any and of Ecology & Evolutionary Biology
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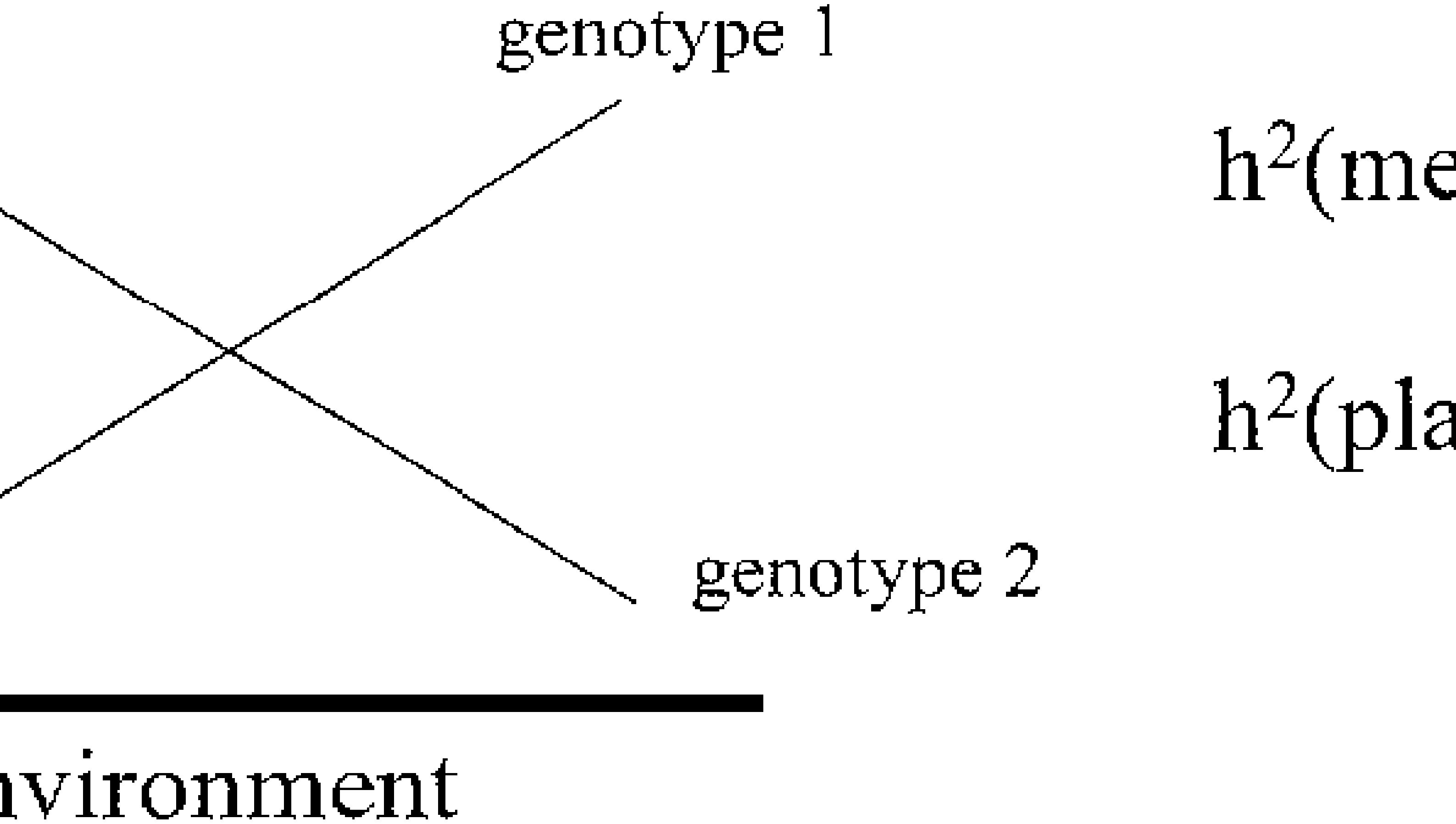
s of phenotypic plasticity has been a controversia
aw [1] proposed the existence of genes controlling
stion was that plasticity is controlled by a set
ent from those underlying variation in the across-e
er. He based this conclusion on the elementary obs
tive genetics experiments - the plasticity and the
y to selection, and/or yield quite distinct heritabili
acterized by a lower heritability than the trait mea
lude that the two aspects of that trait are *indeed g*
simple and apparently innocuous statement h
roversy that has finally erupted in the mid-90s, th
aw's original paper.

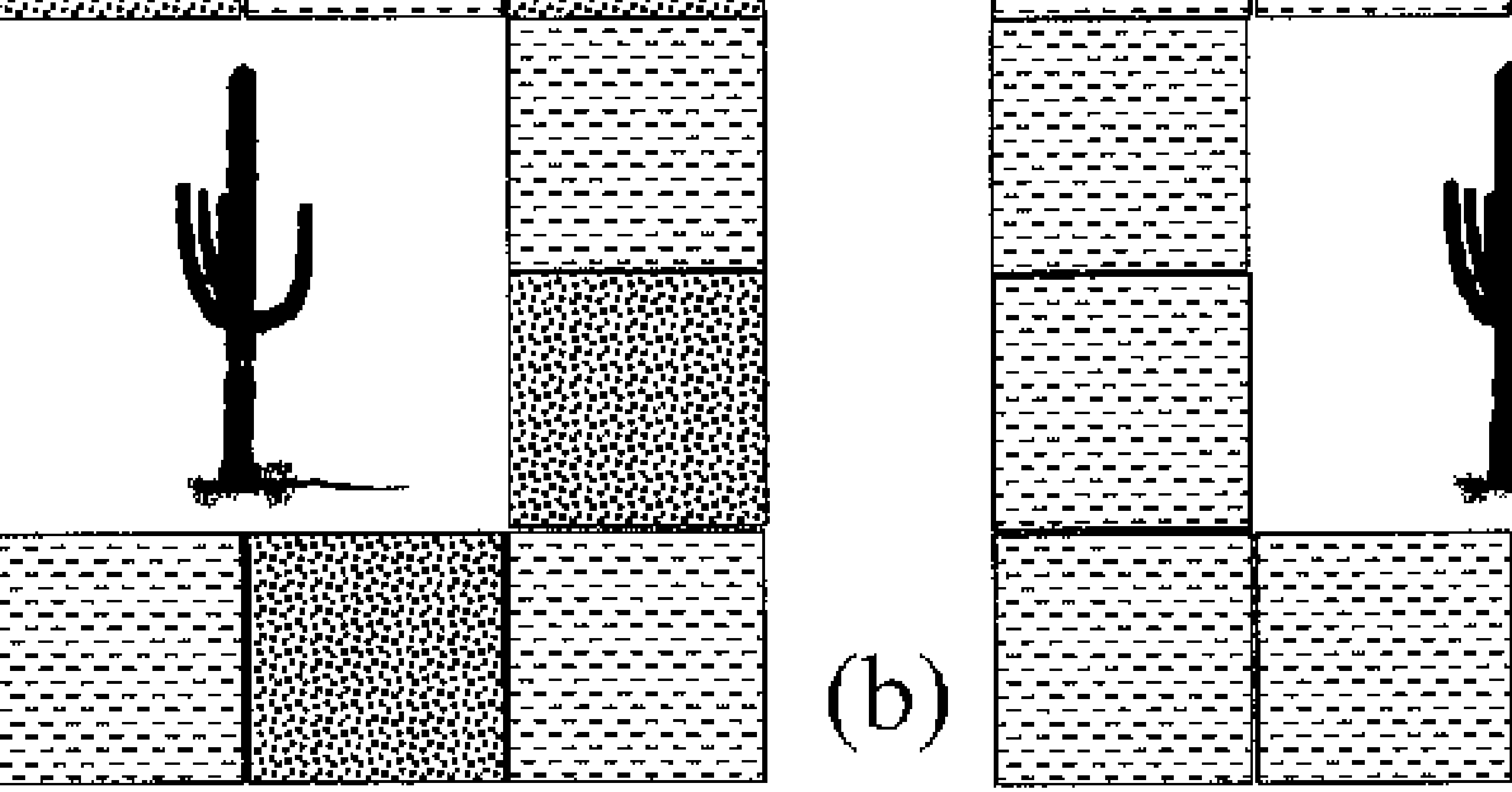
was fired by Via [46] with an article in which
ity is the by-product of selection occurring in disti
efore evolve as a character in its own right. The im
hting and Pigliucci [35], as well as from Schein
cularly strong in their conclusion that phenotypic p
circumstances - evolve as a trait independent of a
rm of a genotype, including and especially the a
Via was referring to the within-environment me

d controversy, but that is - after all - the vital sign



o reaction norms in a environment-phenotype ph
yields very low phenotypic values in the environme
of the diagram, and very high phenotypic val
toward the right end of the diagram. Since Genot
the heritability of phenotypic plasticity will be very
ation for plasticity). However, given that th
means of the two genotype are very similar (the
similar to the average of high + low), the herita
ght") of the reaction norm will be close to zero.

th the bath's water. Heterophylly has historically b
enotypic plasticity to be investigated, and if we s
ition of plasticity along the lines of *the ability of*
nt phenotypes in response to distinct environments,
inition.
pand from the clearest case to a family of similar
ons. First of all, what if instead of a single individu
to experience different environments (Fig. 2)? T
s of kin selection, or as a bet-hedging strategy.
l that evolutionary biologists should account for
s [8,20], and plasticity may increase inclusive fitn
ss. An example is provided by the evolution of plast
eyespots on the wings of butterflies of th
]. These insects sport two seasonal forms (wh
which are characterized by a showy phenotype dur
yptic one during the less active (dry) season. The
s seems to be radically different: attracting the
organs in the first case, helping to avoid the rare
The molecular biology of this system is being wor
fic genes respond to reliable environmental cues suc
opriate developmental pathway. Now, thcsc buttcr
ments", since the progeny of one form experiences
(i.e., there is *temporal* fine grained environmental
therefore makes sense to conclude that this is indee
ense of currently useful and of derived by a hi



Two basic ecological situations leading to the
rgeting directly phenotypic plasticity or to the o
ecotype. In (a) the progeny of the plant in the
xperience one of two environments with a given p
. If such progeny is able to grow well on both env
e the inclusive fitness of the mother plant. This
evolution of an appropriate plastic response. N
nvolved here perceive the environment as fine-g
there may be other kinds of environmental patche
of the mother plant can only lend on one type
is therefore perceived as coarse-grained, and
e mother plant will increase as a result of th
cotypic) specialization. Any plasticity evolving in
lt of occasionally mixing distinct ecotypes, an
and entirely a by-product of selection

nce. Similarly, the debate on the evolution of plast
eral evolutionary ecological question of when c
by evolving locally adapted ecotypes) vs. generalist
nenotypic plasticity or behavioral flexibility). Th
linked to yet another major question in evolutiona
n maintained in natural populations? It has bee
buffer" the action of selection [16]; adaptive plasti
the paradox of natural populations well adapted to
apable of expressing significant heritable gene
.

asis of phenotypic plasticity and why it do

sticity genes, that is of genes whose function is pri
ponse (and that evolved for that purpose), origina
lines of evidence for the fact that plasticity is so
n. The arguments to this effect made above are so f
onable and certainly amenable to modeling. The
published to date which demonstrate selection o
given the experimental difficulties of carrying
chlichting and I had originally in mind while writi
was a compelling demonstration that some types
direct selection. The reasoning goes like this: if
tion only as environmental receptors and conseque
g two or more developmental pathways, then their
n limited to any particular environment, but only u

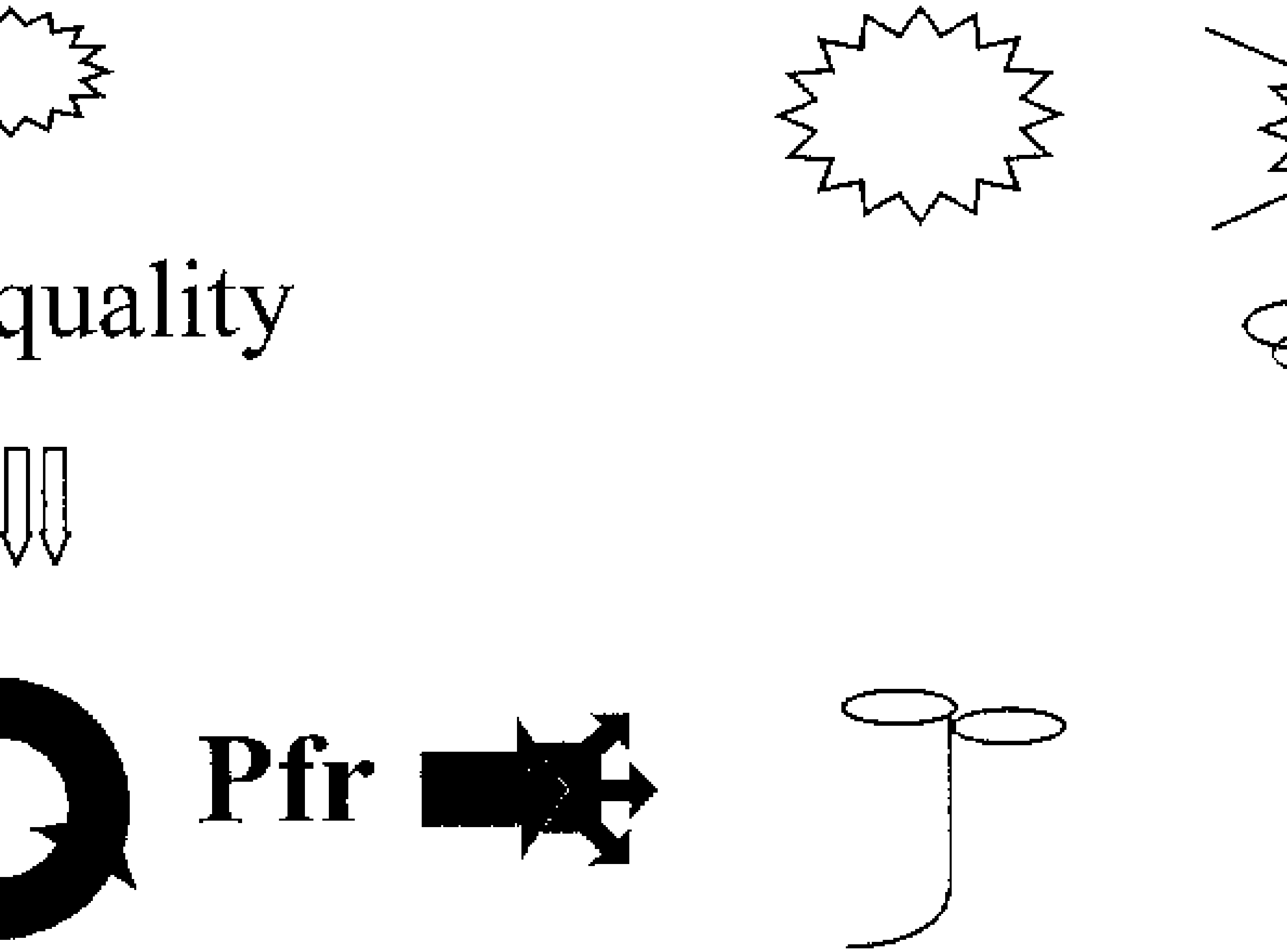
e curves take one or another form. In fact, Schlich
ed that this must be the preliminary step for the
y, even those that eventually come to rely on m
regulate and fine-tune the response.

ecular biologists might cry foul and make the argu
ferent name (plasticity genes) to a phenomenon tha
me, namely the existence of environmental recepto
is it not the classic regulatory element of th
the oldest known case of "plasticity gene"? Yes!
r discussion on plasticity genes is not to give n
bring together two areas of research so far ent
of environmental receptors on one hand, and the
organismal responses to environmental changes o
have known about the *Lac* operon for decades, we
t is in this link between molecular and evolutionar
oncept of plasticity genes.

f plasticity genes and related concepts

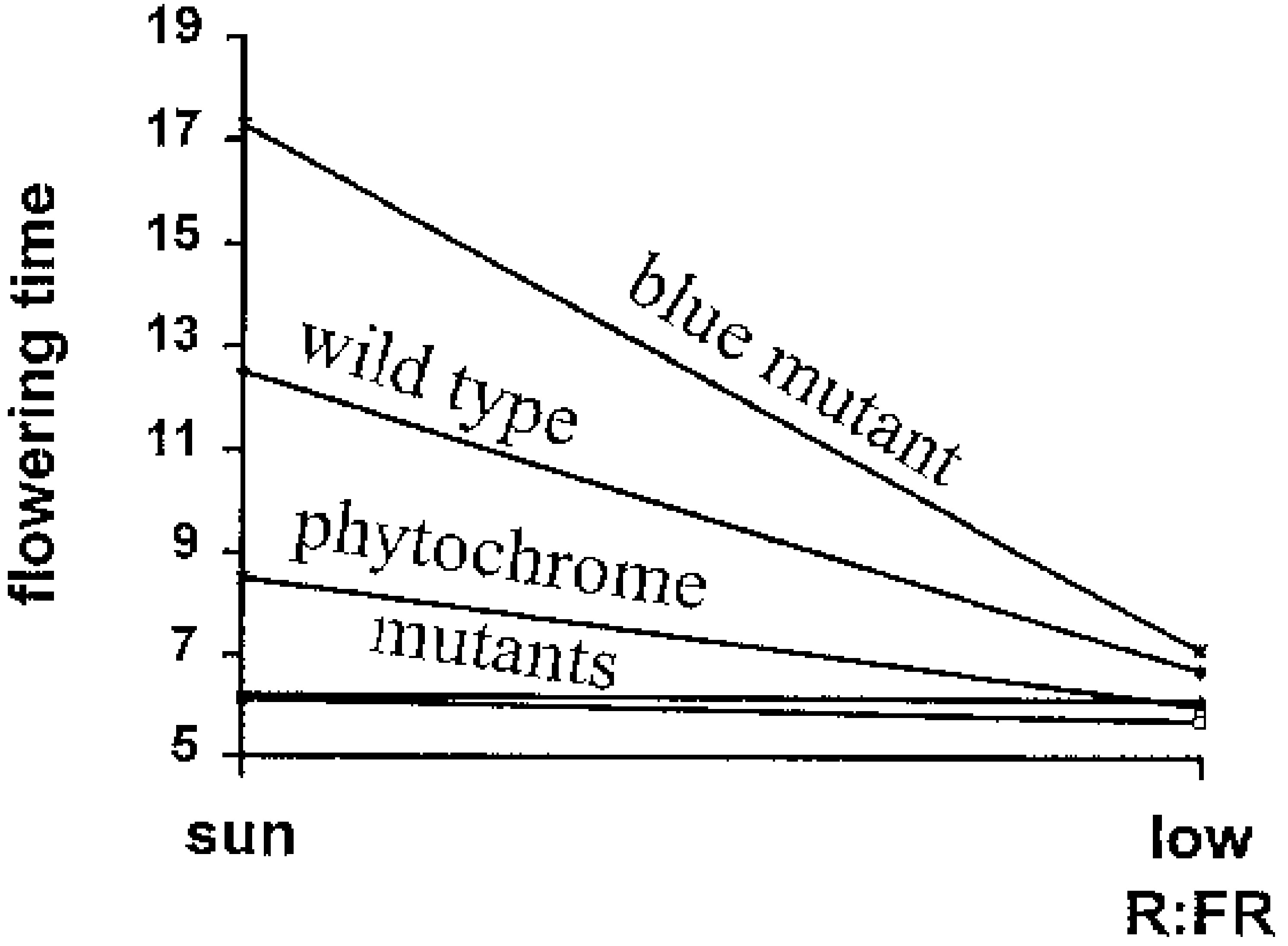
residual confusion, I would like to offer a defin
th the above discussion, as well as outline the oth
any particular plastic response.

genes. These are environmental receptors whose fun
mental signal and trigger a cascade of other genetic
anism down one of a number of alternative



n example of plasticity genes. (Right) The so-c
esponse in plants is a mechanism that allows a
g if the light conditions are not appropriate (l
hile stopping and opening the cotyledons when th
ent. (Left) A class of photoreceptors known as ph
ontrolling the shade avoidance response. The
s as simple as it is effective: if the plant is shaded
ts, the ratio between the red and the far red wav
(normally about 1:1 under sunlight) goes down (l

hese genes may be included in the genetic basis of
y may be structural genes and they may alwa
environment, unlike the previous category).



Experimental study of plasticity genes (from P
press in J Evol Biol). The shade avoidance resp
bidopsis thaliana can be dissected by inducing poi
te the functionality of one or more photorece
phytochromes in this case). The phenotypic plas
then compared to the one displayed by the
e specificity of the candidate genes' action and t

dependently of growth rates. In the same fas
ct a plastic response (e.g., shade avoidance in pla
Schmitt, in press) regardless of growth rates. Ther
ypic plasticity as a genetically unique feature of an

mother of all explanations

ce a possible explanation for the "historical" roo
sy. Via's argument that phenotypic plasticity emerg
hin environments [46,47] is very likely the result
stem she worked with [43,44], and the quantitative
de applied to modeling the evolution of phenotypic
l work was originally on two taxa of phytopha
one of two plant hosts, although occasionally they c
status of these entities is still under discussion, a
ocal ecotypes of the same species, subspecies, or ev
omm.). Whatever the case, Via studied the react
o fitness, such as rates of development, when each
he observation was that each fly was doing better
rnative one. This plasticity for fitness is clearly n
ness is bound to be), and it obviously is the by-pro
ments: each taxon clearly evolved means to ex
host, and simply found life difficult on the other h
e environment is coarse from the point of view of
idual and very likely its progeny experience only

shed framework of quantitative genetic theory. But
y functions connecting a series of experimental poi
re *never* real continuous functions, which in some
rse reification" problem). In the case of plant's resp
an infinite number of possible environments,
nery of the plant is designed to deal with the who
ts along it (incidentally, continuous environment
ative genetics framework, as demonstrated by
Kirkpatrick, [18] on infinite dimensional modeling
valency of different approaches *does not tell us any*
hereof of a reaction norm: only a detailed knowled
direct our biological thinking.

ll pardon me for the clearly out of proportion p
h like the one originating the much broader disput
evolution happening by mass selection on many
niversal pleiotropy [56]. The two rivals started w
ems and theoretical assumptions in mind, and ca
, almost independently of what the other school w
cal evidence was suggesting).

ntics"

the impression that the plasticity genes debate is
ssion sometimes reported to me at informal gatherin
debate was Via's original question [46,47]: is plast
ction? There can be no amount of rhetoric that ma

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