



ELSEVIER



Pgi: the ongoing saga of a candidate gene

Christopher W Wheat and Jason Hill

Numerous studies have found amino acid variation at the phosphoglucose isomerase (PGI) gene associated with organismal performance and fitness. Here we focus upon recent advances in the study of this gene, highlighting novel species being studied, new tools being used, and emerging insights into the evolutionary dynamics acting on this gene. Our synthesis highlights questions that are coming into focus, as well as the need for attention in specific areas, such as manipulative experiments to establish mechanistic insights and a causative role of allelic variation.

Addresses

Department of Zoology, Stockholm University, Svante Arrheniusväg
18 B, 10691 Stockholm, Sweden

Current Opinion in Insect Science 2014, 4:42–47

This review comes from a themed issue on **Environmental physiology**

Edited by **Brent J Sinclair**

For a complete overview see the [Issue](#) and the [Editorial](#)

Available online 25th October 2014

<http://dx.doi.org/10.1016/j.cois.2014.10.003>

2214-5745/Published by Elsevier Inc.

The quest to find and study the genetic variation affecting Darwinian fitness, in an attempt to reveal the gene by environment interactions that maintain and fix such variation in the wild, has been a long one for many research systems [1,2,3]. Yet, allozyme studies have typically found charge-changing amino acid variation at the phosphoglucose isomerase (PGI; E.C. 5.3.1.9) locus that is associated with performance and fitness measures [4,5]. PGI catalyzes the second step of the glycolytic pathway, converting glucose-6-phosphate (G6P) to fructose-6-phosphate, as well as the reverse reaction, and is considered a branch-point enzyme since G6P is also used in other pathways [6]. Over the past decade, there has been an increase in the evolutionary study of the *Pgi* locus. Synthesizing these studies by approach, we find that most studies have conducted some measure of fitness and/or a molecular test of selection, with almost none conducting a manipulation to objectively test whether there is an actual *Pgi* effect (Figure 1). In this review, we start with a general overview of recent advances from insects and other arthropods, discuss emerging causal explanations, and then synthesize these studies in an attempt to generate suggestions for future research.

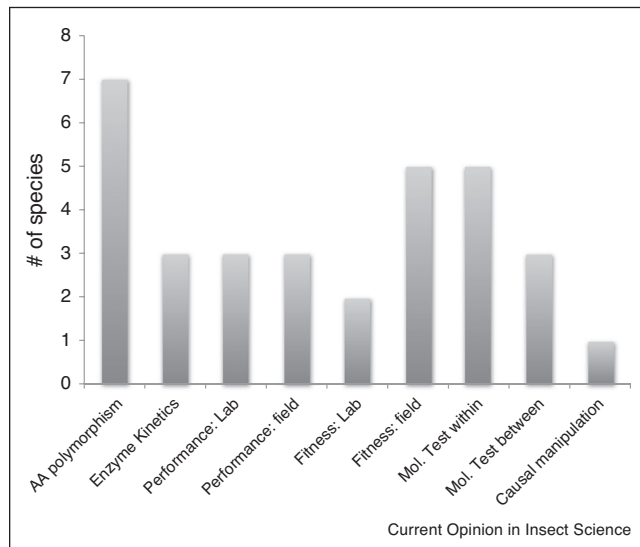
Butterflies (Lepidoptera)

In *Colias* butterflies (Pieridae), Watt and colleagues have contributed the most to our knowledge of PGI and its potential impacts on fitness in the wild, and these studies have been previously reviewed [7]. Recently, Watt and colleagues have integrated population genetic study with enzyme structural modeling by placing the amino acid variation associated with fitness differences in the wild into its native enzyme structural context [8]. Introns in *Pgi* appear to harbor pervasive indel mutations and much lower GC content than surrounding exons, suggesting that rapid sequence turnover could be caused by transposable elements [9]. Furthermore, the evolutionary origins of novel *Pgi* alleles appears to involve occasional hybridization [10].

In *Melitaea cinxia* (Nymphalidae), Hanski and colleagues have investigated *Pgi* effects, recently reviewed in [12]. In particular, they have i) measured resting and peak flight metabolic rate on adult butterflies and found a correlation with *Pgi* genotype only during flight [13,14–16], ii) validated the accuracy of respirometry measures as a proxy for dispersal using radar tracking, finding that *Pgi* genotype interacted with metabolic measures and temperature to explain movement distance [14], iii) developed single nucleotide polymorphism (SNP) genotyping [17], iv) quantified life history variation and fitness components in a large outdoor cage [18], finding that *Pgi* genotypes differed in fecundity [19], v) with the higher fecundity of *Pgi* heterozygotes due to their flying and laying eggs during the earlier, cooler part of the day as indicated by thermal camera imaging [20], vi) measured the growth rate of small, isolated demes associated with SNP genotypes of *Pgi* [21], vii) used molecular population genetics analyses to find evidence for ongoing and long-term balancing selection driven by heterozygote advantage [22]. Studies have also begun to parameterize individual based models using some of these *Pgi* findings, integrating ecological and spatially explicit dynamics [23,24] and significantly advancing the study of eco-evolutionary dynamics [25].

Aside from these in-depth studies on Lepidoptera, three other butterflies have been recently studied. A PGI allozyme allele in *Araschnia levana* (Nymphalidae) was found to be correlated with a higher metabolic rate during flight was also most common at the leading edge of an expansion front in the northern range limit, more common in newly established populations and in the more mobile spring generation [26]. In *Lycena tityrus* (Lycaenidae), a survey of allozyme loci found that only PGI alleles separated low vs. high altitude populations [27],

Figure 1



The number of species that have been studied at a given level of analysis. Each species is only counted once per column in which it may belong. Studies included are those that have been actively published upon in the last 10 years. See Supplemental table for references. Abbreviations: Amino Acid, Molecular tests within species, Molecular tests between species.

with genotypes differing in larval and pupal development time, growth rate, pupal mass and adult chill-coma recovery [28], but not in flight performance [29]. These studies have recently been reviewed with a focus upon high altitude cold stress response [30^{*}]. No amino acid variation was found in *Bicyclus anyana* (Nymphalidae) after extensive DNA sequencing across 80% of the *Pgi* coding region, consistent with previous PGI allozyme surveys in this species.

Beetles (Coleoptera)

An interaction between PGI polymorphisms and heat shock protein (HSP) gene expression, described in *Chrysomela aeneicollis* (Chrysomelidae), found that the more thermally liable genotypes had higher HSP induction at a given temperature [31]. Subsequent studies have investigated how PGI genotype and HSP expression interact with repeated thermal stresses to affect organismal performance and fitness, and these studies have previously been reviewed [32^{*}]. Ongoing studies document apparently strong directional selection on a thermal stability vs. kinetic efficiency tradeoff at PGI, as well as potentially hinting at more intimate interactions between HSP and PGI [32^{*}]. Interestingly, attention to ecologically relevant thermal dynamics has revealed that more thermally stable genotypes increase in frequency after regional thermal stress events [33]. Using respirometry to assess sex specific thermal stress, as well as measures of fecundity in both the field and lab, PGI genotypes appear to have a

strong effect on male running speed and mating frequency [34], as well as female fecundity [33].

Stick insects (Phasmatodea) and bees (Hymenoptera)

A recent comparative genetic study of metabolic genes in the Australasian stick insects (Lanceocercata) has discovered that the PGI locus has undergone at least three rounds of paralogous gene duplication that are nearly 100 million years old [38]. Using a codon based, maximum likelihood analysis of sequence evolution, the authors found evidence of positive selection acting upon *Pgi*. While the codons identified as being positively selected in two of the three *Pgi* orthologs have a moderate overlap with the previous findings in butterflies, these sites at the surface are also where amino acid replacements are expected to occur via drift. The authors conclude that these signatures of selection likely reflect branch-point dynamics with the pentose phosphate shunt [38]. Finally, in an attempt to develop *Pgi* as a molecular marker for conservation purposes [5] a genetic survey was conducted in five species of bumblebee (Hymenoptera: Apidae), which found little to no amino acid variation within each of the species and only moderate levels of divergence among them [39^{*}]. Thus, *Pgi* could not be used as a marker and this may be due to the haplodiploid nature of Hymenoptera and/or the altered thermoregulatory physiology of bees.

Other Arthropods: Coepopods (Harpacticoida) and Barnacles (Sessilia)

Allozyme studies of the marine copepod *Tigriopus californicus* suggest potential habitat specific selection on PGI [35]. Recent DNA study [36] found high levels of population structure, with the same allozyme alleles from different populations being derived from evolutionarily independent charge changes located in different regions of the PGI enzyme. Several molecular tests of selection found evidence of positive selection in the evolutionary origins of alleles, while balancing selection appears to be actively maintaining them [36].

Genotype-by-microhabitat associations have also been found in the barnacle *Semibalanus balanoides*, with PGI allozyme alleles exhibiting significant allele frequency differences between high vs. low intertidal habitats that differ in thermally stressful conditions. Interestingly, this work was conducted with a primary focus upon the genotype-by-microhabitat associations of mannose phosphate isomerase, which converts mannose-6-phosphate to fructose-6-phosphate, and thus engages in branch-point dynamics with PGI [37].

Causal hypotheses

The diverse associations reviewed above call for an explanatory hypothesis of why they should exist. Watt and colleagues have developed the primary working hypothesis for *Pgi* effects. Using metabolic control theory to

Download English Version:

<https://daneshyari.com/en/article/4508287>

Download Persian Version:

<https://daneshyari.com/article/4508287>

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