

The roles of positive and negative selection in the molecular evolution of insect endosymbionts

Adam J. Fry¹, Jennifer J. Wernegreen*

Josephine Bay Paul Center for Comparative Molecular Biology and Evolution, Marine Biological Laboratory, 7 MBL Street, Woods Hole, MA 02543 United States

Received 23 February 2005; received in revised form 29 March 2005; accepted 17 May 2005

Available online 21 July 2005

Received by H. Musto

Abstract

The evolutionary rate acceleration observed in most endosymbiotic bacteria may be explained by higher mutation rates, changes in selective pressure, and increased fixation of deleterious mutations by genetic drift. Here, we explore the forces influencing molecular evolution in *Blochmannia*, an obligate endosymbiont of *Camponotus* and related ant genera. Our goals were to compare rates of sequence evolution in *Blochmannia* with related bacteria, to explore variation in the strength and efficacy of negative (purifying) selection, and to evaluate the effect of positive selection. For six *Blochmannia* pairs, plus *Buchnera* and related enterobacteria, estimates of sequence divergence at four genes confirm faster rates of synonymous evolution in the ant mutualist. This conclusion is based on higher dS between *Blochmannia* lineages despite their more recent divergence. Likewise, generally higher dN in *Blochmannia* indicates faster rates of nonsynonymous substitution in this group. One exception is the *groEL* gene, for which lower dN and dN/dS compared to *Buchnera* indicate exceptionally strong negative selection in *Blochmannia*. In addition, we explored evidence for positive selection in *Blochmannia* using both site- and lineage-based maximum likelihood models. These approaches confirmed heterogeneity of dN/dS among codon sites and revealed significant variation in dN/dS across *Blochmannia* lineages for three genes. Lineage variation affected genes independently, with no evidence of parallel changes in dN/dS across genes along a given branch. Our data also reveal instances of dN/dS greater than one; however, we do not interpret these large dN/dS ratios as evidence for positive selection. In sum, while drift may contribute to an overall rate acceleration at nonsynonymous sites in *Blochmannia*, variable selective pressures best explain the apparent gene-specific changes in dN/dS across lineages of this ant mutualist. In the course of this study, we reanalyzed variation at *Buchnera groEL* and found no evidence of positive selection that was previously reported.

© 2005 Elsevier B.V. All rights reserved.

Keywords: *Blochmannia*; *Camponotus*; *Buchnera*; Genetic drift; Purifying selection

1. Introduction

Accelerated rates of molecular evolution characterize many endosymbiotic bacteria (Canback et al., 2004; Clark et

al., 1999; Itoh et al., 2002; Moran, 1996; Woolfit and Bromham, 2003). The first rigorous demonstration showed accelerated evolutionary rates in five endosymbiont lineages compared to their free-living relatives (Moran, 1996). A consistent rate elevation in endosymbionts and a concentration of changes in nonsynonymous sites of genes available supported the hypothesis that mutation alone could not entirely explain the observed rate increase. Rather, small effective population sizes (N_e) in endosymbionts compared to free-living bacteria are expected to increase the fixation of deleterious mutations due genetic drift. That is, small N_e reduces the efficacy of negative selection against deleterious

Abbreviations: N_e , effective population size; dN, nonsynonymous divergence; dS, synonymous divergence.

* Corresponding author. Tel.: +1 508 548 3705x6650; fax: +1 508 457 4727.

E-mail address: jwernegreen@mbl.edu (J.J. Wernegreen).

¹ Current address: Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT, USA.

mutations before these changes become fixed as substitutions between species (Ohta, 1973; Ohta, 1992). Namely, the probability that a deleterious mutation fixes will be less than the neutral expectation ($1/N_e$) but is greater in a small population than in a large one (Kimura, 1983). This effect may be exacerbated by reduced recombination and Muller's Ratchet in obligately intracellular bacteria (Moran, 1996). Strong impacts of genetic drift in small populations has been supported by subsequent studies (e.g., Abbot and Moran, 2002; Funk et al., 2001; Mira and Moran, 2002) and is the most widely discussed hypothesis to explain the elevated evolutionary rate in endosymbionts (e.g., Brynne et al., 1998; Moran, 1996; Peek et al., 1998; Rispe and Moran, 2000; Wernegreen and Moran, 1999).

An equally important implication of small N_e is a reduced efficacy of positive selection favoring beneficial mutations. For beneficial mutations, the substitution rate depends on the product of the selective advantage of the mutation, the rate at which beneficial mutations arise, and on N_e (Kimura and Ohta, 1971). All else being equal, a small N_e in endosymbionts will lower this product and decrease the rate of adaptive evolution compared to the rate in free-living bacteria. Thus, the hypothesis that small N_e is the primary determinant of endosymbiont molecular evolution predicts that both negative and positive selection will be less efficient in endosymbionts than in free-living bacteria.

The various approaches developed to test for positive selection (Anisimova et al., 2001; Nielsen and Hubisz, 2005; Nielsen and Huelsenbeck, 2002; Nielsen and Yang, 1998; Massingham and Goldman, 2005; Yang and Swanson, 2002; Yang et al., 2005) aim to identify genes or specific codons that show an excess of nonsynonymous over synonymous substitutions (e.g., $dN/dS > 1$). This criterion has been used to identify diversifying selection genes whose products are involved in reproduction (Biermann, 1998; Mah et al., 2004; Metz et al., 1998; Swanson et al., 2004; Tsaour and Wu, 1997), surface antigens (Anisimova and Yang, 2004; Elsheikha and Mansfield, 2004; Tosh et al., 2003), toxicity (Riley et al., 2000; Zhu et al., 2004), among other functions. The prediction of reduced efficacy of positive selection in endosymbionts was challenged with the report of such selection on the *groEL* gene from *Buchnera*, the endosymbiont of aphids. Fares et al. (2002) identified codon sites in the protein binding and co-chaperone regions of *groEL* with $dN/dS > 1$. GroEL is a key chaperonin that facilitates the folding of numerous cellular proteins into their proper conformations. This chaperonin is constitutively overexpressed in *Buchnera* and other intracellular bacteria (Aksoy, 1995; Baumann et al., 1996) and may help to mask the effects of deleterious mutations in other proteins (Moran, 1996).

Given the central role of GroEL in endosymbiont biology and its interaction with a wide range of substrates, the precise mechanism for diversifying selection is not entirely

transparent. It has been suggested that adaptive evolution of *Buchnera groEL* may improve the interaction of this chaperonin with an ever-changing endosymbiont proteome (Fares et al., 2004). In addition, similar findings have been made for eukaryotic CTT chaperonins, in which diversifying selection has been associated with functional divergence following gene duplication events (Fares and Wolfe, 2003). However, an alternative hypothesis that *groEL* is evolving under strong negative selection was tested using a different set of *Buchnera* host taxa and no evidence for positive selection was found (Herbeck et al., 2003). Thus, the evidence for positive selection in endosymbionts remains unclear. The role of such selection at *groEL* or at other endosymbiont genes has important implications for understanding the potential of endosymbionts to adapt to their hosts.

Here, we investigate the roles of positive and negative selection in shaping the molecular evolution of *Blochmannia*, an independent endosymbiont lineage associated with the ant genus *Camponotus*, and re-evaluate the role of positive selection at *Buchnera groEL*. The ant mutualist shares several features with *Buchnera*, including a phylogenetic position in the γ -3 Proteobacteria (Schroder et al., 1996), a strictly intracellular existence (Sauer et al., 2002), stable maternal transmission to host offspring, and long-term cospeciation with its insect hosts (Degnan et al., 2004; Sameshima et al., 1999; Sauer et al., 2000). However, several distinct aspects of the *Blochmannia*–ant association may influence the balance between selection and drift compared to other insect mutualists. For example, their *Camponotus* hosts span a diversity of habitats, including soil under rocks and within rotting wood, and have variable diets ranging from plant-feeding species to omnivores (Davidson et al., 2003; Hölldobler and Wilson, 1990). As a group, these ant hosts may have more varied diets compared to hosts that specialize on nutritionally unbalanced diets (e.g., phloem-feeding aphids, blood-feeding tsetse flies) (Zientz et al., 2004). This variation among *Camponotus* species in diet and life history may lead to variable N_e and variable selective pressures among *Blochmannia* strains. However, all *Camponotus* spp. likely experience two starvation phases (colony founding and metamorphosis) when metabolic demands exceed food supply (Wheeler and Buck, 1995).

In order to assess the role of selection on endosymbionts associated with phylogenetically and ecologically diverse *Camponotus* hosts, we compared maximum likelihood approaches to estimate dN and dS for four *Blochmannia* genes across a broad sample representing several host subgenera. We used estimates of dN/dS to test the influence of positive and negative selection at each *Blochmannia* gene, and compared patterns of molecular evolution in *Blochmannia* to *Buchnera* and free-living relatives. Because questions of positive selection in endosymbionts have centered on *groEL*, we give special emphasis to the molecular evolution of this chaperonin in *Blochmannia*

Download English Version:

<https://daneshyari.com/en/article/9127031>

Download Persian Version:

<https://daneshyari.com/article/9127031>

[Daneshyari.com](https://daneshyari.com)