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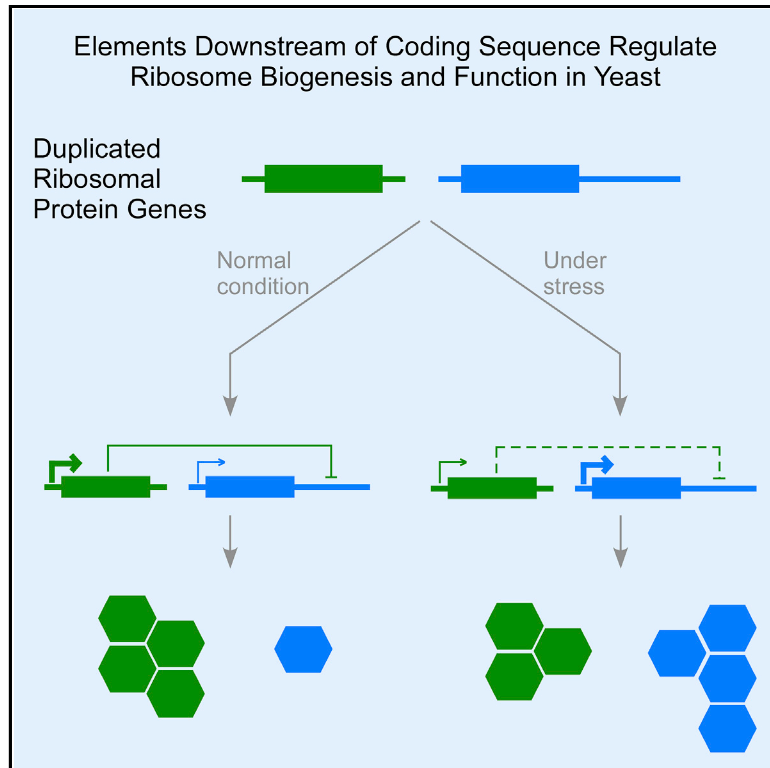
Preservation of Gene Duplication Increases the Regulatory Spectrum of Ribosomal Protein Genes and Enhances Growth under Stress

Graphical Abstract



Highlights

- Duplicated ribosomal protein genes (RPGs) are asymmetrically expressed and regulated
- Transcription termination regulates the expression of non-intron-containing RPGs
- Differences in expression levels enforce the subfunctionalization of duplicated RPGs
- Duplication of RPGs improves cell fitness and growth under stress

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In Brief

Parenteau et al. describe the mechanism regulating the expression of non-intron-encoding ribosomal protein genes (RPGs) and explain the basis of the copy-specific function and expression patterns of the duplicated RPGs. Paralog-specific phenotypic effects are generated by differences in expression patterns supporting growth under stress.

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Preservation of Gene Duplication Increases the Regulatory Spectrum of Ribosomal Protein Genes and Enhances Growth under Stress

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SUMMARY

In baker's yeast, the majority of ribosomal protein genes (RPGs) are duplicated, and it was recently proposed that such duplications are preserved via the functional specialization of the duplicated genes. However, the origin and nature of duplicated RPGs' (dRPGs) functional specificity remain unclear. In this study, we show that differences in dRPG functions are generated by variations in the modality of gene expression and, to a lesser extent, by protein sequence. Analysis of the sequence and expression patterns of non-intron-containing RPGs indicates that each dRPG is controlled by specific regulatory sequences modulating its expression levels in response to changing growth conditions. Homogenization of dRPG sequences reduces cell tolerance to growth under stress without changing the number of expressed genes. Together, the data reveal a model where duplicated genes provide a means for modulating the expression of ribosomal proteins in response to stress.

INTRODUCTION

Ribosomes are traditionally viewed as uniform units of ribonucleoprotein complexes composed of four rRNAs (18S, 5S, 5.8S, and 25S rRNA) and ~80 proteins (Ben-Shem et al., 2010). However, recent studies indicate that eukaryotic cells may produce ribosomes with different compositions and functions (Xue and Barna, 2012). For example, inclusion of the tissue-specific ribosomal protein L38 was shown to facilitate cap-independent translation of mRNA featuring internal ribosome entry site (IRES)-like structures (Xue et al., 2015). Modification of ribosome functions could also be achieved through the association with non-ribosomal proteins like the receptor for activated C kinase 1 (RACK1), which promotes mRNA-specific repression of translation via the recruitment of microRNA (miRNA) (Jannot et al., 2011). Similarly, the stress-induced protein mazEF was shown to modulate the function of bacterial ribosomes by removing the anti-Shine-Dalgarno (aSD) sequence required for the translation of normal mRNAs (Vesper et al., 2011). In yeast, the majority of ribosomal protein genes (RPGs) are duplicated (dRPGs, Figure S1A), and this leads to the generation of ribosomes with different protein configurations (Wapinski et al., 2010). However, the reason behind the preservation of this ribosomal gene duplication and its impact on cell functions remain unclear.

The duplication of RPGs in *Saccharomyces cerevisiae* is believed to be the consequence of a whole-genome duplication event that occurred before the *Saccharomyces* and *Kluyveromyces* lineages diverged from each other about 150 million years ago (Langkjaer et al., 2003). This presumed polyploidization was followed by substantial losses of duplicated genes through degenerative processes, except for a few gene classes like the RPGs. Approximately 10% of the surviving ohnologs (i.e., paralogs generated by whole-genome duplication events) encode ribosomal proteins (RPs) (Evangelisti and Conant, 2010). The majority of the surviving RPG ohnologs produce proteins with more than 95% sequence identity (Wapinski et al., 2010) due to gene conversion events that maintain similarity between the duplicated genes (Evangelisti and Conant, 2010). Despite this high similarity between protein sequences, deletions of yeast ohnologs result in different phenotypes, suggesting that they may have developed specialized functions responsible for their preservation (Komili et al., 2007; Parenteau et al., 2011). However, the mechanism by which dRPGs might preferentially affect cell function remains largely unexplored. It was proposed that duplicated genes could be preserved through partitioning of ancestral gene functions by qualitative or quantitative subfunctionalization or by neofunctionalization of the duplicated genes (Force et al., 1999; Lynch, 2007). In the first model, the dRPGs in *S. cerevisiae* would be preserved because they complement each other's expression levels or functions, while, in the second, the dRPGs would be preserved because one or both genes developed new functions not found in their ancestral gene but at the expense of ancestral gene functions.

Unlike most genes in *S. cerevisiae*, 81% of dRPGs include introns and require splicing for expression (Parenteau et al., 2011). Analysis of intron-encoding RPGs suggested that the functional specialization of ohnologs may result at least in part from differences in expression patterns (Parenteau et al., 2011). Intron deletions affected the expression of dRPGs in different ways leading to the modification of ohnolog expression

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