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SPECIAL FEATURE: DARWINIAN CORE AND POST-DARWINIAN EXTENSIONS

Is the evolutionary theory still useful? A review with examples

¿Es todavía útil la teoría evolutiva? Una revisión con ejemplos

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ABSTRACT

Evolutionary biology is experiencing an exceptional process of revision and outreach because of the 200-anniversary of the birth of Charles Darwin. As a consequence, the study of organic evolution and also its teaching are being discussed at several levels, by evolutionary biologists, biologists and scholars outside evolutionary biology and by the general public. In this scenario, a didactic explanation of how biologists address evolutionary research in real populations seems to be useful. Using actual research examples, here I tried to outline how the classic theory (termed here as the “basic scheme”) is useful to answer relevant questions in biology and how a less dogmatic paradigm (or a more versatile one) would be needed when dealing with the most recent and extravagant cases of gene, genotype, phenotype and environment interactions. Specifically, I used three in-extenso examples of research driven by hypothesis-testing: (1) the changes in genetic architecture induced by sexuality in a cyclically parthenogenetic insect; (2) the test of the energetic definition of fitness through phenotypic selection studies; and (3) the assessment of the underlying causes of character displacement in Darwin finches. In the former two cases, it is argued that the basic scheme is useful and sufficient for testing relevant evolutionary hypotheses. In the third case, it is argued that something else is needed to explain the observed genetic variation that *Geospiza* species exhibit in Daphne major island (Galapagos). Finally, I outline some “extravagant” cases biological entities interacting, such as horizontal gene transfer, epigenetic inheritance, adaptive anticipatory conditioning, evolutionary capacitance and niche construction. This “post-modern” biology has been seriously proposed and demonstrated to be widespread in nature, which would justify an extended evolutionary synthesis.

Key words: character displacement, microevolution, modern synthesis, natural selection, population genetics.

RESUMEN

La biología evolutiva está experimentando un inédito proceso de revisión y difusión debido al aniversario del natalicio de Charles Darwin. Como consecuencia, el estudio de la evolución orgánica y también su enseñanza están siendo discutidos a varios niveles, por biólogos evolutivos, biólogos y académicos fuera de la biología evolutiva, y por el público en general. En este escenario, una explicación didáctica de cómo los biólogos enfocan su investigación evolutiva en poblaciones reales podría ser útil. Usando ejemplos reales, he intentado presentar cómo la teoría clásica (definida como el “esquema básico”) es útil para responder preguntas relevantes en biología y cómo un paradigma menos dogmático (o más versátil) podría ser necesario al tratar los casos más extravagantes de interacciones gene, genotipo, fenotipo y ambiente. Específicamente, he usado tres ejemplos in extenso de investigaciones guiadas por prueba de hipótesis: (1) los cambios en la arquitectura genética inducidos por sexualidad en un insecto partenogenético cíclico; (2) la puesta a prueba de la definición energética de la adecuación biológica a través de estudios de selección fenotípica; y (3) el estudio de las causas subyacentes al desplazamiento de caracteres en los pinzones de Darwin. En los dos primeros casos se argumenta que el esquema básico es útil y suficiente para probar hipótesis evolutivas relevantes. En el tercer caso se argumenta que algo más es necesario para explicar la variación genética observada en las especies de *Geospiza* que habitan en la isla Daphne mayor (Galápagos). Finalmente, se explican algunos casos “extravagantes” de interacción entre entidades biológicas, tales como transferencia horizontal de genes, herencia epigenética, condicionamiento anticipatorio adaptativo, capacitancia evolutiva y construcción del nicho. Esta biología “postmoderna” ha sido seriamente propuesta y de gran generalidad en la naturaleza, lo cual justificaría una síntesis evolutiva extendida.

Palabras clave: desplazamiento de caracteres, genética de poblaciones, microevolución, selección natural, síntesis moderna.

INTRODUCTION

The 200-anniversary of Darwin birth has provoked the most vivid reactions both in the general public and within the academic

community. In many academic circles (but not among evolutionary biologists) it has become common to hear some erroneous statements about modern evolutionary science. In fact, there exists some concern of specialized

scholars in evolutionary research, about the common view that evolution is only natural selection, argued by people outside evolutionary biology, who adds that the discipline needs to be reconstructed from its principles. In fact, the evolutionary biologist Michael Lynch lucidly synthesized the opinion of many scholars regarding the year of Darwin and the need of an “extended” theory of evolution (see: Pigliucci 2007, Gowaty et al. 2008, Whitfield 2008):

“A lot has occurred during the last 150 years but the basic frame of evolutionary biology is rock solid. There not a single observation in the cell, molecular biology, or developmental biology that has provoked a significant change in our understanding of evolutionary principles. Of course, this does not means that molecular, cellular biologists, and developmental biologists are not needed to complete the understanding of the evolution process –they are needed most than ever– but to recognize that there are unsolved issues would be an ignorant mistake.”

Thus, a not-so-technical explanation is in order. The evolutionary theory, also known as the modern synthesis, is one of the most successful scientific theories, but also one of the most complex. What we call modern synthesis today is a body of knowledge developed by biologists after the Darwinism and new-Darwinism (Pigliucci 2007). There are a number of biological phenomena that are appropriately managed by the modern synthesis whereas there are a number of other processes that are not explained by this theory, especially those that have been discovered with modern technologies. Here, I will try to exemplify both, biological phenomena that are appropriately explained with the “basic scheme” of the modern synthesis, and also some phenomena that need some refinements.

The “classic” theory is not incorrect

What is commonly known as the modern synthesis, is the term generally applied to the fusion of neo-Darwinism, with the theoretical population genetics developed in great deal by J.B.S. Haldane, Sewal Wright and Ronald Fisher in the first part of the 1900 century (Haldane 1924, Fisher 1930, Wright 1931, Haldane 1932, Wright 1932, Wright 1943, Wright 1982,

Gustafsson 1986, Wright 1988, Ewens 1989, Crow 1991, Wade & Goodnight 1991, Frank & Slatkin 1992, Price & Langen 1992, Edwards 1994, Coyne et al. 1997, Kirkpatrick & Barton 1997, Wade & Goodnight 1998, Leigh 1999, Coyne et al. 2000). This body of knowledge proposed the “language” by which phenotypes are read from genotypes, in the context of the change in allele frequency of individuals in populations. Hence, this was a unidirectional premise, where phenotypes are the fixed ends of genotypes, which are re-organized after recombination in each (generally sexual) reproduction. Several advancements in ecological research, theoretical biology and molecular ecology were included in the modern synthesis late in the twentieth century, especially after the development and optimization of the polymerase chain reaction (PCR) procedure. This technique, together with the development of a great variety of genetic markers, provoked a revolution in population genetics and phylogeography, as many old theoretical models were now possible to be tested in actual populations. However, the recent advancement of genomics, developmental genetics and information technologies applied to the evolutionary science, has revealed a superbly varied picture of the reciprocal association between genes and phenotypes in organisms, populations and ecosystems. Still, it would be erroneous to indicate that this new insight negates in some way the original statements of the modern synthesis. In other words, genes are still important determinant of phenotypes; recombination, drift, population size and gene flow are still basic forces behind the observed gene-frequencies; and natural selection has never been seriously questioned as the most important mechanism behind the appearance of adaptations (Seeley 1986, Sinervo et al. 1992, Laland et al. 1999, Filchak et al. 2000, Higgie et al. 2000, Sinervo et al. 2000, Rice & Chippindale 2001, Abzhanov et al. 2004, Abzhanov et al. 2006, Seehausen et al. 2008, Harmon et al. 2009). Hence, what is probably under way is, according to Pigliucci (2007) an extended evolutionary synthesis rather than a replacement. Since this need is appropriately presented by this and other authors, here I explain some cases that I believe exemplify the basic scheme of the modern synthesis.

THE BASIC SCHEME: THE POPULATION/ QUANTITATIVE GENETICS MODEL

Imagine an individual plant or an animal, in which we measure two metric traits that we can graphically depict as in Fig. 1A. Now suppose that those phenotypic measurements are somewhat weighed by the degree by which this particular trait is under genetic influence. This can only be conceived assuming that the trait is determined by many genes of small effect (i.e., polygenic inheritance). Also, we are supposing the absence of any kind of interaction between genes (e.g., epistasis, dominance) and that the population is reasonably large to avoid the effects of genetic drift. Whatever the scale of this new variable is, this would be a magnitude that depends on both, the phenotypic value and how much heritable is the trait. This weighed attribute is commonly known as the breeding value, and a sample of such breeding values from a population would look as in Fig. 1B (Arnold et al. 2008). Now suppose that we are talking about two negatively correlated traits, such as clutch size and offspring size, and we represent the whole breeding values of the whole population, as in Fig. 1C. If we were considering just traits (not breeding values), Fig. 1C would be known as a negative phenotypic correlation. However, we are talking about a bivariate distribution of breeding values which shows a negative correlation, which is also known as the genetic correlation (Cheverud et al. 1983, Houle 1991). The variance of breeding values in each axis is also known as the genetic variance, which is usually summarized as heritability: the ratio between genetic variance and phenotypic variance (Houle 1992). Now imagine an adaptive landscape (Fig. 1D): some combinations of traits (here in dark) maximize survival and reproduction (= fitness), and others minimize it (white) leading to "maladaptive" zones (also known as fitness valleys, in analogy of a contour landscape) (Wright 1932, Wright 1988, Arnold et al. 2008). If we over-impose our whole population of breeding values and the adaptive landscape (Fig. 1E), we would be witnessing an imminent outcome: an evolutionary change by natural selection (Fig. 1F). This representation shows directional natural

selection acting on one trait but the distribution of breeding values (i.e., the negative genetic correlation) provoked a change in the mean phenotype of both traits. But not only there was a change in the mean, but also in the variance of both traits, which was reduced. More striking, the original genetic correlation disappeared after this selective event. The representation of Fig. 1 is a cartoon of what is supposed to happen (under the basic scheme) during the origin of adaptations: a drastic reduction of genetic variance because of the fixation of alleles in the population and a reduction of the potential for response to selection. However, it is possible that other processes, such as recombination, gene flow, and mutation increase genetic variation, compensating its reduction by selection, and contributing to its maintenance. The structure of genetic variances and covariances, its analytical treatment and statistical procedures aimed to compare and estimate them are the aims of comparative quantitative genetics (Arnold 1983, Stepan et al. 2002, Arnold et al. 2008).

USING THE BASIC SCHEME I: STUDYING THE EFFECT OF SEXUALITY ON GENETIC ARCHITECTURE

There are many examples and case studies showing how the structure of genetic variances and covariances (also known as the "G" matrix) encapsulates the potentials and restrictions for adaptive evolution (Caswell & Sinauer 1989, McDonald et al. 1993, Roff 2000, Begin & Roff 2001, Phillips et al. 2001, Stepan et al. 2002, Begin & Roff 2003, Jones et al. 2003, Begin et al. 2004, Cano et al. 2004, Bochdansky et al. 2005b, Revell 2007, Arnold et al. 2008, Ovaskainen et al. 2008). Here I provide as example, our results in the clonal aphid *Rhopalosiphum padi* and the effect of sexuality on it (Nespolo et al. 2008, 2009). Aphids are cyclic parthenogenetic organisms that reproduce continuously by parthenogenesis, but reduction in temperature and photoperiod can provoke episodes of sexual reproduction. Clonal animals and plants have the advantage that individuals can be replicated in a pedigree, being the clonal means of the trait, analogous to breeding

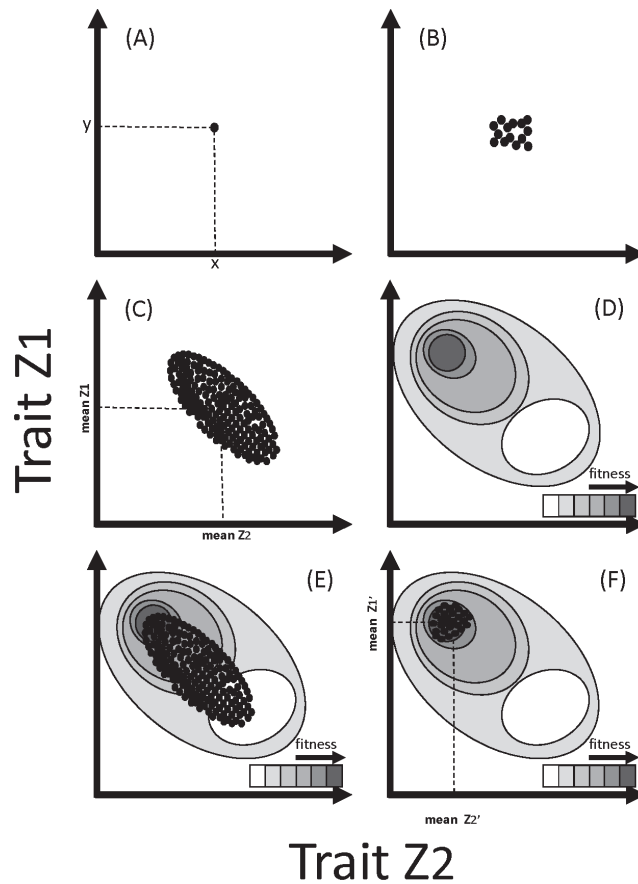


Fig. 1: A graphic simulation of the distribution of breeding values in a population, two traits and an adaptive landscape. A: a single individual with breeding value y for trait Z_1 and breeding value x for trait Z_2 . Breeding values could be considered phenotypic values weighed by how much heritable is the trait. B: fourteen individuals in the same population, with evident variation in their breeding values for both traits. C: the distribution of breeding values in the whole population, showing a negative genetic correlation between Z_1 and Z_2 , and their means. This is what is known as an “evolutionary trade-off”. D: an adaptive landscape, where fitness peaks (red) and valleys (blue) are shown for different traits combinations. E: the distribution of the breeding values over-imposed on the adaptive landscape showing that a proportion of individuals falling in the fitness valley (which would have minimum fitness) and other fraction falling in the fitness peak (which would have maximum fitness). F: the consequence of selection, within one generation (i.e., without reproduction), where the means Z_1 and Z_2 change to Z_1' and Z_2' . Three key consequences should be noted: (1) the change in the mean phenotype could be interpreted as natural selection on trait Z_1 but as a consequence of the genetic correlation, trait Z_2 is also affected; (2) a drastic reduction in genetic variance occurred, which limits future adaptive changes (and producing an adaptation when all the alleles become fixed) and (3) that the genetic correlation disappeared.

Simulación gráfica de la distribución de los valores de cría en una población, dos rasgos y un paisaje adaptativo. A: un individuo con valores de cría y para el rasgo Z_1 y valor de cría x para el rasgo Z_2 . Los valores de cría pueden ser considerados valores fenotípicos ponderados por el grado de control genético que ellos poseen. B: catorce individuos de la misma población, mostrando variación en sus valores de cría para ambos rasgos. C: la distribución de los valores de cría en la población completa, mostrando las medias y una correlación genética negativa entre Z_1 y Z_2 . Esto es lo que se conoce como un “compromiso evolutivo”. D: un paisaje adaptativo, donde los picos (rojo) y valles (azul) de adecuación se muestran para diferentes combinaciones de rasgos. E: la distribución de los valores de cría superpuesta en el paisaje adaptativo, mostrando una proporción de los individuos cayendo en el valle de adecuación (los cuales tendrán adecuación mínima) y otra proporción cayendo en el pico de adecuación (los cuales tendrán adecuación máxima). F: la consecuencia de la selección, dentro de una generación (i.e., sin reproducción), donde las media Z_1 y Z_2 cambian a Z_1' y Z_2' . Tres consecuencias clave deben notarse: (1) el cambio en la media fenotípica se puede interpretar como selección natural en el rasgo Z_1 pero como consecuencia de la correlación genética, el rasgo Z_2 también cambia (se reduce su media); (2) una reducción drástica de la varianza genética, lo cual limita futuros cambios adaptativos (y produciendo una adaptación cuando todos los alelos se fijen por selección) y (3) que la correlación genética desapareció.

values. This fact simplifies considerably the study of genetic (co) variances, since several individuals in a sample from an aphid population could be clones among them. Taking advantage of microsatellite markers and PCR, it is possible to sample individuals from nature and to determine how many clones are in a given population. After that, individuals can be asexually reproduced in the laboratory in order to obtain "living replicates" for a given clone and their traits can be measured. Then, genetic variance would be the variance of clonal means and genetic correlation would be its correlation (between two traits). Among other interesting features of aphids, different morphs (i.e., sexual and asexual) can be induced in replicates of the same genotype, under specific environmental conditions. We used this system, considering the possibility to manipulate sexual reproduction as a fixed treatment, to address the question of how much differences in the genetic architecture are expressed by different reproductive modes (see the complete study in Nespolo et al. 2009). Life history theory indicates that traits such as age at maturity and fecundity are fitness components, which in some insects can be modulated by the capacity of dispersion by producing winged individuals (Roff & Fairbairn 2007). This is the case of many species of aphids, where winged individuals are produced after a number of environmental and genetic determinants (Dixon & Kindlmann 1999). Thus we chose those traits in order to test whether evolutionary trade-offs are present, in the form of negative genetic correlations among those traits (Fig. 2), and whether they change in response to sexuality. To accomplish this, we sampled a population of aphids and identified 23 different genotypes by PCR amplification and using seven microsatellite loci, and we further reproduced them asexually during several generations. Then, also by asexual reproduction, we produced two set of replicates that were submitted to two treatments: sexual and asexual induction (for details see Nespolo et al. 2009). Interestingly, during the asexual phase we found important evolutionary trade-offs between fecundity, age at maturity and production of winged individuals (Fig. 2). But (in the same genotypes) these trade-offs disappeared during

sexual reproduction, possibly because of a re-allocation energy pattern due to the expensive sexual forms. Recalling the adaptive landscape and distribution of breeding values depicted in Fig. 1, the presence of a fitness optimum at the upper-left area of the graph (i.e., high dispersion capacity, high age at maturity and low fecundity in Fig. 2; a general reaction to crowding in insects) would produce, based on our results, an evolutionary shift towards reducing fecundity, delaying maturity and increasing the production of winged individuals during the asexual phase (Fig. 2B and 2D). However, this is not predicted to occur during sexuality, given the radically different distribution of clonal means (Fig. 2C and 2C). This is an example of the application of the basic scheme with little deviations from the modern synthesis. Perhaps the use of PCR amplification, microsatellite markers and clonal design could be considered as later advancements, but the rationale and the predictions are just as in Fig. 1. However, these results, which test the constancy of the G-matrix in response to reproductive mode, were considered novel and useful without needs to invoke any new paradigm.

USING THE BASIC SCHEME II: VALIDATING THE ENERGETIC DEFINITION OF FITNESS

Natural selection is perhaps the most commonly known proposition of Darwin, and no other mechanism has been seriously proposed to explain the origin of adaptations. In fact, the oldest and also the most recent studies addressing the origin of adaptations gives to natural selection a central role (Williams 1966, Gadgil & Bossert 1970, O'Donald 1973, Boag & Grant 1981, Morris 1985, Endler 1986, Schluter & Smith 1986, Seeley 1986, Mousseau & Roff 1987, Fox 2000, Gubitz et al. 2000, Higgie et al. 2000, Kentner & Mesler 2000, Kohn et al. 2000, Szekely et al. 2000, Conner 2001, Kirk et al. 2001, Merila et al. 2001b, Rice & Chippindale 2001, Hey & Kliman 2002, Parsonage & Hughes 2002, Sheldon et al. 2003, Sinervo & Calsbeek 2003, Abzhanov et al. 2004, Cano et al. 2004, Ceplitis & Bengtsson 2004, Brommer et al. 2005, Abzhanov et al. 2006, Saldana et al. 2007, Anisimova & Liberles 2008).

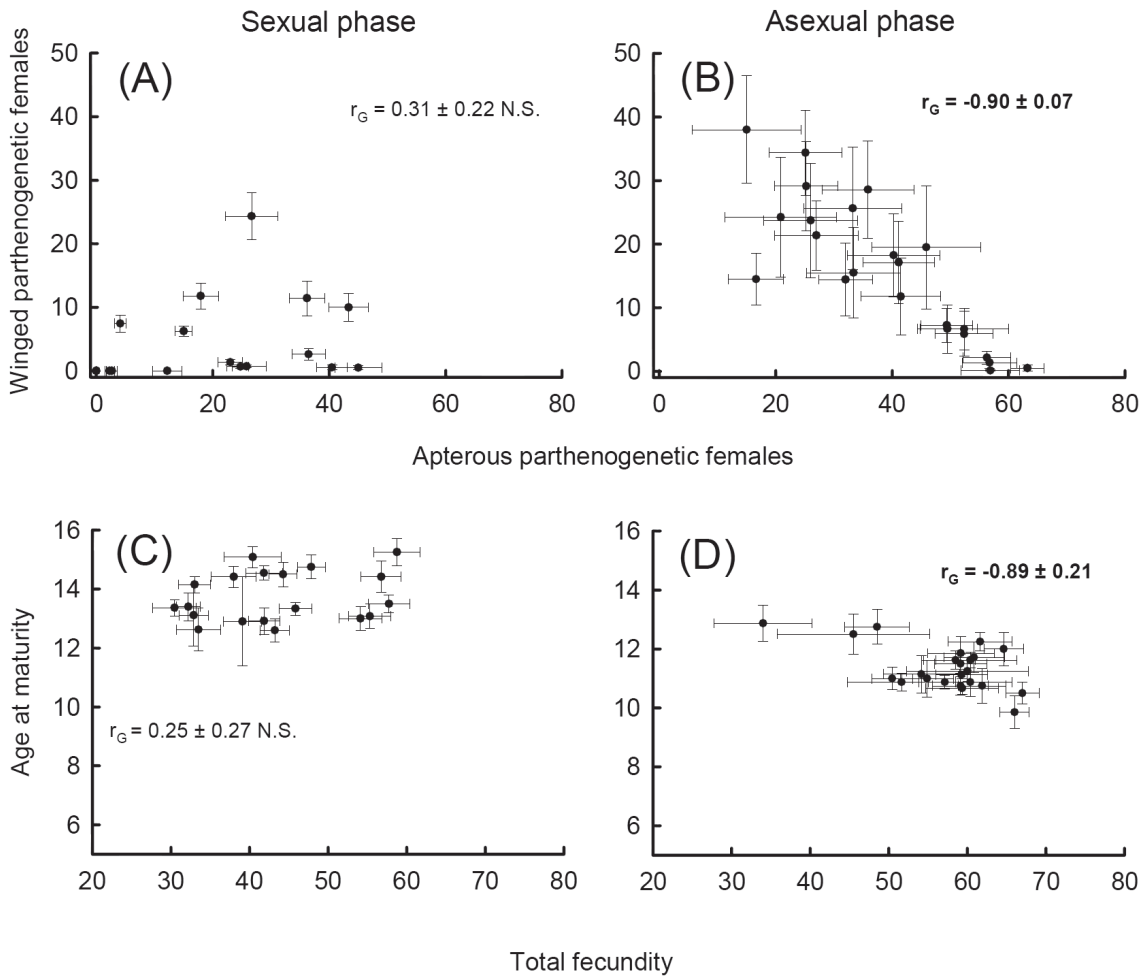


Fig. 2: The potentials and restrictions to evolution in life histories of a cyclic parthenogenetic aphid (*Rhopalosiphum padi*), as analyzed by comparative quantitative genetics. In this case, breeding values (each datapoint) are represented by clonal means (\pm SE; $N = 8-12$ measured individuals per clone), and genetic correlations ($r_G \pm$ SE of the estimate) are the Pearson product-moment correlation of clonal means between traits. This population alternates continuous parthenogenetic reproduction with episodes of sexual reproduction, a study case where the same population and even the same genotypes express radically different genetic architecture, which in turn predict different evolutionary trajectories. This is an example of fluctuating trade-offs in classic life-history traits: age at maturity and fecundity (lower panel) and specific life histories such as the production of winged and apterous individuals (upper panel). It can be seen that fairly high negative genetic correlations (constraints for adaptive evolution) are present during the asexual phase (B and D) but disappear during the sexual reproduction (A and C) (see details in Nespolo et al. 2009).

La potencialidad y restricciones a la evolución de historias de vida en un áfido partenogenético cíclico (*Rhopalosiphum padi*), analizada desde la perspectiva de la genética cuantitativa comparada. En este caso, los valores de cría (cada punto) están representados por las medias clonales (\pm EE; $N = 8-12$ individuos medidos por clon), y las correlaciones genéticas ($r_G \pm$ EE del estimador) son las correlaciones de producto-momento de Pearson de las medias clonales entre rasgos. Esta población alterna reproducción partenogenética continua con episodios de reproducción sexual, un caso de estudio donde la misma población e incluso el mismo genotipo expresa arquitecturas genéticas radicalmente diferentes, lo cual a su vez predice trayectorias evolutivas diferentes. Este es un ejemplo de compromiso fluctuante en rasgos de historia de vida clásicos: edad de la madurez y fecundidad (abajo) y rasgos de historia de vida específicos como la producción de individuos alados o ápteros (arriba). Se puede ver que correlaciones genéticas altas y negativas (restricciones a la evolución adaptativa) están presentes durante la fase asexual (B y D) pero desaparecen durante la reproducción sexual (A y C) (véase detalles en Nespolo et al. 2009).

The study of contemporary natural selection in wild populations, also known as “phenotypic selection studies” took its form after the theoretical framework introduced by Robertson and Price (Robertson 1966, Price 1970), who demonstrated that directional selection is equivalent with the covariance of fitness and the trait of interest. This approach was later applied to real data and non-linear fitness surfaces, and also to other forms of selection (Arnold 1983, Arnold & Wade 1984, Brodie et al. 1995). A great number of natural selection studies have been performed since then, which suggest that natural selection is strong, can fluctuate in sign, form and magnitude, and is widespread in all kind of organisms. Another conclusion of these studies was that almost every possible attribute of animals and plants can be target of natural selection, depending on its impact on fitness (Primack & Kang 1989, Wiggins 1991, Lindén 1992, Sorci & Clobert 1999, Barbraud 2000, Svensson & Sinervo 2000, Hoekstra et al. 2001, Kingsolver et al. 2001, Kirk et al. 2001, Kruuk et al. 2001, Medel 2001, Kruuk et al. 2003). However, the great majority of those studies were performed on morphological traits.

Physiological ecologists, during a long time worked making an important assumption regarding organisms in populations: that plants and animals optimize the use of energy in order to maximize fitness. This was formerly known as the allocation principle, but later was renamed as the energetic definition of fitness (Cody 1966, Gadgil & Bossert 1970, Sibly & Calow 1986, Brown et al. 1993), and suppose that available energy is limiting in ecosystems, and organism need to allocate it to either biological functions (e.g., growth, reproduction, maintenance, movement). Hence, an important prediction of the hypothesis is that natural selection will promote those genotypes that optimize energy use. In other words, individuals that minimize the cost of living (i.e., maintenance metabolism in the case of animals) would be promoted by selection since the surplus energy will maximize survival and fecundity (i.e., increasing fitness). To test this hypothesis, natural or phenotypic selection on (maintenance) energy consumption needs to be measured.

The problem to study natural selection in animals relies on the fact that it is critical to mark, measure and recapture a great number of individuals. The obvious limitations of measuring energy metabolism in many individuals (which in most cases need to be measured in the lab) worsen the picture and have made these kinds of studies, prohibitive. Few indirect evidences suggesting that animals optimize their energy budget by reducing maintenance costs, came from ectotherms such as fish (Bochdansky et al. 2005) and terrestrial snails (Czarnoleski et al. 2008). The only direct attempts of testing the hypothesis through phenotypic selection studies, were done in endotherms (wild rodents) (Hayes & O'Connor 1999, Jackson et al. 2001, Boratynski & Koteja 2009). However, none of them yielded conclusive results. With this idea in mind, we took the challenge of testing the energetic definition of fitness in animals, choosing the common terrestrial snail (*Helix aspersa*) as model. We chose this model because one of the problems of phenotypic selection analyses is related with the inherent low statistical power of the technique. This is a consequence of the uncertainty of assuming non-recaptured animals as died animals (when the fitness is measured as survival, which is the majority of the cases, e.g., Janzen 1993, Kruuk et al. 2000, Merila et al. 2001a, McAdam & Boutin 2003, Reale et al. 2003). By using an animal which does not move much (and hence, it is easily found), and more important, the deads are readily identified by the tagged empty shells, we obtained enough statistical power using a couple of hundreds snails. After capturing those individuals, we took them to the laboratory and we measured Standard Metabolic Rate at the routine temperature for snails (see Artacho & Nespolo 2009). We also characterized them morphologically in order to discard correlational selection with other traits. The final results of the survival analysis are presented in Fig. 3 (Artacho & Nespolo 2009). This “fitness profile” shows that selection promoted individuals with low-to-medium energy metabolism. In other words, natural selection seemed to act against “wasteful” individuals.

In terms of the basic scheme in Fig. 1, the snails study would be the kind of evidence needed for drawing the actual fitness

landscape (related with the physiological phenotype, in this case). Of course, it has obvious limitations such as the fact that we were using trait-values and not breeding values, and the fact that the proxy of fitness is just survival (assuming that fecundity is constant). Still, these results were considered useful, since they summarize one of the few empirical supports to the energetic definition of fitness. These results were obtained exclusively using the basic scheme (fitness, genetic variances and covariances, see Fig. 1), as in measuring the effects of sexuality on aphids genetic architecture (Fig. 2).

USING THE BASIC SCHEME III (AND BEYOND): DARWIN FINCHES

One of the most classic examples of adaptive radiation and character displacement are the great variety of beak sizes and shapes, of Darwin finches, endemic to Galapagos Islands (Grant & Grant 2002, Grant 2003, Grant & Grant 2003). Among them, six species belong to the genus *Geospiza* (ground finches) and exhibit a continuous gradient in beak size and shapes, which matches closely the main food they usually consume. Hence, one extreme could be represented by the large ground finch (*Geospiza magnirostris*) which consumes big, hard seeds and uses its strong, short beak to crack their hard shells. The other extreme would be the cactus finch (*Geospiza scandens*), which use their small, long and pointed beak to feed almost exclusively on the pollen and nectar obtained from the flowers of cactuses. In the middle, a myriad of beak sizes and shapes are diversely related to their ecological (trophic) niche, exhibiting variation even at the population level (Grant & Grant 2002, Grant 2003, Grant & Grant 2003). From generalists to extreme specialists, the species of Darwin finches are distributed in the Galapagos archipelago as unique textbook examples showing sometimes striking niche separation when sympatric, and niche overlap when allopatric (Grant et al. 2000, Grant & Grant 2006).

Given the natural laboratory for studying evolutionary processes that they are, a number of evolutionary biologists did their careers studying Darwin finches in Galapagos,

especially in Daphne Major Island, most of them inspired, or associated with Rosmary and Peter Grant (Weiner 2002). These researchers applied the whole battery of procedures based on ecological theory and the modern synthesis, including quantitative genetics (Boag & Grant 1978, Grant & Grant 2000b, Keller et al. 2001), population genetics (Grant et al. 2000, Keller et al. 2001), niche theory

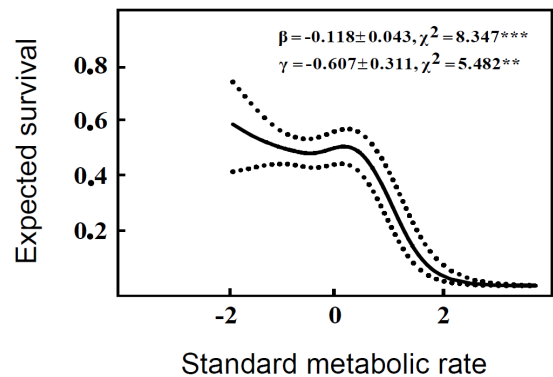


Fig. 3: Natural selection acting against high standard energy metabolism in the terrestrial snail *Helix aspersa*. A study showing that a physiological trait could be target of directional natural selection, in this case supporting the energetic definition of fitness which suggests that natural selection would promote energy optimization. This “fitness profile” shows a dichotomous fitness value (survival; 0 = dead; 1 = survived) in function of the trait value (standardized values to mean = zero and SD = 1), adjusted with a cubic-spline (non-parametric) procedure and 95 % confidence interval computed by bootstrap. As the fitness profile suggest, there was a combination of negative directional and stabilizing selection, as the linear (β) and non-linear (γ) selection gradients confirmed (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). See details in Artacho & Nespolo (2009).

Selección natural actuando en contra de alto metabolismo estándar en el caracol terrestre *Helix aspersa*. Un estudio mostrando que un rasgo fisiológico puede ser blanco de la selección natural, en este caso apoyando la definición energética de la adecuación biológica, la cual sugiere que la selección natural promovería la optimización de la energía. Este “perfil de adecuación” muestra valores de adecuación dicotómicos (sobrevivencia; 0 = muerto; 1 = sobrevive) en función del valor del rasgo (valores estandarizados para media = 0 y SD = 1), ajustados mediante un procedimiento de spline cúbico (no paramétrico) e intervalos de confianza del 95 % calculados mediante bootstrap. Como el perfil de adecuación sugiere, existió una combinación de selección direccional negativa y estabilizadora, tal como los gradientes de selección lineal (β) y no lineal (γ) confirmaron (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$). Véase detalles en Artacho & Nespolo (2009).

(Grant et al. 2000) and phenotypic selection studies (Boag & Grant 1981, Gibbs & Grant 1987, Grant & Grant 2000) to understand the processes behind the adaptive radiation that they observed, mostly in beak shape and body size, but also in song variation (Grant et al. 2000). This evidence suggests that directional selection was strong on beak morphology, but oscillating in sign (Fig. 4). In fact, the same directional selection gradient that we measured for the snails (see Fig. 3), but during 18 years in *G. fortis* and *G. scandens* indicate a highly fluctuating pattern of selection (Fig. 4, Grant & Grant 2002). Considerable amount of additive genetic variation in beak size and shape, and in body size provoked rapid responses to selection to opposite sides, depending on how dry or rainy were the years. This fact surely maintained the genetic variance in those traits, but several other factors, revealed with allozyme, microsatellite and mitochondrial DNA markers indicated large effective population sizes, introgression and hybridization which should have contributed to the maintenance or increase in genetic variation (Grant & Grant 1994, Grant & Grant 1996, Sato et al. 1999, Keller et al. 2001). Then, Darwin finches appeared to be living examples of the basic scheme (Fig. 1): additive genetic variation (i.e., the variance in breeding values for beak shape and body size) was high, and classic population genetic factors were demonstrated to be maintaining it. However, now the adaptive landscape was not static, changing dark zones (i.e., fitness peaks) into white (i.e., fitness valleys) depending on environmental conditions each year (see Fig. 1).

It turned out, however, that the expression of the beak morphology was not under the effects of many genes of small effect, as would be the logic of “breeding values” (and the basic scheme). After a number of elegant experiments on *Geospiza* embryos, and through a combination of gene-expression patterns using microarray technology, Abzhanov and collaborators showed how the tridimensional structure of the beak in Darwin finches is determined by two gene-expression factors (Abzhanov et al. 2004, Abzhanov et al. 2006). In fact, in the chicken a zone of cell proliferation in the frontonasal mass is associated with the bone morphogenetic

protein 4 (BMP4) activity, which determines how “robust” (i.e., the deepness and width) is the beak (Abzhanov et al. 2004, Wu et al. 2004). Calmodulin, on the other hand, appears to be the molecule whose expression levels

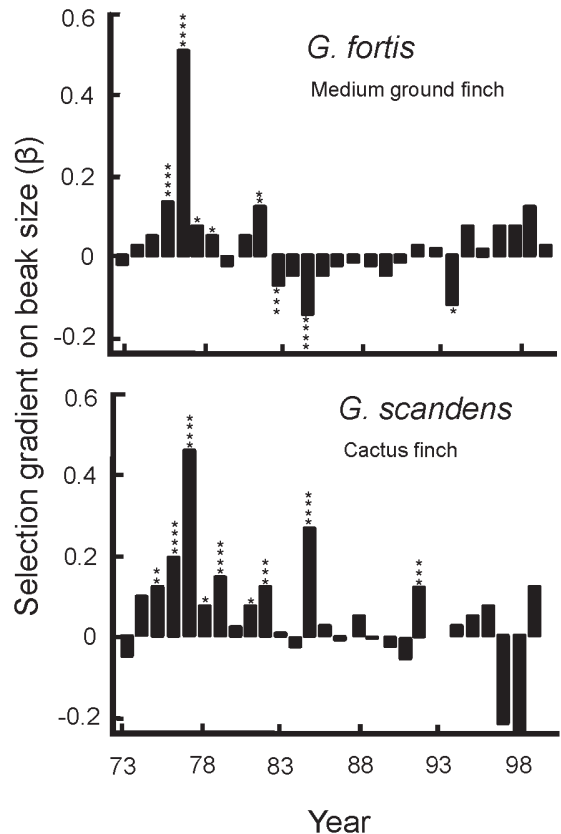


Fig. 4: Long term dataset of Grant & Grant (2002) experiment in two species of Darwin finches in Galapagos Islands. Each bar represents the magnitude of the directional selection gradient, showing how fluctuating could be natural selection across time, depending on environmental conditions. During dry years, positive selection (i.e., promoting big beaks) was the strongest (modified from Grant & Grant 2002). The authors also found a similar fluctuating pattern of selection in beak shape and body size (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.005$; **** = $P < 0.001$).

Experimento de largo plazo, de Grant & Grant (2002), en dos especies de pinzones de Darwin en las islas Galápagos. Cada barra representa la magnitud del gradiente de selección lineal () sobre el tamaño del pico, mostrando cuán fluctuante puede ser la selección en el tiempo, dependiendo de las condiciones ambientales. Durante los años secos, la selección positiva (i.e., promoviendo picos grandes) fue máxima (modificado de Grant & Grant 2002). Los autores encontraron un patrón similar en la forma del pico y el tamaño corporal (* = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.005$; **** = $P < 0.001$).

determine elongated beaks (Abzhanov et al. 2006) (Fig. 5). The levels of these two molecules vary independently of each other, explaining the pointed beaks of cactus finch and the blunt beak of the large ground finch. In other words, the inter-individual differences in beak size were apparently related with the

same genes behind the expression of proteins BMP4 and calmoduling, but differentially expressed. Then, it appears that the high quantitative genetic variation detected in several populations of *Geospiza* was not explained by variation in genes of small effects that codify for beak shape and size, but

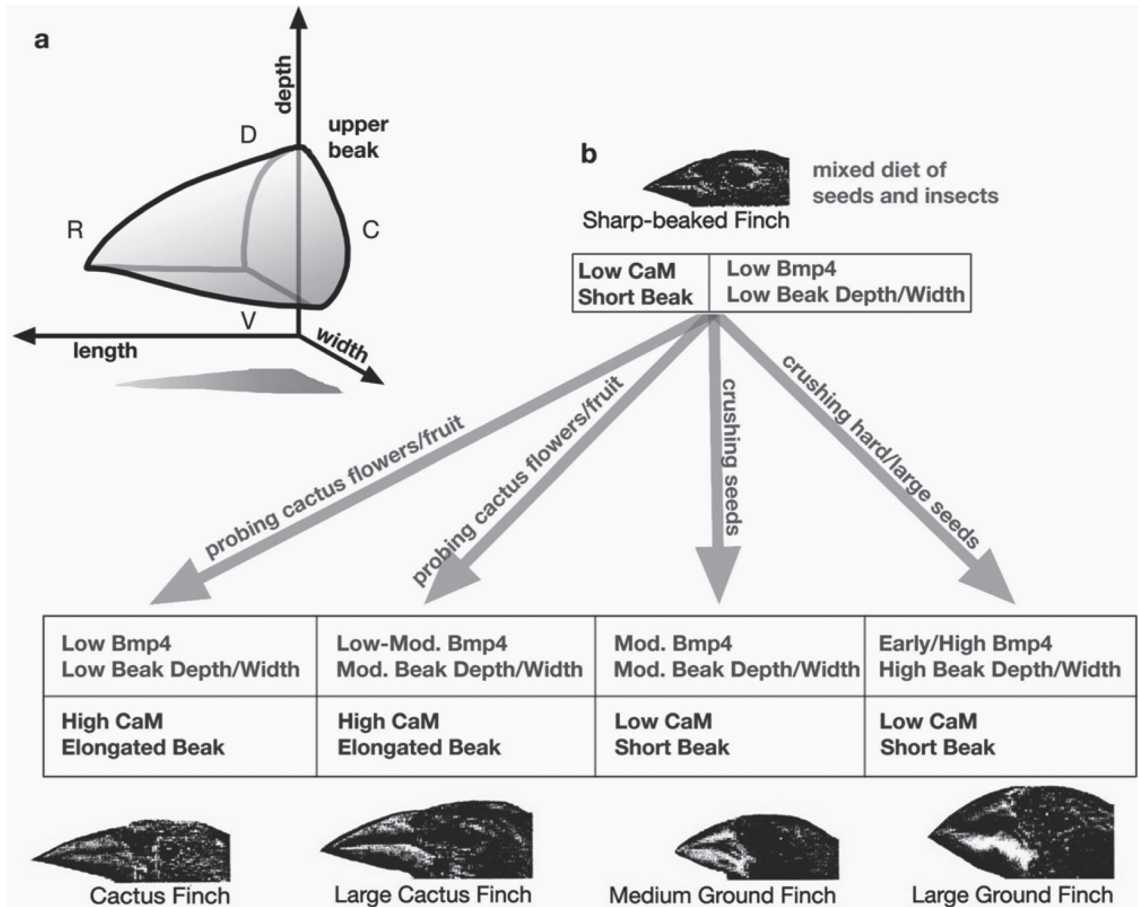


Fig. 5: Abzhanov and colleagues (Abzhanov et al. 2006, Abzhanov et al. 2004) discovered that the classic example of adaptive radiation in the beak of Darwin finches was not explained by the basic model of population and quantitative genetics, which supposes that selection acts on additive genetic variation (as in Fig. 1). On the contrary, they found that the shape and size of the beak in finches appear to be a function of several structural genes that do not vary in their allele composition, but in their levels of expression. This expression is function of two factors: calmodulin (which determines beak length) and bmp4 (which controls beak height and width). Different combinations of expression of calmodulin and bmp4 produce the complete range of observed beak shapes and sizes (reproduced from Abzhanov et al. 2006, with permission from the first author and from Nature publishing group).

Abzhanov y colegas (Abzhanov et al. 2006, Abzhanov et al. 2004) descubrieron que el ejemplo clásico de radiación adaptativa en los picos de los pinzones de Darwin no estaba explicado por el modelo clásico de la genética de poblaciones y cuantitativa, el cual supone que la selección actúa sobre la variación genética aditiva (como en Fig. 1). Por el contrario, ellos encontraron que la forma y el tamaño del pico en los pinzones es función de varios genes estructurales que no varían en su composición alélica, sino que en sus niveles de expresión. Esta expresión es función de dos factores: calmodulina (que determina el largo del pico) y bmp4 (que determina el alto y ancho del pico). Diferentes combinaciones de la expresión de calmodulina y bmp4 producen el rango completo de formas y tamaños de picos (reproducido de Abzhanov et al. 2006, con permiso del primer autor y de Nature publishing group).

explained by differential levels of gene expression in the same groups of genes across populations and species. This is an example where the basic scheme does not apply: heritable variation is not a consequence of standard genetic variation. The consequences of this fact in terms of the model depicted in Fig. 1, supposing that the width and height of the beak is represented in one of the axis, and the length in the other axis, would be more complex (Fig. 6). Given that the length of the beak varies independently of its robustness, the only limitation to a given beak shape would be the aberrant forms or physically impossible beaks. As a result, a superb amount of variation in beak shape and size is evident not only between species but also within populations (Fig. 6A). A hypothetical adaptive landscape of Darwin finches would look as in Fig. 6B, and would produce beaks as in Fig. 6C.

BEYOND THE BASIC SCHEME: EXTRAVAGANT BIOLOGY

Darwin finches are interesting examples of the application of developmental biology to understand evolutionary patterns, but it would be still within the “acceptable framework” of classic biology. In fact, ecologists and evolutionary biologists are used to observe the most varied expression of life forms, as a product of experimentally varying gene composition, and gene-expression patterns. A photosynthetic green animal would be such example, but perhaps something hard to conceive in nature. However, this is exactly what appeared in the cover of the November issue in 2008, of the *Proceedings of the National Academy of Sciences*. In this issue, a paper described the amazing case of a sea slug that acquires photosynthetic capacity by sequestering the chloroplasts of an alga in its digestive epithelium (Rumpho et al. 2008). This amazing case of horizontal gene transfer, in which the transferred gene is integrated into the predator’s genome, is just one of several cases where genes are described to be translocated between organisms, generating evolutionary novelties at an unparalleled rate. As impressive as these examples, a myriad of alternative modes reciprocal association

between genes, organisms and environment in addition to varying genotypes and gene expression patterns have been elucidated during the last decades. For instance, epigenetic inheritance or the inheritance of some acquired experience is a common phenomenon induced in early development, as DNA methylation (Jablonka & Lamb 1998, Wang & vom Saal 2000). Dramatic evidence supports epigenetic inheritance, such as the fact that individuals who were prenatally exposed to famine during the winter of 1944-45 had, six decades later, significantly less DNA methylation of an imprinted gene compared with their unexposed, same-sex siblings (Heijmans et al. 2008). Other kinds of inheritance of acquired experience, such as adaptive anticipatory conditioning are even more spectacular, as it shows that microorganisms can learn from history, evolving the adaptive (i.e., by natural selection) capacity of anticipating environmental changes, as in Pavlov conditioning (Mitchell et al. 2009).

Genetic variation in populations, on the other hand, not only changes as consequences of classic mutation, recombination and selection forces. Several proteins are thought to produce evolutionary capacitance, a phenomenon by which genetic variation is buffered or hidden under stable condition and suddenly released under environmental changes (Le Rouzic & Carlborg 2008). Formerly, chaperones Hsp90 were identified as the main evolutionary capacitors but recently, it has been proposed to be a general consequence of complex gene networks (Bergman & Siegal 2003). A related phenomenon, genetic slippage occurs in facultative asexual organisms such as some invertebrates and plants under directional selection. In these populations, sudden episodes of sexual reproduction generate explosions of variability and phenotypic changes contrary to the direction of previous selection (i.e., maladaptive evolution; Dickerson 1955, Lynch & Deng 1994, Deng & Lynch 1996).

Possibly the most revolutionary idea beyond the basic scheme is niche construction, and related concepts describing the impact of organism functioning on their environments. This constructivist view of

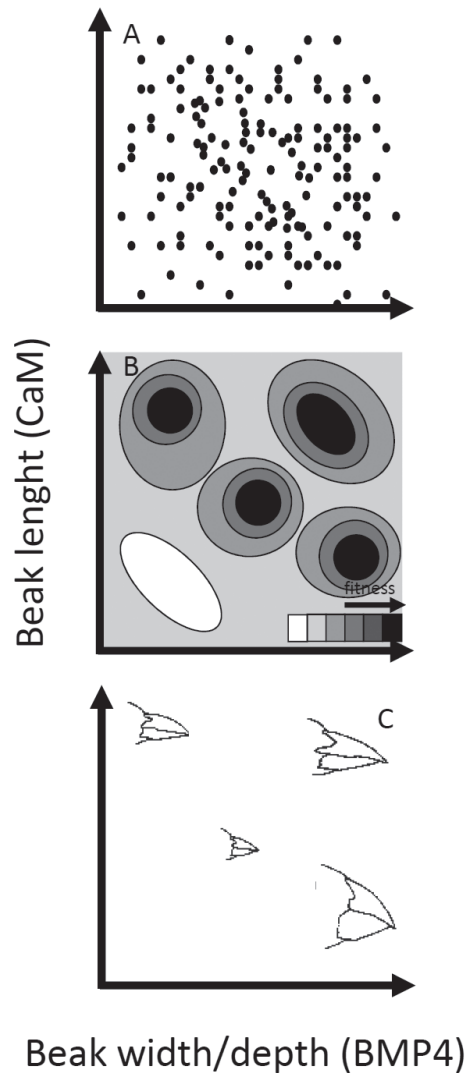


Fig. 6: According to Sato et al. (1999), the six species of Darwin finches of the *Geospiza* genus (ground finches) are monophyletic, being *G. fuliginosa* (small ground finch) the most basal species, which is also the less specialized. Given that the shape of the beak is generated by two gene clusters, differentially and independently expressed (see Fig. 5), there would be a great variety of beak shapes that can be produced, even at the population level. This would be traduced in a “cloud” of breeding values without clear restrictions other than deleterious forms due to physical impossibilities (A). According to the selection gradients measured in the field, a hypothetical adaptive landscape for such situation would be B, where different diet items would produce several adaptive peaks, which would appear especially during dry years (see Fig. 4). This landscape would produce generalized, small beaks as in some individuals of *G. fuliginosa* (C: center); robust, short beaks as in some individuals of *G. fortis* (C: bottom, right); large, long beaks as in some individuals of *G. conirostris* (C: upper, right); and long beaks as *G. scandens* (C: upper, left).

De acuerdo a Sato et al. (1999), las seis especies de pinzones de Darwin del género *Geospiza* (pinzones terrestres) tienen origen monofilético, siendo *G. fuliginosa* (pinzón terrestre pequeño) la especie más basal, la cual es además la menos especializada. Dado que la forma del pico es generada básicamente por dos grupos de genes, expresados diferencialmente (véase Fig. 5), existirá una gran variedad de formas y tamaños de picos que se pueden generar, incluso a nivel poblacional. Esto se traduciría en una “nube” de valores de cría sin claras restricciones más que las formas deletéreas debidas a imposibilidad física (A). De acuerdo a los gradientes de selección medidos en terreno, un paisaje adaptativo hipotético en esta situación sería B, donde diferentes ítemes dietarios producirían varios picos adaptativos, los cuales aparecerían especialmente durante los años secos (véase Fig. 4). Este paisaje produciría picos generalizados y pequeños, como en algunos individuos de *G. fuliginosa* (C: centro); picos robustos y cortos, como en algunos individuos de *G. fortis* (C: abajo, derecha); picos grandes y largos, como en algunos individuos de *G. conirostris* (C: arriba, derecha); y picos largos como en algunos individuos de *G. scandens* (C: arriba, izquierda).

evolution, in which organisms can modify their environments and “construct” their niche have been proposed several times during the last 30 years, mainly by ecologist (Jones et al. 1997), theoretical evolutionary biologists (as system-dependent selection, Lansing et al. 1998) but also by social scientists such as Cavalli-Sforza explaining cultural evolution (Vandermeer 2004). But perhaps the most well developed conceptual body, explaining how, when and at what levels niche construction is determinant for ecology and evolution is the research agenda presented by the anthropologist John Odling-Smee, the biologist Kevin Laland and the population geneticist Marcus Feldman in their book and website <http://lalandlab.st-andrews.ac.uk/niche/bookoverview.html> (Laland et al. 1999, Laland et al. 2001, Vandermeer 2004, Laland et al. 2008, Krakauer et al. 2009).

Niche construction is based on the idea that some consequences of organisms functioning are based on the genetics of each individual, but the temporal modifications of the gene pool and these consequences are distinct processes that are affected by natural selection. The second part of “niche construction” theory, however, indicates that the environment generates the selective pressures on genes and organism’s consequences, which are themselves constructed by organisms functioning. Theoretical developments and some empirical evidence suggest that niche construction should be considered seriously as auto-organization factor which affects evolution, with consequences in all known types of ecological interaction (e.g., competence, positive interactions; Laland et al., 1999). For instance, Rezende et al. (2007) demonstrated that the (self-assembled) architecture of pollination networks is a good predictor of extinction cascades. On the other hand, Harmon et al. (2009) demonstrated how the adaptive radiation in sticklebacks (freshwater fishes) had profound effects on ecosystem primary production, an example of how organisms modify irreversibly their global environments. In fact, Crisp et al. (2009) talked about phylogenetic biome conservatism, when referring to the tendency of species to retain their ancestral ecology, a common process in many past speciation events.

The last examples make reasonable the following question (in the context of long-term-evolutionary change) what determines what: species or ecosystems?

CONCLUSIONS

The task of trying to explain the enormous variety of mechanisms that the new avenues of science and technology opened in evolutionary biology is a tough one, especially when old paradigms are still appropriate in an enormous part of the cases. Here I tried to use examples to show how that old paradigms, termed the modern synthesis (or the “basic scheme”, in this review) can coexist with the new possible models that explain the exotic biological phenomena outlined above. Perhaps the easiest way to see why an extended evolutionary theory is needed is to list the phenomena that were not considered to occur in the modern synthesis, some of which I just outlined: the modern synthesis does not suppose: (1) that genes are transmitted outside the generational axis, (2) that some genes have major effects, especially affecting the expression of other genes, (3) other form of inheritance than genes, (4) mechanisms of maintenance/release of genetic variation different than gene mutation and recombination, (5) that organisms can modify their environments importantly enough to be of evolutionary relevance in further generations and (6) other forms of inheritance outside organisms (e.g., niche construction) that are relevant to the evolutionary process.

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