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## ***Daphnia* comes of age: an ecological model in the genomic era**

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### **Abstract**

Scientists in various subdisciplines of biology have long relied on model organisms to push the frontiers of knowledge forward as far as possible in their specific field. Today, interdisciplinary science requires model organisms that can push our understanding on multiple frontiers and help us formulate and address more complex questions. Members of the genus *Daphnia* represent just such an interdisciplinary model. *Daphnia* are aquatic microcrustaceans (also known as water-fleas) that have long been central to the study of ecology and toxicology and have recently been developed as a genomic model. A recent survey of both nuclear and mitochondrial markers in populations of the *Daphnia pulex* complex from high-altitude lakes in South America (Mergeay *et al.* 2008, this issue) provides an excellent example of how genetic data and ecological information can be used to push the boundaries of our understanding in molecular ecology. In this species complex, extensive hybridization has occurred resulting in polyploidization and, consequently, asexuality. Their data reveal high levels of genetic diversity, incongruence in phylogenetic signal among genomes (nuclear and mitochondrial), cryptic species in the complex, and a new model for the historical spread of the species throughout the Americas. Their data indicate that genome-level changes have occurred in this species which have profound consequences in an ecological context, the implications of which can be more fully appreciated because of our extensive knowledge of the ecology and natural history of the genus *Daphnia*.

### **Keywords**

asexuality; cryptic speciation; cyclical parthenogen; *Daphnia* phylogeny; *Daphnia pulex*; glacial refugia; hybridization; microsatellites; mitochondria; polyploidy

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Among the *Daphnia* populations sampled in this study, a central outcome of hybridization is polyploidization. Although most species of *Daphnia* reproduce via cyclical parthenogenesis (clonal asexual reproduction punctuated by seasonal bouts of sex), polyploids consistently lose the ability to reproduce sexually. Obligate asexuality is not uncommon in this species complex and can occur even in the absence of polyploidization. The mechanism underlying the switch to asexuality is not known in polyploids (nor is it known for diploid asexuals as of yet), but this phenomenon is widespread among many other distinct clades. Asexuality may provide an ecological advantage for hybrids because it may allow them to colonize marginal habitats, thereby increasing the species range. Isolated populations along the edges of the species distribution may, in turn, experience discontinuous gene flow and ultimately result in cryptic species. The phylogenetic analysis based on sequencing mitochondrial DNA (mtDNA) presented by Mergeay *et al.* 2008 (this issue) suggests there are at least three distinct, previously unknown clades in this species complex. In addition, their phylogeny overturns former notions about the pattern of colonization of the Americas by *Daphnia pulicaria* (a sister species to *D.*

*pulex*) suggesting that colonization proceeded from south to north, and not vice versa as previously hypothesized (Adamowicz *et al.* 2002).

Based on the nuclear and mtDNA data, Mergeay *et al.* 2008 observe extremely high overall levels of genetic diversity among the populations they sampled in the Bolivian Andes compared to those collected in southern South America (Fig. 1). This diversity could be explained by several factors, including the addition of genetic material resulting merely from the genetic admixture that occurred during the initial hybridization event. It may also simply reflect the different evolutionary dynamics of the two genomes from which the data are derived, given that differences in the natural history of nuclear vs. mitochondrial genomes are known to influence levels of polymorphism at the genetic level (Lynch *et al.* 2006). In this case, however, Mergeay *et al.* interpret the results in light of the unique ecological context in which these populations were found. They suggest that the high genetic diversity and haplotype distribution likely reflects the role of high-altitude lakes in this region as refugia during glaciations, the last of which occurred in this area approximately 25 000 BP.

The abiotic environment may also explain the apparent success of polyploids in this region, since polyploidy is associated with increased cold tolerance and hardiness (Dufresne & Hebert 1998). Polyploids also tend to be larger in size and may therefore be capable of outcompeting their diploid ancestors in competitive environments. The ecological advantages of polyploidy, however, could be short-term, given the associated switch to asexuality. Theoretically, asexuals carry the burden of accumulating deleterious mutations relative to their sexually reproducing counterparts. Recent evidence, however, suggests asexuality in *Daphnia* may not be the genetic dead-end it was originally thought to be because of the unexpectedly high frequency of ameiotic recombination (Omilian *et al.* 2006). In this survey, there is certainly no evidence for a disadvantage for asexuals given that Mergeay and coworkers found only these asexual polyploid lineages and no trace of diploid sexuals that may have served as potential parent species for the hybrids. The occurrence of polyploids in this area is consistent with previously identified patterns indicating increased polyploidy and asexuality at high elevations. It does not, however, mirror the large-scale cline of polyploidism with increasing latitude that has been documented in *Daphnia* in the northern hemisphere (Beaton & Hebert 1988).

Using genetic markers, Mergeay *et al.* 2008 uncover the phylogenetic relationship among populations of the *D. pulex* complex from the Bolivian Andes, and between this and other species of the genus in both North and South America. In doing so, they highlight the cascade of effects resulting from hybridization in this species including polyploidy, asexuality, cryptic speciation and potential fitness advantages in certain habitats. The interplay among genetic phenomena and their ecological consequences highlights the power of unifying our ecological understanding and genetic information in a single model organism in order to understand the implications of results in a natural context. With the recent release of the *D. pulex* genome sequence, the construction of a genetic map and the development of numerous genetic tools including molecular markers, microarrays, cell culture and virus-mediated transgene expression, such an interdisciplinary approach is now possible (Colbourne *et al.* 2004; Cristescu *et al.* 2006; Robinson *et al.* 2006; Soetaert *et al.* 2006). *Daphnia* has ceased to be merely a classical ecological model and sentinel of toxicology, but instead has arrived as a fully fledged ecological genomics model organism in which genetic and ecological inferences generate a feedback and lead to further questions and deeper understanding.

## Biography

Sarah Schaack is a PhD candidate at Indiana University currently investigating questions related to genome evolution, the evolution of sex, and mutation in *Daphnia*. Her main interests are in the role of recombination in transposable element evolution in sexual and asexual *D.*

*pulex* throughout North America. Previously, she has conducted research in the field of aquatic ecology in both temperate and tropical habitats.

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**Fig. 1.** Nuclear microsatellite markers and mtDNA loci from members of the *Daphnia* species complex from high-altitude lakes in Bolivia reveal extensive hybridization has led to a cascade of genetic and ecological consequences for members of this group. (Photo credit: Joachim Mergeay and Adam Petrusek.)