating that speciation can proceed without ecological divergence (**Chapter 4**). The key findings of this thesis are that inversions are widespread in their geographic and taxonomic distributions, and that most of them have roles in local adaptation. *Littorina* is a good system for studying the roles of inversions throughout speciation, as each inversion tells a separate, yet linked story over a long process of divergence.

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