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Macroevolutionary Freezing and the Janusian Nature of Evolvability: Is the Evolution (of Profound Biological Novelty) Going to End?

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Abstract In a macroevolutionary timescale, evolvability itself evolves. Lineages are sorted based on their ability to generate adaptive novelties, which leads to the optimization of their genotype-phenotype map. The system of translation of genetic or epigenetic changes to the phenotype may reach significant horizontal and vertical complexity, and may even exhibit certain aspects of learning behaviour. This continuously evolving semiotic system probably enables the origin of complex yet functional and internally compatible adaptations. However, it also has a second, "darker", side. As was pointed out by several authors, the same process gradually reduces the probability of the origination of significant evolutionary novelties. In a similar way to the evolution of societies, teachings, or languages, in which the growing number of internal linkages gradually solidifies their overall structure and the structure or interpretation of their constitutive elements, the evolutionary potential of lineages decreases during biological evolution. Possible adaptations become limited to small "peripheral" modifications. According to the Frozen Evolution theory, some of the proximate causes of this "macroevolutionary freezing" are more pronounced or present exclusively in sexual lineages. Sorting based on the highest (remaining) evolvability probably leads to the establishment of certain structural features of complex organisms, e.g. the modular character of their development and morphology. However, modules also "macroevolutionary freeze" whereas the hypothetical "thawing" of modules or their novel adaptive combinations becomes rarer and rarer. Some possible ways out of this dead end include the rearrangement of individual development, e.g. neoteny, radical simplification, i.e. sacculinization, and transition to a higher level of organization, e.g. symbiosis or

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symbiogenesis. The evolution of evolvability is essentially a biosemiotic process situated at the intersection of the genocentric modern synthesis and the evo-devo-centric extended synthesis. Therefore, evolvability may eventually connect these three not necessarily contradictory approaches.

Keywords Evolvability · Evolutionary theory · Extended synthesis · Macroevolution · Stability-based sorting · Frozen evolution theory

Introduction: Evolvability and (Macro)Evolutionary Potential

Modern Synthesis, Extended Synthesis and Evolvability

The central topics of modern synthesis, today's mainstream of evolutionary biology, encompass the character of natural selection, genetic inheritance, the origin and fate of genetic variability, gene flow, the problematics of speciation and other essentially population-genetic topics (see, e.g. Mayr 2003). On the other hand, the so-called extended synthesis, which proposes a fundamental revision of evolutionary biology, emphasizes especially nontrivial relationships between genotype and phenotype and accounts for a significant role for individual development, life cycle and modifications of these processes in evolution. It also focuses on the evolutionary aspects of nongenetic inheritance, the backward influence of phenotype on genotype, genomic evolution, the feedbacks between organisms and their environment, multiple levels of selection, macroevolutionary processes and other formerly omitted directions of research (see, e.g. Pigliucci 2009; Pigliucci and Müller 2010; Laland et al. 2015). Extended synthesis comprises all findings of modern synthesis. The relevance of "canonical" evolutionary mechanisms, such as natural selection, is only rarely disputed by its proponents. However, both approaches differ in the importance attributed to particular evolutionary processes. With some degree of simplification, proponents of the older concept usually consider the phenomena emphasized by extended synthesis to be secondary compared to the core topics of modern synthesis, whereas the proponents of extended synthesis consider them essential (see, e.g. Laland et al. 2014). In the middle of this struggle, evolvability, a phenomenon situated on the borderline of both approaches, quickly becomes one of the centrepieces of modern evolutionary biology.

Evolvability seems almost trivial on first sight. It is a necessary condition for natural selection to play its role in evolution. It was defined, for example, as: "the ability of random variations to sometimes produce improvement" or "the genome's ability to produce adaptive variants when acted upon by the genetic system" (Wagner and Altenberg 1996), and eventually "an organism's capacity to generate heritable, selectable phenotypic variation" (Kirschner and Gerhart 1998). Other proposed definitions of evolvability were summarized, e.g. by Pigliucci (2008) or Hansen (2016). However, the phenomenon itself is not easy to grasp because the term evolvability relates to several somewhat different evolutionary mechanisms. Wagner and Altenberg (1996) and Wagner (2005) outlined that various understandings of evolvability stress either the degree to which heritable genetic variation is capable of responding to natural selection or the variability of certain genotype-phenotype maps, i.e. the potential for gaining new functions or evolutionary innovations. Pigliucci (2008) went even further and distinguished three somehow different understandings of the term: Evolvability can be understood as (1) a standing pool of genetic variation and covariation on the population level that determines its response to natural selection (i.e. a concept similar to heritability), (2) the type of genotype-phenotype map (or genetic architecture) coupled with the extent and character of constraints acting upon possible adaptive solutions on the species level, or (3) the capacity to overcome evolutionary constraints and produce major evolutionary novelties or new hierarchical levels of organization. As we will show later in this paper, all these "levels of evolvability" are deeply intertwined. Sometimes, however, they can evolve to some extent separately, even in opposing directions.

Like nearly all topics of modern evolutionary biology, the problematics of evolvability were first outlined by Charles Darwin (1859). According to the Oxford Dictionary (OED Online 2017), the term was first applied in the 1930s by John A. Thomson. However, it was used only sporadically during the twentieth century. The investigation of construction criteria that enable the evolution of organisms, or the evolution of these criteria and the ways they canalize evolution, stood outside the main focus of evolutionary biological research. Nevertheless, these topics were touched by some researchers that followed embryological, structuralist and macroevolutionary investigations from the turn of the century, as was recently summarized, e.g. by Sharov (2014) or Hansen (2016). Ivan Schmalhausen's idea of stabilizing selection, i.e. the selection on phenotypic plasticity and robusticity necessary in heterogeneous environments, is especially worthy of mentioning in this regard. However, a deep interest in the study of evolvability came later with the development of computer simulations of evolution and evolutionary developmental biology (evo-devo) in the 1980s and 1990s. Paradoxically, the term "evolvability" was highlighted in this context for the first time by Richard Dawkins, one of the leading proponents of modern synthesis (Dawkins 1989).

Two Faces of Evolvability

Differences and similarities among genomes of related evolutionary lineages and their interactions with various internal and external factors show that evolvability itself evolves over time (Wagner and Altenberg 1996; Kirschner and Gerhart 1998; 2007; Pigliucci 2008; Hansen 2016). There is, however, currently no consensus on the causes of this process. It is clear that numerous properties of complex biological systems contribute to their evolvability: robusticity, versatility, flexibility, and redundancy, as well as compartmentalization (modularity), complex regulatory properties (weak linkage), delegation of some functions to exploratory mechanisms (from particular mechanisms such as maturation of vertebrate antibodies to integrated nature of metazoan development that enable phenotypic accommodation), integration of "correctional" systems that may act as evolutionary capacitators (e.g. Hsp proteins, Rutherford and Lindquist 1998) and other properties (see, e.g. Kirschner and Gerhart 1998; Hansen 2016). Proposed drivers of evolution of evolvability, which range from neutral explanations and side-effects of the evolution of other features to direct selection on evolvability on various levels, were summarized, e.g. by Kirschner and Gerhart (1998), Pigliucci (2008), or Hansen (2016). Nevertheless, various proposed processes may complement each other both on the same level and on different levels.

The immediate cause of the evolution of evolvability is the establishment of complex and to some degree optimised genetic architecture on multiple levels of an organism's functioning (nucleotide, chromatin and its modifications, regulation and regulatory pathways etc.) during the life of evolutionary lineages. This architecture then serves as a transducer between genotype and phenotype. According to numerous authors (e.g. Riedl 1977, 1978; Wagner and Altenberg 1996; Kirschner and Gerhart 1998; Turney 1999; Pigliucci 2008; Davies 2014; Hansen 2016), the structure of a genome evolves to most effectively reflect the structure of a phenotype and the environment with all its selective pressures. This increases the odds that the eventual changes in the genome will be adaptive and reduces the odds of these changes being maladaptive or lethal. It also reduces the number of mutations necessary to produce an adaptive phenotype. The same process, however, leads to the establishment of constraints that canalise the degree and character of subsequent evolutionary changes. Genetic architecture, or the map of genotype-phenotype relations, is thus probably necessary for the production of any complex phenotypes and their adaptive evolution. On the other hand, the establishment of such a map or architecture constrains, or at least complicates, the emergence of significant innovations for the same reasons.

The evolution of evolvability, or more precisely its product, evolutionary constraints, thus have, just like the Roman god Janus, two faces. The "dark" one drew the attention of researches first. Many possible limitations caused by the long-term one-way constraining of clade evolution were studied, e.g. by Riedl (Riedl 1977; 1978; Wagner and Laubichler 2004; Budd 2006; Schoch 2010), Arthur (1982, 1984), (Wimsatt 2013; Schank and Wimsatt 1986; Wimsatt and Schank 2004), or Shcherbakov (2012, 2013). According to these authors, an evolutionary lineage might ultimately deplete its (macro)evolutionary potential and reach a state in which the origin of significant evolutionary novelties becomes extremely improbable.

In contrast, the "bright" face of evolvability is more appreciated today. Constraints associated with evolvability are, as the source of robusticity, considered a necessary condition for the further evolution of complex organisms (Kirschner and Gerhart 1998; Wagner 2005; Schoch 2010; Davies 2014; Brigandt 2015). The first signs of this approach could be seen, e.g. in Riedl's idea of imitating epigenotype and similar concepts (Riedl 1978; Wagner and Laubichler 2004; Budd 2006; Schoch 2010). However, this approach manifests much later in its full extent – e.g. in Sharov (2014) or the theory of facilitated variation (Kirschner and Gerhart 2005; 2007). The theory of facilitated variation goes even further and argues that the development and other aspects of organismal function, as well as the character of evolutionary reactions on selective pressures that might be met by the members of the lineage during its evolution, are canalised and optimised on the basis of the earlier evolutionary experiences of the lineage (West-Eberhard 2003; Jablonka and Lamb 2005; Budd 2006; Pigliucci 2008; Watson et al. 2014, 2016; Watson and Szathmary 2016). Constraints on various levels might limit the evolutionary potential but are always redeemed by more pronounced de-constraints in other aspects of organismal structure or function, and, consequently, the increased evolvability of the whole organism (Kirschner and Gerhart 1998; Sharov 2014).

In other words, evolutionary lineages learn[1] to "read" the character of their environment during their evolution, so that they can react to its changes with increasing efficacy. This is enhanced by the fact that organisms co-create their environment and coevolve with it (West-Eberhard 2003; Jablonka and Lamb 2005; Davies 2014; Watson et al. 2014, 2016; Watson and Szathmary 2016). A prominent example of this phenomenon on the individual level is the Baldwin effect. However, many other processes take place, and many of them are completely analogous to learning (Davies 2014; Lindholm 2015).

In any case, evolutionary lineages keep memories of their previous states. This memory is gradually lost by mutation meltdown and analogous processes on other levels. However, one result of the process of the evolution of evolvability is a protection of certain core processes against such loss of information. This manifests in the rare cases of structural or functional re-evolutions – e.g. the wings of Phasmatodea (Whiting et al. 2003), sexuality in mites (Domes et al. 2007), or eggs in viviparous boas (Lynch and Wagner 2010). Only the most essential features of adaptations are usually preserved whereas accompanying fine-tunings are lost.

Biosemiotic Aspects of Evolvability

Of course, the process through which particular evolutionary lineages are able to learn, which characterizes the evolution of evolvability, is neither active nor conscious. It is clear that neither evolutionary lineages nor the whole biosphere live or learn in the same way individual organisms do. Nevertheless, the course of this process and its results are almost completely analogous to conscious learning (Davies 2014; Watson et al. 2014, 2016; Watson and Szathmary 2016).[2]

With some exaggeration, evolution can be described as a process during which the biosphere learns, recognizes and builds both itself and an outside world through the process of the evolution of evolvability. Processes related to the evolution of evolvability are complex and multilevel, and integrate elements of signalization (weak linkage, Kirschner and Gerhart 1998) with both the genetic and non-genetic memory of a particular evolutionary lineage. It was demonstrated that similar processes in the natural wold, if they reach a certain level of complexity, are better described by a biosemiotic approach than by the optics of cybernetics (see, e.g. Markoš and Faltýnek 2011; Markoš and Cvrčková 2013; Markoš 2014, 2015; Markoš and Das 2016). Therefore, the evolutionary reactions of particular lineages could be understood as their interpretation of current conditions, or the changes in these conditions, on the basis of past experience and with the aim of producing the most effective adaptation.

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[1] This is not to say evolutionary lineages or the whole biosphere live or learn in the same way individual organisms do. However, in order to avoid any anthropomorphic tone, it would be necessary to discuss these aspects of evolution of evolvability purely in terms of mutually responsive interactions. This would make the exposition less clear and possible analogies with individual learning less obvious. Therefore, we (as numerous authors before us) stuck with the term "learning", which, however, should not be thought as identical to individual learning but only analogous with it some degree (see, e.g. Davies 2014; Watson et al. 2014, 2016; Lindholm 2015; or Watson and Szathmary 2016 for more detail).

[2] It remains an open question whether all forms of learning and similar processes in living nature are based on the same principle – "domesticated" natural selection. Broad array of processes, e.g. the affinity maturation of antibodies in our immune system (Manser 1990) or "testing" of hypotheses about outside world that define Dennett's (1995) Popperian organisms, seems to support this possibility.

From the classic viewpoint of modern synthesis, this process is based on random mutations occurring on the lowest level of biological organization. However, the frequency of mutations in different places within the genome and the potential effects of these mutations on phenotype are canalised by the preceding rounds of the evolution of evolvability. Alternatively, we can grant primacy to higher levels of organismal structure and functions – epigenetic, developmental, physiological, the level of learning, culture and others. From this vantage point, the genome serves only as a more or less passive library that secondarily fixates adaptive changes (see, e.g. West-Eberhard 2003; Jablonka and Lamb 2005).

Conceiving of the evolutionary reactions of lineages as a biosemiotic process might seem unusual at first sight. However, at second glance it is not surprising at all. The course of evolution has given rise to countless forms of biosemiotic processes in the strict sense, and it is even possible that semiosis is inseparably connected to the origin of life itself (see, e.g. Markoš 2014; Markoš and Das 2016; Sharov 2016). For example, Markoš (2014) or Markoš and Das (2016) denote life to be semiotic category, “a system born, endowed with semiosis, with history” (Markoš 2014). This might be a rather poetic delimitation, but it touches several essential aspects of organisms – they are born only from other organisms (today), they are capable of semiotic acts (usually on multiple levels), and they are endowed with multiple kinds of memory (individual, multiple types of genetic and non-genetic memory of the evolutionary lineage etc.). Therefore, semiosis, comprehended as “the ability of interpretation based in memory, history, experience and context” (Markoš 2014), might be the feature that distinguishes living organisms from simple replicators. Sharov (2016) proposed one way such organisms might originate from simple self-constructing semiotic networks that gradually complexified themselves.

At the same time, particular biosemiotic processes have a major impact on the evolvability of their bearers – either by the interpretation of momentary inputs on the basis of various types of memory, individual learning, transgenerational transfer of knowledge and culture, or other organismal properties with biosemiotic character (see, e.g. Shcherbakov 2012; Hoffmeyer and Stjernfelt 2016). Even if all sub-organismal and supra-organismal biosemiotic processes are left aside and consideration is only applied at the level of individual, it is clear that every organism “reads” its environment differently. The specific character of these differences is determined by organism’s individual experience, the species it belongs to, the adaptations and evolutionary history of the species etc. (von Uexküll 1909). This all affects the course of the species’ further evolution including its evolvability (West-Eberhard 2003; Jablonka and Lamb 2005; Budd 2006; Pigliucci 2008; Watson et al. 2014, 2016; Watson and Szathmary 2016). The most extreme example of this process is probably the origin of beings capable of conscious semiosis and reflection of this ability, i.e., humans. Cultural evolution largely isolated humans from the influence of natural selection. On the other hand, it represents a whole new sphere of evolution and it is already beginning to give us tools to change our own genetic basis. The influence on human evolvability is therefore enormous.

However, the relationship between biosemiotic processes and evolvability is not unidirectional. Any factors that influence the evolution of evolvability in general, and especially factors that might even canalize this process to some degree, should be of great interest to biosemiotics. The reason is that such factors (or their more general analogues) might affect the evolution and characteristics of any biosemiotic system. The application of some non-trivial evolutionary-biological principles in a more general manner to all biosemiotic systems was already proposed, e.g. by Ostdiek (2011), or Markoš (2014, 2015), and we will elaborate the idea later in this paper with our concept of Frozen Evolution Theory (FET). In sum, evolvability and biosemiotic processes are deeply interconnected and the evolution of evolvability can be described as an essentially biosemiotic process.

Janus Comes Back on a Stage

As we showed above, evolvability is currently considered a creative force, a source of robusticity and a necessary condition for the further evolution of complex organisms. Earlier, it was perceived predominantly on the basis of a species' ability to produce profound evolutionary innovations. This is related to the "paradox" of evolvability, i.e. the fact that despite the existence of body plans and other evidence of the conservatism of genetic architecture (see, e.g. Kirschner and Gerhart 1998; Davidson and Erwin 2006), the actual values of heritability and related measures of quantitative evolvability used in modern synthesis (see, e.g. Hansen 2016) does not support the notion of any essential limitations of evolution. The same can be said about the potential of evolutionary lineages to generate interclade diversity in time (see, e.g. Erwin 2007). The explanation of this "paradox" is most likely that the conservation of elements manifests only in macroevolution, i.e. on higher taxonomic levels (Davidson and Erwin 2006; Erwin 2007). The evolution of evolvability therefore maximizes evolvability only in its first understanding (sensu Pigliucci 2008). (Macro)evolutionary potential for profound evolutionary novelties and rearrangements, which is much more difficult to quantify, most likely has a different character and decreases during the evolution of evolvability. This is mirrored in the fact that most mutations causing interspecific and interclade variability represent changes to regulatory elements, whereas changes in protein coding sequences are more common in the interspecific (micro)evolution (Stern and Orgogozo 2008, 2009).

The radical and limiting conception of constraints became one of the sources of criticism on the basis of the older, "darker", understanding of the evolution of evolvability (see, e.g. Schoch 2010; Brigandt 2015). However, rejecting these ideas might have been premature. In this article, we propose that decreasing evolvability is probably inescapable at least in certain forms and in certain evolutionary lineages. As follows from our Frozen Evolution Theory (FET) (Flegr 2010, 2013, 2015), macroevolutionary "freezing" of evolvability that may lead, in the extreme case, to the complete depletion of the (macro)evolutionary potential of particular lineage, is effectively irreversible in the long term. Numerous patterns of the terrestrial biosphere indicate that this freezing might be a real macroevolutionary phenomenon. Nevertheless, evolutionary lineages probably have a limited set of ways to avoid a fatal decrease of evolutionary potential. The main aim of this article is therefore to present sources of macroevolutionary freezing, its evidence, and some possible routes by which organismal evolution may proceed from this (nearly) "dead end".

Unlike most earlier concepts, FET does not suspect some form of selection to be the source of this decrease; rather, its source is predicted to be stability-based sorting (SBS), a phenomenon that will be described later in this article. As SBS proceeds on all levels in all evolving systems, it should be noted that FET might serve as the common linkage between modern synthesis, extended synthesis and biosemiotics: FET describes the evolution of evolvability, which is one of the central concepts of extended synthesis (but also, as we argued above, essentially a biosemiotic phenomenon), whereas it is based on the population-level genetic changes emphasized by modern synthesis. This unification might well appear elusive. Nevertheless, the second message of this article is that the three approaches to evolutionary research might be distinct, however they need not be contradictory in the end.

Results and Discussion: Inevitability of Macroevolutionary Freezing

Stability-Based Sorting and Frozen Evolution Theory

SBS (Toman and Flegr 2017) it often a neglected process that acts constantly at all levels and in all historical systems – e.g. biological evolution, its computer simulations, cultural evolution, or the development of societies. On first sight, SBS is essentially a rather trivial phenomenon that was termed by Richard Dawkins as the “survival of the stable” (Dawkins 1976, p. 13): Changeable entities change and disappear, whereas stable or rapidly emerging entities accumulate and predominate in the system. To state it more thoroughly, SBS is the process that affects, regardless of their origin, all living and non-living material and immaterial entities. During the course of SBS, the elements of the system are sorted on the basis of their contextually dependent stability. Entities with the lowest probability of expiration or transformation into something else (further unchangeable genetic modules, characters that increase the persistence of their holders, more persistent species etc.) accumulate in the system, whereas less stable entities are sorted out. It is true that this “law” is probably axiomatic: more stable (or persistent) entities last longer. However, this does not reduce the significance of the fact it is one of the most general rules that affect biological evolution (and more). Various aspects of SBS were historically studied by researchers in numerous fields, however, they were not analyzed thoroughly and comprehensively until Toman and Flegr (2017).

Understanding the role of SBS in evolution is challenging – even natural selection is a special case of this process. Natural selection represents sorting based on the dynamic stability (the highest difference between the speeds of origination and the disappearance of new entities) that takes place in systems of entities reproducing with heritability. However, SBS in its strict sense and usual conception, i.e. sorting based on static stability (slowest disappearance among sorted entities), still takes place even in the systems of such entities. This process leads to the accumulation of contextually more persistent (stable) elements on all levels of evolution (Shcherbakov 2012, 2013; Toman and Flegr 2017). SBS cannot produce adaptations as spectacular as those produced through natural selection. However, it can sort traits (characters) of organisms – that play the role of exaptations and spandrels – on the basis of their contribution to long-term persistence (stability) of sorted evolutionary lineages. Therefore, it always has the upper hand over opportunistic selection (Toman and Flegr 2017).

SBS may be the cause of, or explanation for, many enigmatic properties of organisms – e.g. the universality of genetic code, broad distribution and long-term persistence of sexual reproduction, or some forms of altruistic behaviour. However, the most important implications of SBS are probably those described by FET (Flegr 2010, 2013, 2015; Toman and Flegr 2017) – a macroevolutionary concept that examines the long-term consequences of SBS on all levels of biological evolution. These consequences are 1) a macroevolutionary trend of decreasing (macro)evolutionary potential of sexual lineages accompanied by a decreasing probability of profound biological innovations and 2) a macroevolutionary trend of decreasing disparity, i.e. morphological and functional richness (e.g. the number of body plans), during the evolution of sexual clades. In other words, the consequences may be understood as the "dark" side of the evolution of evolvability.

Various traits (morphological, developmental, physiological and other) exhibit varying degrees of evolvability, and this degree may further change in the evolution of the lineage (Wagner and Altenberg 1996; Kirschner and Gerhart 1998, 2005; 2007; Pigliucci 2008; Sharov 2014). It follows from the principle of SBS that more stable, i.e. macroevolutionary "frozen", traits and their combinations would preferably accumulate in the evolution of the lineage. Therefore, FET predicts that most traits are very changeable at the beginning of the lineage's evolution, some are less changeable, and only few of them are changeable minimally or not at all. SBS then causes unchangeable traits to accumulate, so that the lineage continually loses most of its ability to respond to selection pressures (or at least most of its degrees of freedom in responding to such pressures).

As Toman and Flegr (2017) showed, the trend of "macroevolutionary freezing" is universal and effectively irreversible in the long term. Although some lineages might temporarily stop or partially reverse this trend (as we will show later in this article), statistically speaking, it applies universally. Successful significant reversals of the trend are probably very rare and associated with a transition to a higher level of organization. The accumulation of frozen traits has a ratchet-like character and this accumulation occurs simultaneously on all levels. Lineages with the largest remaining (macro)evolutionary potential are advantageous in species selection over more frozen lineages. Such lineages are more prone to extinction and also probably speciate less often. Their eventual daughter species are less likely to significantly differentiate in their phenotype, colonize new environments and adaptively radiate. However, in the long term, species selection can only slowdown the decrease of (macro)evolutionary potential. Persistent frozen traits and their groups accumulate in all lineages simultaneously and it is not possible to avoid this process by "pruning" (Wimsatt and Schank 2004). In fact, the accumulation of frozen traits is analogous to the accumulation of mildly deleterious mutations by Muller's ratchet (Muller 1964). Mildly deleterious mutations appear selectively neutral in realistically sized populations, cannot be eliminated by selection, and accumulate in their gene pool. In the same way, small changes that lead to the decrease of (macro)evolutionary potential probably stay below the resolution of species selection.

The negative effects of Muller's ratchet are avoided by organisms with huge populations in which selection determines even the fate of very mildly deleterious mutations (Lynch et al. 1993). Asexual organisms in which (leaving apart horizontal gene transfer) each individual establishes its own evolutionary lineage may be resistant to the decrease of (macro)evolutionary potential for similar reasons: Species selection is equivalent to individual selection in these organisms, and they usually have huge populations and undergo intense competition. This applies especially to prokaryotes. In sexual and usually less numerous populations of eukaryotes, SBS probably progresses with full strength. Moreover, as will be shown later, other processes that further accelerate macroevolutionary freezing may take place in such organisms.

Reasons of Macroevolutionary Freezing

According to FET, SBS causes, especially in sexual eukaryotic lineages, the accumulation of traits that are unable to further respond to directional selection (Flegr 2010, 2013, 2015). These traits are coded especially by genes that would considerably decease the fitness of an individual if altered (see, e.g. the model of Wimsatt and Schank 2004) or would not manifest on its phenotype at all. These may be the genes that are functionally (pleiotropically) interconnected with many other genes in their effects, genes whose slightest change would strongly decrease the fertility or viability of the individual, or genes that are actively held in a multiple-backed state, so that the change in the coded trait would require simultaneous changes in many mutually substitutable genes (Flegr 2010, 2013, 2015; Haiyang et al. 2017). As was pinpointed by earlier researchers, these are usually genes and their natural groups that affect a higher number of functions, characters, and processes especially important for the organism (Kirschner and Gerhart 1998, 2005; Davidson and Erwin 2006; Erwin 2007; Gerhart and Kirschner 2007; Haiyang et al. 2017). More specifically, these are usually genes and their groups that act early in the individual organism's development and affect a high number of functions, characters, and processes. Additionally, they are also usually phylogenetically older (i.e. phylogenetically conserved) (Riedl 1977, 1978; Arthur 1982, 1984; Schank and Wimsatt 1986; Wagner and Laubichler 2004; Wimsatt and Schank 2004; Budd 2006; Schoch 2010; Wimsatt 2013; Haiyang et al. 2017).

Under these conditions, lineages with genetic architectures that confer lower evolvability are sorted out whereas those who confer higher evolvability accumulate. The most common way of achieving genetic architectures with higher evolvability is the structuring of unchangeable genes into henceforth largely unchangeable quasi-independent modules (Lewontin 1978; Schank and Wimsatt 1986; Wimsatt and Schank 2004; Davies 2014). This increases evolvability on a higher level of organismal organization. Therefore, we usually observe that distinguishable traits are coded by natural groups of genes with closely related phenotypic effects organized in a modular manner, i.e. with strongly interrelated pleiotropic effects among the members of the module and weaker in relation to surroundings (see, e.g. Simon 1962; Bonner 1988; Wagner and Altenberg 1996; McShea 2000; Schlosser 2002; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005). These genetic modules are subsequently reflected in functional, developmental, morphological and evolutionary modules. For example, gene regulatory network kernels that take place in development have been shown to exhibit extreme interconnection and low redundancy (Davidson and Erwin 2006; Erwin 2007), whereas the conserved core components of Kirschner and Gerhart (Kirschner and Gerhart 1998; 2005; 2007) represent their more general equivalent. Other examples on multiple levels of organismal structure and functioning are discussed, e.g. by Carroll (2001).

Modules can be deployed as repeatable and to a large extent independently combinable and regulateable wholes (Simon 1962; Lewontin 1978; Bonner 1988; Wagner 1995; Wagner and Altenberg 1996; Kirschner and Gerhart 1998; McShea 2000;

Schlosser 2002, 2004; Wagner et al. 2005). Evolution has reached modular solution many times independently. Modularly arranged processes and wholes occur on all levels of individual development, morphology, and function of sexual organisms, especially (Kirschner and Gerhart 1998). The most significant phenotypic changes therefore occur by changing genomic regulatory elements, respectively by differentially regulating genes and whole developmental and functional modules, deleting them, multiplicating, or deploying on other places and in different times (see, e.g. Carroll 2005; Hoekstra and Coyne 2007; Stern and Orgogozo 2008, 2009; Marshall and Valentine 2010; Haiyang et al. 2017).

In the short to middle term, the accumulation of macroevolutionary frozen elements may be advantageous even for individuals, since it can increase the robusticity of development, i.e. decrease its sensitivity to inner and outer changes. Additionally, it can be advantageous for the population, because it increases the evolvability of the evolutionary lineage (Kirschner and Gerhart 1998, 2005; Wagner 2005; Gerhart and Kirschner 2007; Wimsatt 2013). Accumulation of such genes, their groups, modules, and consequently traits by SBS thus may be accelerated by individual and species selection under many conditions. Moreover, the establishment of further unchangeable modules may paradoxically increase the evolvability of a lineage.

Modules and their groups, however, differ in their evolvability just as single genes do. Elements are sorted on the basis of their stability on all levels simultaneously, including the level of modules themselves and their differential regulation. Therefore, according to the FET, not only modules themselves but, on a large scale and in the long term, also the entire modular arrangement gets frozen. This leads to a further decrease of (macro)evolutionary potential (Flegr 2010, 2013, 2015; Toman and Flegr 2017).

Another source of macroevolutionary freezing, in this case exclusively for sexual clades, may be the accumulation of polymorphic alleles and their functionally integrated groups. Such groups have frequency dependent effects on fitness so strong (especially when supplemented with pleiotropy, epistasis, and contextually dependent effect on fitness) that they cannot be fixed or eliminated in the population under any realistic conditions. The role of such alleles and their groups is accentuated by the theory of frozen plasticity (FPT) (Flegr 1998, 2010, 2013), an evolutionary theory describing the microevolution of sexual species and specific aspects of their adaptive evolution (Flegr 2015).[3]

According to FPT, alleles may be fixed or eliminated only under specific conditions – for example, under a very strong and long-lasting pressure of directional selection. These are, however, only alleles coding simple traits with a low number epistatic and pleiotropic interactions. And even then, their fixation is expected to manifest negatively on other aspects of the fitness of species representatives. Profoundly and without the tendency of alleles with frequency-dependent fitness values to return to their original distribution (i.e. plastically in Flegr's 1998, 2010, 2013, terminology; not to be confused with phenotypic plasticity), sexual species are able to respond to directional selection only temporarily. Specifically, they are able to do so after the separation of a small part of

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[3] FPT is, in some regards, close to older punctuational theories of evolution (for systematic review, see Flegr 2013). However, it is based on the existence of alleles with frequency dependent effects on fitness rather than on the existence of epistasis and offers the most complex scenario of related events.

the original population that holds only a fraction of the original genetic polymorphism due to the founder effect and a population bottleneck, then surviving in a small number of individuals long enough to lose the remaining polymorphism by genetic drift, and ultimately the final expansion accompanied by the rising strength of selection in a large (temporarily) genetically uniform population (Flegr 2010, 2013, 2015).[4] Moreover, the same scenario also likely facilitates the evolution of traits coded by pleiotropically and epistatically interconnected alleles with contextually dependent effects on fitness even without the involvement of frequency-dependent selection (see, e.g. Wimsatt and Schank 2004).

From the macroevolutionary point of view, it is essential that some alleles may have such a strong frequency-dependent effect on fitness that their fixation or elimination would require an unrealistically large decrease in population size or unrealistically long time of surviving in a population of an extremely small number of individuals. Such alleles, together with functionally interconnected alleles, would even survive events associated with the transition to the plastic phase of species existence in a polymorphic state. Therefore, they would gradually accumulate and constrain the evolvability of the lineage (Flegr 2010, 2013, 2015; Toman and Flegr 2017).

Moreover, there could be a non-trivial relationship between both the abovementioned types of macroevolutionary freezing. It is possible that alleles maintained in a polymorphic state by frequency-dependent selection form a kind of “crystallization core” that may continuously “adhere” functionally connected alleles of other genes by increasing their persistence in a gene pool. It was proposed that genomic modularity may originate on the basis of similar interdependencies (see, e.g. Pepper 2000). Such modules may, but need not, be adaptive, whereas those non-adaptive may, but need not, be co-opted later (such concepts were summarized, e.g. by Schlosser 2004). Moreover, the aggregation of unchangeable evolutionary modules is probably accelerated by high genetic polymorphism of sexual populations that cause growing pressure for robusticity, in this case the ability to produce a desired phenotype on various genetic backgrounds (see, e.g. Azevedo et al. 2006; Wimsatt 2013; Ikemoto and Sekiyama 2014). Such an understanding also calls to mind the hypothesis that evolvability may evolve predominantly or exclusively as a by-product of sexuality (see Pigliucci 2008).

It is also noteworthy that macroevolutionary freezing has, with the necessary specifics, close analogies in cultural evolution (e.g. the evolution of languages, societies, teachings etc.) in which SBS also takes place. Mutually interconnected elements accumulate in the evolution of such systems as well, which leads to a decreasing probability of significant changes both in the particular building elements (institution, ritual, interpretation of meaning etc.) and also in the overall structure (Toman and Flegr 2017). On the other hand, small gradual changes based on shared experiences (language, history etc.) are facilitated, often by the means of modularization (of language elements, institutions etc.). The essential transformation of such system is probably possible only after its radical simplification (Ostdiek 2011; Markoš 2014, 2015; Toman and Flegr 2017).

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[4] Compare to levels of evolvability in Pigliucci (2008), intraclade vs. interclade innovations in Davidson and Erwin (2006) or Erwin (2007) and interspecific vs. intraspecific and interclade genetic diversity in Stern and Orogozo (2008; 2009).

Macroevolutionary Phenomena Supporting FET

Numerous distinct macroevolutionary phenomena support the predictions of FET. For example, it was proposed on the basis of theoretical models (see, e.g. Riedl 1978; Wagner and Laubichler 2004; Budd 2006; Schoch 2010; Wimsatt 2013), as well as empirically observed (see, e.g. Erwin et al. 1987; Gould 1989; DiMichele and Bateman 1996; Foote 1997; Eble 1998, 1999; Rasnicyn 2005; Erwin 2007; Hughes et al. 2013) that the (macro)evolutionary potential of evolutionary lineages (i.e. taxa) decreases in the course of their existence. A manifestation of this process is the decrease of their interspecific and intraspecific disparity.

This pattern and its course are universal in the macroevolution of eukaryotic organisms (Toman and Flegr 2017). All branches of the evolutionary tree, both those that originated by speciation and those with more exotic origin, e.g. symbiosis or symbiogenesis, have minimal diversity and disparity at the beginning of their evolution. Diversity, reflecting the number of species, as well as disparity, reflecting the morphological and functional richness of the whole lineage, then rise and, consequentially, also the number of phenotypically distinct branches and the number of higher taxa demarcated by paleotaxonomists. However, as individual sublineages of the evolutionary lineage die off in time, newly originated species (potential founders of new evolutionary lineages) in the remaining sublineages differ in a decreasing number of increasingly derived traits. Therefore, diversity may still rise for some time. Disparity, however, more or less irreversibly declines under such circumstances. Taxon continually abandon particular areas of morphospace until perhaps only one branch remains, often highly specialised and phenotypically very uniform.

This evolutionary trend was documented and widely discussed in Metazoa. This widespread and highly successful group did not produce any new phylum (evolutionary branch profoundly different from other branches) since the Cambrian. Further, it did not produce any radically new body plans since the Cambrian, apart from some markedly simplified groups of parasites (Canning et al. 2004; Glenner and Hebsgaard 2006; Murchison 2008). On the other hand, many Cambrian lineages that are morphologically very distinct, and which would probably be classified as phyla today, became extinct (see, e.g. Gould 1989; Kirschner and Gerhart 1998). The same trend was documented in many individual taxa of multicellular animals and plants (Erwin et al. 1987; DiMichele and Bateman 1996; Eble 1999). Other examples were summarized, for example, by Gould (1989) or Erwin (2007). According to Hughes et al. (2013), this trend is characteristic for phanerozoic clades of Metazoa in general. McShea (1996) presented evidence in favour of the slowing down of metazoan morphological evolution, whereas the deceleration of post-Cambrian metazoan evolution on both genotypic and phenotypic level was documented by Lee et al. (2013).

The proposed explanations of decreasing disparity can be distinguished between ecospatial and developmental (or genetic). The explanations from the two groups need not exclude each other and both were supported by evidence (Valentine 1995; Davidson and Erwin 2006; Erwin 2007; Jablonski 2007; Webster 2007; Budd and Jackson 2016). However, another closely related pattern speaks in favour of the developmental group of explanations – the global trend of a gradual decrease of intraspecific variability during the evolution of taxa known as Rosa's rule (Rosa 1899). Except for some older anecdotal evidence, this rule was also documented quantitatively. Webster (2007) showed that the number of intraspecifically variable characters and the degree of their variability in trilobites (Trilobita) was markedly higher in older species when compared to younger ones. The trend of the decreasing disparity and (macro)evolutionary potential is thus probably not only a taxonomic artefact caused by the subjectivity of our view from the recent perspective and the way paleotaxonomists delimit taxa of higher and lower level (older combinations of characters delimit higher taxa and vice versa). It is most likely associated with the decreasing variability on the species level, which is based on differences in genetic architecture between younger and older taxa.

General Discussion: Restoring Evolutionary Potential

“Thawing” of Modules

We showed in the previous section that, according to FET, especially sexual eukaryotic lineages gradually and effectively irreversibly freeze, i.e. decrease their (macro)evolutionary potential. However, there are several ways to cope with this process.

It cannot be ruled out that some species, even those belonging to macroevolutionary lineages that are strongly frozen, may reach new, very advantageous, combinations of considerably frozen traits that were not yet sorted on the basis of stability (Toman and Flegr 2017). Such a situation is probably most often associated with the transition to a new, mostly unoccupied part of the ecospace – a new ecological strategy or biome, e.g. active flight throughout Phanerozoic or terrestrial environment in Palaeozoic. Such “experimenting” lineages are protected from the excessive selective pressures of competitors, predators, and parasites under these conditions and may survive and adapt even if the new combination of traits would be suboptimal in the original environment. Such events may appear as the so-called mosaic evolution phenomenon (de Beer 1954) in the paleontological record. The new ecospace usually appears to be invaded by many related lineages of one preadapted group simultaneously. However, usually only one is spectacularly successful at the end – probably the lineage that combined several frozen traits in a beneficial way. This lineage may become the “king of the hill” and hamper an invasion of other (even considerably more perspective) groups.

Another, probably even rarer, possibility is the occasional thawing of some seemingly irreversibly frozen module. Since the individual modules differ in the depth of their freezing, even this possibility is imaginable. Some later adaptations may appear to directly or indirectly relieve internal pressures that have kept the module in a frozen state for the majority of its existence (see, e.g. Wimsatt and Schank 2004; Budd 2006). Wimsatt and Schank (2004) identified numerous factors that may contribute to the “thawing” of seemingly irreversibly frozen genes, traits, or modules. Relatively rare nonlethal positive changes are essential in this regard. These positive changes can be ensured, or at least helped, by small population size, modularity, redundancy, duplications, capacitators of evolution such as Hsp proteins, genetic canalization, maternal effect, symbioses, sociality, behavioural plasticity, the relaxation of competition, predation or parazitation, hybridization, and other factors. Such macroevolutionary thawing could have occurred, for example, at the beginning of the evolution of birds, whose ancestor probably considerably decoupled the evolution of anterior and posterior limbs

(Dececchi and Larsson 2013). The question of the possibility of essential transformations of genetic architecture that would comprise even changes in the modules themselves is therefore still an open one. However, the magnitude of the potential change should always be inversely proportional to the degree of modular freezing.

More pronounced thawing, e.g. thawing that would disengage the ties in deep modules responsible for body plan, is probably extremely rare and associated with the radical simplification of individual development. Such events probably occurred at the beginning of the evolution of Rhizocephalia (Glenner and Hebsgaard 2006), Myxozoa (Canning et al. 2004), and biting- or sexually-transmitted mammalian cancers (Murchison 2008). We can call this phenomenon "sacculization" after the most famous instance of these cases, rhizocephalan *Sacculina*. These radically simplified organisms may become the founders of a new, initially macroevolutionary very plastic but gradually freezing clade. We know of no large, diverse and successful metazoan lineage with a radically different body plan that would have evolved from a lineage with an already established body plan in the last 490 million years (i.e. since the end of Cambrian). Therefore, it seems probable that these macroevolutionary events play only a very limited role in evolution, at least in the metazoan case. However, in light of the FET, it remains an open question whether this is not only a temporary state and a consequence of the fact that sexual evolutionary lineages have not yet reached the critical point of abandoning sufficiently large parts of the ecospace they hold as the "kings of the hill".

One possible and less radical variation of the simplification of body plan could be neoteny (or generally any heterochrony), as was summarized by Budd (2006). Such an event enables its carriers to change their phenotype relatively simply and eventually to expand into a new environment. It is, moreover, often associated with the releasing of some modules for new purposes.[5] Similar processes might cause, for example, the diversification of major chordate (Chordata) clades (see Haiyang et al. 2017).

In sum, even though lineages differ in the speed of their macroevolutionary freezing and some clades are probably able to temporarily slow this freezing down or reverse it, it can be said that it applies universally, statistically speaking. None of the abovementioned options can completely stop the decreasing of (macro)evolutionary potential. Returning to the analogy of the accumulation of slightly deleterious mutations by Muller's ratchet, the original function of the gene can be restored by reverse mutations. However, such events are extremely rare and cannot completely stop the accumulation of slightly deleterious mutations, at least not in populations of eukaryotic size (Lynch et al. 1993). Sexual organisms can significantly slow down Muller's ratchet by the means of sexual reproduction that enables the accumulation of deleterious mutations in certain individuals and their removal from the population. However, we know of no similar process on the level of whole evolutionary lineages.

Alternatives to Freezing Modular Organization

Organismal architecture consisting of quasi-independent modules is very common but not the only way that the evolution of evolvability may proceed. It is not universally

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[5] Compare with the role of SBS in the development of societies and their options of restoring evolvability (Ostdiek 2011; Markoš 2014, 2015; Toman and Flegr 2017).

true that a genetic architecture with the most articulated modular elements and lowest number of pleiotropic interactions between them is the most evolvable. The structure and direction of pleiotropic interactions is a more important factor (see, e.g. Hansen 2003; Rasskin-Gutman 2005). Certain elements of modularity apply almost universally in genetic architecture. However, modularity itself is not an easily delimited natural phenomenon and always represents only a relative property (Hansen 2003).

Moreover, complex (compound, major, irreducibly complex etc.) adaptations, i.e. not only minor changes of phenotype but profound evolutionary innovations deeply integrated in it, may originate even by means other than by the (re)arrangement of modularly organized elements and processes. According to some authors, this is the reason why (macro)evolutionary potential need not decrease despite an accumulation of constraints in the evolution of evolvability (Budd 2006). These alternative ways were summarized, e.g. by Budd (2006). Leaving apart "hardly structuralistic" evolutionary theories that completely reverse the relationship between genotype and phenotype, either the existence of exceptional key adaptations, or at least an occasional origin of "hopeful monsters" (i.e. individuals that reached significantly altered but viable phenotype by major shift in their genotype-phenotype map) must be postulated (Budd 2006). Some authors also speak of "correlated progression", i.e. the gradual tandem evolution of loosely interconnected traits (Kemp 2007). Several other explanations that usually incorporate some elements of modularity but are not necessarily based on them were also proposed to explain the evolvability of organisms, as was summarized, e.g. by Hansen (2003) or Sharov (2014).

From a general point of view, the fulfilment of several requirements which are not directly conditioned by strictly modular structure is probably necessary for the evolution of a complex trait (Budd 2006). Nevertheless, a key condition for changes of complex traits to occur with a realistic probability is redundancy – generally, a backup of components that is conditioned by their modular build. Therefore, complex traits without modular structure may evolve in theory. However, the native advantages of modular organization ensure its vast predominance among genomic architectures.

Transition to a Higher Level of Hierarchical Complexity

It currently seems that the only way to efficiently avoid irreversible macroevolutionary freezing and the decreasing of (macro)evolutionary potential remains in the transition to a higher hierarchical level of complexity (see, e.g. McShea 2001a, 2001b). The first type of these transitions that enable evolutionary lineages to avoid SBS on a given level is the internal modularization of their structure and function. This process was described above in association with the evolution of evolvability, especially in the chapter "Reasons of Macroevolutionary Freezing".

The direct mechanism of the origin of modules, or the role of various proposed ways of modularization, have been discussed intensively (Lewontin 1978; Wagner and Altenberg 1996; McShea 2000; Schlosser 2002; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005; Wagner et al. 2005, 2007; Clune et al. 2013; Espinosa-Soto 2014). Generally speaking, modules may originate in two different ways: by parcellation or integration. Specific versions of both processes take place in evolution (see, e.g. Vermeij 1973; Erwin et al. 1987; Wagner and Altenberg 1996; Foote 1997;

Eble 1998, 1999; Thomas 2005; Budd 2006). Moreover, both processes may alternate on subsequent levels (Wagner and Altenberg 1996; Eble 2005). Strong SBS induced integration on the lower level accompanied by macroevolutionary freezing may lead to the multiplication of a whole integrated structure and consequently the origin of parcellated modular organization on the higher level. The possibilities of such cumulative modularization were sketched, e.g. by Kirschner and Gerhart (1998). One extreme case of such restructuralization of genomic architecture is the duplication of the whole genome. This event is quite common in some lineages and might have played a key role, e.g. in the potentiation of the early evolution of vertebrates or actinopterygian fish (Meyer and Van de Peer 2005).

The second way evolutionary entities may reach a higher level of organization and restoration of their (macro)evolutionary potential is a combination of several originally independent entities of the lower level. There are essentially two ways to achieve this. Queller (1997, 2000) termed them fraternal and egalitarian transitions in individuality. Fraternal transitions in individuality are based on the conjoining of related individuals, e.g. clones or progeny of one individual or pair, into higher level entity (Queller 2000). Examples of such entities are, for example, colonies of unicellular prokaryotes or eukaryotes, multicellular organisms, or eusocial organisms. On the lower level, fraternal transitions could lead to pre-cellular compartments consisting of identical molecules, or cells with multiplied organelles. Egalitarian transitions in individuality are based on the conjoining of unrelated individuals coming from distant evolutionary lineages (Queller 2000). Their examples are, for example, various kinds of symbiotic and symbiogenetic events. On the lower level, egalitarian transitions could lead to pre-cellular compartments consisting of different molecules, or chromosomes consisting of various genes. However, even looser nearly obligate symbioses such as those among fungi and plants (mycorrhizae, lichens etc.), dinoflagellates and corals, various unicellular organisms and their metazoan hosts (termites, blood- and sap-sucking insects, ruminants etc.), or flowering plants and their pollinators also play an important evolutionary role and, in some sense, constitute a higher level organism (Szathmáry and Maynard Smith 1995; Calcott and Sterelny 2001; Maynard Smith and Szathmáry 2010; Szathmáry 2015). After all, most metazoans are composite organisms that are no longer viable without their symbionts, i.e. holobionts, and symbioses are essential even for the majority of remaining organisms (Margulis and Fester 1991). Macroevolutionary freezing that facilitates these processes thus may be a crucial evolutionary factor.

Conclusions

Evolvability and its evolution are two of the most important topics of evolutionary biology. The association of evolvability with the origin of evolutionary novelties makes it one of the central themes of evo-devo and the whole field of extended synthesis. Evolvability, albeit in a slightly different understanding, is also established in the field of modern synthesis. Moreover, its evolution happens to be an essentially biosemiotic process that involves elements of memory, learning and interpretation. Therefore, any factors that influence the evolution of evolvability are highly relevant for biosemiotics because they might be analogous to more general factors that affect the evolution, structure, and function of any biosemiotic system.

At the same time, evolvability is not a simple concept. The term covers several interrelated but not completely identical processes on microevolutionary and macroevolutionary levels, and, in a similar way to the Roman god Janus, it has two faces. The "bright" one presents evolvability as a process that creatively canalizes evolutionary change, increases robusticity and facilitates the origin of complex adaptations. This "bright" conception depicts a process that evolves over the long term and maximizes these properties on the basis of past experience. The "dark" face of evolvability tells another story. In this light, evolvability seems to be a process that reduces the (macro)evolutionary potential of a lineage, i.e. it limits the origin of profound evolutionary novelties and deep transformations of phenotype. In the extreme case, it might limitally restrict possible evolutionary changes down to zero.

These two aspects of evolvability constantly intermingle. According to FET, SBS causes a constant and inevitable accumulation of further, effectively unchangeable, macroevolutionary frozen elements. Lineages with the most effective genetic architecture, i.e. lineages with the highest evolvability, predominate in competition with other linages. SBS, however, continues on the level of newly originated and more or less modular genotype-phenotype map. It leads to a radical limitation of (macro)evolutionary potential of the evolutionary lineage. SBS thus may represent a long-sought factor leading to the origin and structuration of (macro)evolutionary limiting genomic interdependencies.

Under normal circumstances, evolutionary lineages can only slow the macroevolutionary freezing down, temporarily stop it, or partially reverse it – e.g. by implementing new combinations of frozen traits, rare thawing of seemingly irreversibly frozen modules, or heterochrony. Completely, albeit also only temporarily, macroevolutionary freezing can be reversed only by the radical simplification of development, i.e. sacculinization, or fraternal and egalitarian transition to a higher level of hierarchical complexity.

All of these assumptions and implications of FET can be tested, for example, on the basis of new findings regarding the genetic architecture of organisms, fossil material, or the ecology of particular evolutionary lineages. It has been previously presented that this theory can coherently explain many mysterious phenomena from a variety of biological disciplines (Flegr 2010, 2013, 2015). FET, however, promises much more. Its foundation stone, SBS, acts in all historical systems and it is thus reasonable to assume that these systems also exhibit processes analogous to macroevolutionary freezing. A small outline of this approach was made, for example, by Flegr (2015) or Toman and Flegr (2017). In any case, FET has the potential to play the role of a bolt uniting modern synthesis, extended synthesis and biosemiotics: three distinct but not necessarily opposing approaches to evolutionary research.

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Compliance with Ethical Standards

Conflict of Interest The authors declare that they have no conflict of interest.

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