

## **Plants red list indicates species extinction as a sink for selfish DNA**

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*Abstract.* An antagonism between different selection levels was demonstrated on the example of selfish DNA and species selection. Notwithstanding an average evolutionary increase of genome size in the higher plants due to activity of transposable elements, the threatened plant species (those which are nowadays on the brink of extinction) were found to have on average larger genomes than their relatives, which indicates that redundant DNA in plant genomes is selected against at the species level.

The role of noncoding DNA, which constitutes the most part of eukaryotic genomes, remains enigmatic. Although the larger genome is known to relate to a number of phenotypic traits [1,2], some of which, especially in the plants, can be interpreted as adaptive [3-5], it is still unclear whether genome enlargement is selected for on the organismal level or is a result of activity of transposable elements just tolerated by the organismal-level selection [6]. Even in the latter case, in contrast to other neutral traits, the accumulation of selfish DNA in the genome is still promoted by selection albeit it is a selection of genomic parasites behaving as Darwinian units. Therefore, the usual (indirect) tests for traits neutrality based on population size, breeding system, generation time et cetera, are inconclusive. The direct evidence of (mal)adaptive nature of redundant DNA for the organism is needed. Here it is shown that threatened plants (those which are nowadays on the brink of extinction) have on average larger genomes than their relatives, which indicates that the excess of noncoding DNA in the plant genome is selected against at the species level.

The data on plant genome sizes were taken from the Plant DNA C-values Database (<http://www.rbgekew.org.uk/cval/homepage.html>). After exclusion of polyploid and poorly determined, there remained 2976 species. (The records with "sp.", "af.", "cf.", "?" in the species field were excluded. The data of different authors and for infraspecies forms were averaged.) They were checked against the United Nations Environment Programme - World Conservation and Monitoring Centre (UNEP-WCMC) Species Database (<http://quin.unep-wcmc.org/isdb/taxonomy/>) in two ways: first, against the subset of plants of global conservation concern, and second, against the total data set, which includes both plants of global and local concerns. From the total 2976 species, 293 species were found to be of global concern, and 999 species were of

local concern (i.e., they are threatened only in particular countries). The phylogenetic conservatism is a usual complication of any comparative analysis [7], therefore genome size values were tested as within-families contrasts (i.e., as ratios to families means). The spectacular "dose-dependent" relationship between genome size and conservation status was found (Fig. 1). (A similar relation between genome size and conservation status held also at the level of raw species points and at the level of within-families contrasts for monocots, dicots and gymnosperms, taken separately, and at the level of within-genera contrasts for the whole dataset, at least between species of no conservation concern and species of global concern.)

To establish whether this is a recent trend, the number of species in each genus was determined using the International Plant Names Index (<http://www.ipni.org/ipni>). The negative correlation between mean genome size and number of species in a genus was found (Spearman  $r=-0.11$ ,  $p<0.001$ ,  $n=756$ ; for angiosperms only:  $r=-0.11$ ,  $p<0.001$ ,  $n=716$ ), which indicates that the association of a larger genome with extinction (or depressed origination) is not unique to the recent time. This result is surprising because earlier the family-level phylogenetic analysis suggested that genome size of angiosperm (flowering) plants was increasing in the evolution [8]. The analysis of paleontological data using the Fossil Record 2 database (<http://palaeo.gly.bris.ac.uk/frwhole/FR2.html>) confirms this conclusion: there is a negative correlation between mean genome size of angiosperm families and the upper limit of their first appearance in geological time ( $r=-0.39$ ,  $p<0.001$ ,  $n=74$ ), i.e., more recent families have on average larger genomes. Thus, it can be concluded that a pressure of transposable elements, which expands genomes of plants in the course of evolution and which metaphorically was called "a one-way ticket to genomic obesity" [6], impairs speciosity. While analyses of the above-species level

cannot distinguish between extinction and depressed origination, the red list clearly demonstrates that excess of selfish DNA in the plant genome increases the likelihood of extinction. It seems to be a first documented case of antagonism between different selection levels, which thereby supports the recently developed concept of hierarchical selection [9].

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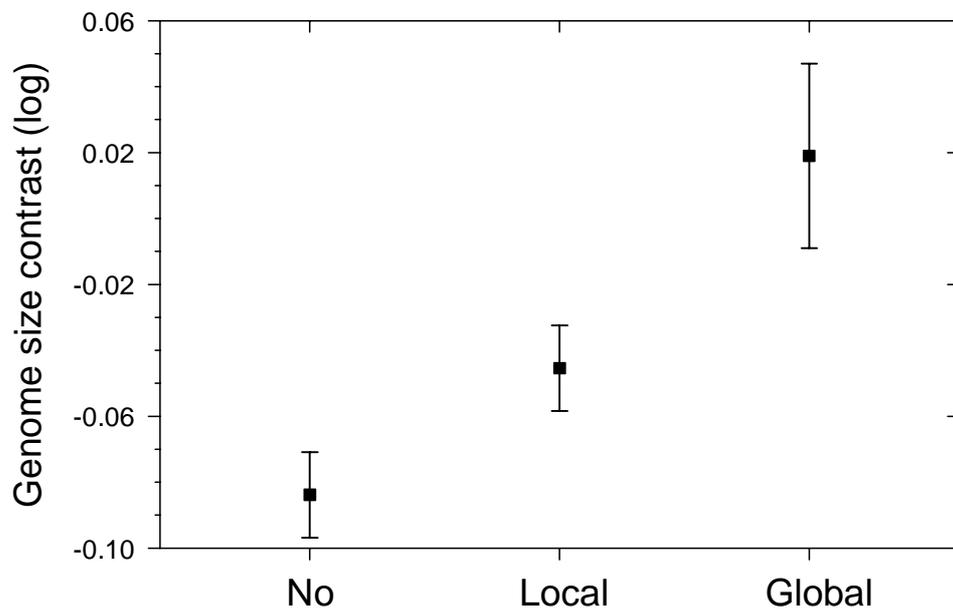


Fig. 1. Within-families genome size contrasts (ratios) for plants of different conservation status (means with 95% LSD intervals; Kruskal-Wallis,  $p < 10^{-4}$ ).