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Colonisation of subterranean ecosystems leads to larger genome in waterlouse (Aselloidea)

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A recommendation of

Lefébure T, Morvan C, Malard F, François C, Konecny-Dupré L, Guéguen L, Weiss-Gayet M, Seguin-Orlando A, Ermini L, Der Sarkissian C, Charrier NP, Eme D, Mermillod-Blondin F, Duret L, Vieira C, Orlando L, and Douady CJ. 2017. **Less effective selection leads to larger genomes.** *Genome Research* 27: 1016-1028. doi: [10.1101/gr.212589.116](https://doi.org/10.1101/gr.212589.116)

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The total amount of DNA utilized to store hereditary information varies immensely among eukaryotic organisms. Single copy genome sizes – disregarding differences due to ploidy - differ by more than three orders of magnitude ranging from a few million nucleotides (Mb) to hundreds of billions (Gb). With the ever-increasing availability of fully sequenced genomes we now know that most of the difference is due either to whole genome duplication or to variation in the abundance of repetitive elements. Regarding repetitive elements, the evolutionary forces underlying the large variation 'allowing' more or less elements in a genome remain largely elusive. A tentative correlation between an organism's complexity (however this may be adequately measured) and genome size, the so-called C-value paradox [1], has long been dismissed. Studies testing for selection on secondary phenotypic effects associated with genome size (cell size, metabolic rates, nutrient availability) have yielded mixed results. Nonadaptive theories capitalizing on a role of deleterious insertion-deletion mutations and genetic drift as the main drivers have likewise received mixed support [2-3]. Overall, most

evidence was derived from analyses across broad taxonomical scales [4-6].

Lefébure and colleagues [7] take a different approach. They confine their considerations to a homogeneous, restricted taxonomical group, isopod crustaceans of the superfamily Aselloidea. This taxonomic focus allows the authors to circumvent many of the confounding factors such as phylogenetic inertia, life history divergence and mutation rate variation that tend to trouble analyses across broad taxonomic timescales. Another important feature of the chosen system is the evolutionary independent transition of habitat use that has occurred at least 11 times. One group of species inhabits subterranean ecosystems (groundwater), another group thrives on surface water. Populations of the former live in low-energy habitats and are expected to be outnumbered by their surface dwelling relatives. Interestingly – and a precondition for the study - the groundwater species have significantly larger genomes (up to 137%). With this unique set-up, the authors are able to investigate the link between genome size and evolutionary forces related to a proxy of long-term population size by removing many of the confounding factors a priori.

Upfront, we learn that the dN/dS ratio is higher in the groundwater species. This may either suggest prevalent positive selection or lower efficacy of purifying selection (relaxed constraint) in the group of species in which population sizes are expected to be low. Using a series of population genetic analyses the authors provide compelling evidence for the latter. Analyses are carefully conducted and include models for estimating the intensity and frequency of purifying and positive selection, the DoS (direction of selection) and α statistic. Next the authors also exclude the possibility that increased dN/dS of the subterranean groundwater species may be due to nonfunctionalization, which may result from the subterranean lifestyle.

Overall, these analyses suggest relaxed constraint in smaller populations as the most plausible alternative to explain increased dN/dS ratios. In addition to the efficacy of selection, the authors estimate the timing of the ecological transition under the rationale that the amount of time a species may have been exposed to the subterranean habitat may reflect long term population sizes. To calibrate the 'colonization clock' they apply a neat trick based on the degree of degeneration of the opsin gene (as vision tends to get lost in these habitats). When finally testing which parameters may explain differences in genome size all factors – ecological status, selection efficiency as measured by dN/dS and colonization time - turned out to be significant predictors. Direct estimates of the short term effective population size N_e from polymorphism data, however, did not correlate with genome size. Ruling out the effect of other co-variables such as body size and growth rate the authors conclude that genome size was overall best predicted by long-term population size change upon habitat shift. In that the authors provide convincing evidence that the increase in genome size is linked to a decrease in long-term reduction of selection efficiency of subterranean species. Assuming a bias for insertion mutations over deletion mutations (which is usually the case in eukaryotes) this result is in agreement with the theory of mutational hazard [4-6]. This theory proposed by Michael Lynch postulates that the accumulation of non-functional DNA has a weak deleterious effect that can only be efficiently opposed by natural selection in species with high N_e .

In conclusion, Lefébure and colleagues provide novel and welcome evidence supporting a 'neutralist' hypothesis of genome size evolution without the need to invoke an adaptive component. Methodologically, the study cautions against the common use of polymorphism-based estimates of N_e which are often obfuscated by transitory demographic change. Instead, alternative measures of selection efficacy linked to long-term population size may serve as better predictors of genome size. We hope that this study will stimulate additional work testing the link between N_e and genome size variation in other taxonomical groups [8-9]. Using genome sequences instead of the transcriptome

approach applied here may concomitantly further our understanding of the molecular mechanisms underlying genome size change.

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