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Makroevoluční a ekologické implikace teorie zamrzlé plasticity
Macroevolutionary and ecological implications of the theory of frozen plasticity

Disertační práce

Vedoucí práce: prof. RNDr. Jaroslav Flegr, CSc.

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V Praze dne …......................   …................................

Jan Toman

ABSTRAKT

Teorie zamrzlé plasticity je punktuacionalistickou teorií adaptivní evoluce, podle které se v evoluci pohlavních druhů střídají dlouhá období stáze, během kterých reagují populace na selekční tlaky pouze elastickou změnou ve frekvenci již přítomných alel, s krátkými obdobími plastické evoluce, během kterých může docházet k fixaci a eliminaci alel působením usměrněného výběru. Nepohlavní druhy by si podle tohoto konceptu sice neměly dlouhodobě udržovat tak vysoký genetický polymorfismus, zase by ale měly vykazovat potenciál plasticky reagovat na selekční tlaky v průběhu celé své existence. Tento rozdíl mezi dynamikou evoluce pohlavních a nepohlavních kladů má celou řadu ekologických a makroevolučních implikací. Co se ekologie týče, mohli bychom očekávat odlišné environmentální preference pohlavních a nepohlavních druhů. V naší první práci jsme v souladu s tím na základě srovnávací studie statisticky významně podpořili hypotézu, že se (starobyle) nepohlavní skupiny (eukaryot) vyskytují přednostně ve stabilnějších a homogennějších habitatech než jejich příbuzné pohlavní kontroly. Zásadním faktorem se přitom ukázalo vycházet ze skutečně zažívané, tj. subjektivní, heterogenity prostředí. Z hlediska makroevolučních implikací teorie zamrzlé plasticity je zásadní předpoklad, že se v průběhu existence evolučních linií efektivně nevratně hromadí polymorfní alely a dále neproměnlivé prvky genotypovo-fenotypové mapy. Jak argumentujeme v naší druhé, teoretické, práci, toto „makroevoluční zamrzání" je důležitým faktorem evoluce evolvability pohlavních linií. Výsledkem tohoto procesu je snadnější adaptace, modulární organizace a robustnost organismů. Zároveň se ale projevuje poklesem makroevolučního potenciálu, tj. pravděpodobnosti vzniku zásadních evolučních novinek. To má za následek mj. snižování proměnlivosti evolučních linií nebo jejich mezidruhové a vnitrodruhové disparity. Makroevoluční zamrzání je výsledkem třídění z hlediska stability – univerzálního procesu hromadění prvků, které vykazují menší pravděpodobnost svého zániku nebo změny v prvky jiné. Teoretické analýze tohoto fenoménu, jeho vztahu k přirozenému výběru a (makro)evolučních důsledků jsme se věnovali v naší třetí práci. Platí přitom, že v relativně malých populacích eukaryotických organismů patrně nedokáže makroevoluční zamrzání zastavit ani druhový výběr na základě nejvyššího zbývajícího makroevolučního potenciálu. V následující čtvrté, rovněž teoretické, práci argumentujeme, že se v pozemské evoluci příliš neuplatňují alternativy zamrzající modulární genetické architektury a makroevolučnímu zamrzání nedokáží zcela zabránit ani občasné kombinace několika do velké míry zamrzlých znaků, vzácná „rozmrznutí" takovýchto elementů tělní stavby či fungování, heterochronické změny, nebo radikální zjednodušení vývoje. Jedinou efektivní cestou, jak obnovit makroevoluční potenciál, tak patrně zůstává postup na vyšší úroveň hierarchické organizace. K makroevolučnímu zamrzání však dochází i na vyšší úrovni, přičemž jedinou cestou ze „slepé uličky" zůstává postup na ještě vyšší úroveň hierarchické komplexity. Makroevoluční zamrzání, respektive třídění na základě stability, proto nabízí ultimátní vysvětlení trendu zvyšování hierarchické komplexity v průběhu existence pozemského života i jeho doprovodných fenoménů jako jsou modulární organizace organismů, zvyšování různorodosti mezi elementy na bezprostředně nižší úrovni, zjednodušování elementů na této úrovni a úrovních nižších, postupné zrychlování trendu se dvěma velkými skoky v neoproterozoiku a kambriu, jeho typičnost pro eukaryota a zejména jejich komplexní zástupce, odlišnost pre-neoproterozoické (a hlavně prekambrické) evoluce od evoluce post-neoproterozoické (a hlavně fanerozoické), nebo odlišný charakter evoluce prokaryot a eukaryot. V samotném závěru této práce dávám do vzájemného kontextu ekologické a makroevoluční implikace teorie zamrzlé plasticity a ukazuji, že nejsou pouze koherentní, ale navíc umožňují načrtnout rozvrh událostí, které mohly vést od biosféry sestávající z relativně jednoduchých nepohlavních prokaryotických organismů až k dnešní biosféře charakteristické přítomností komplexních a stále se komplikujících eukaryotických organismů s mnohoúrovňovou genotypovo-fenotypovou mapou.

Klíčová slova: Teorie zamrzlé plasticity, teorie zamrzlé evoluce, pohlavní rozmnožování, evolvabilita, komplexita, makroevoluční potenciál

ABSTRACT

The frozen plasticity theory is a punctuationalist theory of adaptive evolution. It states that long periods of stasis, during which populations respond to selection pressures only by elastic change in the frequency of already present alleles, alternate in the evolution of sexual species with short periods of plastic evolution, during which alleles can get fixed or eliminated by directed selection. Asexual species are not expected to maintain such high genetic polymorphism in the long term. They should, however, be able to plastically respond to selection pressures throughout their whole existence. This difference between the evolutionary dynamics of sexual and asexual clades has a number of ecological and macroevolutionary implications. Concerning ecology, we could expect different environmental preferences of sexual and asexual species. Accordingly, in our first work that was based on a comparative study, we statistically significantly supported the hypothesis that (ancient) asexual groups of (eukaryotes) inhabit more stable and homogeneous habitats than their related sexual controls. Focusing on actually experienced, i.e. subjective, heterogeneity of the environment turned out to be the crucial factor of this type of research. From the viewpoint of macroevolutionary implications of the frozen plasticity theory, it is essential that irreversibly polymorphic alleles and further unchangeable elements of the genotype-phenotype map accumulate effectively irreversibly in the course of the existence of evolutionary lineages. As we argue in our second, theoretical, work, this "macroevolutionary freezing" is an important factor in the evolution of evolvability of sexual lineages. This process results in easier adaptation, modular organization and increased robustness of organisms. At the same time, however, it manifests as the reduction of macroevolutionary potential, i.e. the probability of producing major evolutionary innovations. This results, among other things, in decreasing variability of evolutionary lineages or their interspecific and intraspecific disparity. Macroevolutionary freezing is the result of stability-based sorting – a universal process of preferential accumulation of elements that are less likely to disappear or change to other elements. Theoretical analysis of this phenomenon, its relation to natural selection and macroevolutionary consequences was the topic of our third work. It is shown that even species selection based on the highest remaining macroevolutionary potential probably cannot stop macroevolutionary freezing in relatively small populations of eukaryotic organisms. In the following fourth, also theoretical, work, we argue that alternatives to freezing modular genetic architecture are not frequent in terrestrial evolution and that macroevolutionary freezing cannot be entirely prevented even by occasional combinations of several considerably frozen traits, rare "thawings" of such elements of body function and organization, heterochronic changes, or radical simplifications of development. The only effective way to restore macroevolutionary potential thus remains a transition to a higher level of hierarchical organization. However, macroevolutionary freezing proceeds also at the higher level, whereas the only way from this "dead end" remains to be a transition to an even higher level of hierarchical complexity. Macroevolutionary freezing, or stability-based sorting, therefore propose the ultimate explanation for the trend of increasing hierarchical complexity during the existence of life on Earth and its accompanying phenomena such as the modular organization of organisms, increasing diversity between elements at an immediately lower level, simplification of elements at this level and lower levels, gradual acceleration of the trend with two large boosts in the Neoproterozoic and Cambrian, its typicality for eukaryotes and especially their complex representatives, the difference of pre-Neoproterozoic (and especially Precambrian) evolution from post-Neoproterozoic (and mainly Phanerozoic) evolution, or the different character of prokaryotic and eukaryotic evolution. At the very end of this thesis I mutually contextualize ecological and macroevolutionary implications of frozen plasticity theory and show that they are not only coherent but also allow us to outline a schedule of events that could lead from a biosphere consisting of relatively simple asexual prokaryotic organisms to the contemporary biosphere characterized by the presence of complex and increasingly complicated eukaryotic organisms with a multi-level genotype-phenotype map.

Keywords: Frozen plasticity theory, frozen evolution theory, sexual reproduction, evolvability, complexity, macroevolutionary potential

OBSAH

1 ÚVOD

Explozivní rozvoj evoluční biologie v posledních desetiletích odsunul do pozadí fakt, že na celou řadu důležitých evolučních otázek stále neznáme spolehlivé odpovědi. Zdaleka se nejedná pouze o záhadu pohlavního rozmnožování, bez kterého se prokaryotické organismy obejdou, ale které navzdory řadě nevýhod dominuje mezi eukaryoty. Na mnoho problémů jsme si zvykli seriózně vůbec neptat. Uplatňují se v evoluci nějaké velké, směrované trendy? Proč se tak liší dynamika prekambrické a fanerozoické evoluce? Mění se evoluční proměnlivost kladů během jejich existence? Z jakých příčin se v historii pozemského života zvyšovala komplexita organismů? A jak je možné, že evoluce nezávisle na sobě několikrát dospěla k modulární stavbě organismů? V této práci se pokusím ukázat, že tyto otázky nemůžeme smést ze stolu jako triviality, nebo zavádějící pozůstatky myšlení 19. století. Koherentně je naopak může zodpovědět teorie zamrzlé plasticity, respektive její makroevoluční rozšíření v podobě teorie zamrzlé evoluce.

V rámci svého doktorského studia jsem se věnoval ekologickým a makroevolučním implikacím teorie zamrzlé plasticity. Tento koncept, jehož základy si představíme v následující kapitole, na přelomu tisíciletí završil řadu punktuacionalistických konceptů, podle kterých pohlavnost komplikuje adaptivní evoluci svých nositelů. Zároveň jim ale může přinášet krátkodobé až střednědobé výhody plynoucí z dlouhodobého udržování vysokého genetického polymorfismu v populaci. Jednou z těchto ekologických výhod by hypoteticky mohla být větší evoluční životaschopnost v proměnlivém a heterogenním prostředí. Tuto možnost jsem testoval už ve své diplomové práci (Toman, 2013; viz také navazující monografie Toman, 2015), data jsme ale nově doplnili, vyhodnotili a výsledky publikovali v článku „*General environmental heterogeneity as the explanation of sexuality? Comparative study shows that ancient asexual taxa are associated with both biotically and abiotically homogeneous environments*“ (Toman & Flegr, 2017a, viz příloha 1), o kterém pojednám v kapitole 3.1.

Možné makroevoluční implikace teorie zamrzlé plasticity nastínil v několika publikacích už její autor (Flegr, 2008, 2010, 2013, 2015). Centrální místo v těchto úvahách zastává myšlenka, že v průběhu evoluce může docházet k hromadění dále neproměnlivých genů, jejich skupin, modulů a celých znaků, tj. „makroevolučnímu zamrzání“. Výsledný koncept, který zastřešuje i původní teorii zamrzlé plasticity, autor nazval teorií zamrzlé evoluce. V sérii teoretických článků jsem tyto úvahy rozpracoval, prohloubil a dal do souvislosti s dalšími makroevolučními fenomény a pozorovanými patrnostmi. Článek „*Macroevolutionary Freezing and the Janusian Nature of Evolvability: Is the Evolution (of Profound Biological Novelty) Going to End?*“ (Toman & Flegr, 2018a, viz příloha 2), ke kterému se dostaneme v kapitole 4.1, pojednává o evoluci evolvability a spojuje ji s makroevolučním zamrzáním. Článek „*Stability-based sorting: The forgotten process behind (not only) biological evolution*“ (Toman & Flegr, 2017c, viz příloha 3), kterého se dotkneme v kapitole 4.2, analyzuje hlavní příčinu makroevolučního zamrzání, fenomén třídění z hlediska stability. Poslední publikace „*A Virtue Made of Necessity: Is the Increasing Hierarchical Complexity of Sexual Clades an Inevitable Outcome of Their Declining*

(Macro)evolutionary Potential?“ (Toman & Flegr, 2018b, viz příloha 4), ke které se dostaneme v kapitole 4.3, potom dává makroevoluční zamrzání do souvislosti s trendem zvyšování hierarchické komplexity organismů v průběhu evoluce a završuje makroevoluční část doktorského projektu popisem bezprecedentní řady dosud spolehlivě nevysvětlených makroevolučních fenoménů, pro které teorie zamrzlé evoluce nabízí koherentní vysvětlení.

Tato práce nemá za cíl vyčerpávající popis mého bádání na poli teorií zamrzlé plasticity a evoluce. Na dalších řádcích se pokusím spíše o představení souvisejících článků, jejichž jsem prvním autorem, a jejich zařazení do kontextu – jak vzájemného, tak kontextu moderního evolučně-biologického bádání. Tyto články čtenář nalezne v příloze na koci práce. Na některých místech rozvedu naše myšlenky ve větší šíři, než nám dovolil omezený rozsah odborných článků, většinou ale bude následující text představovat spíše průvodce po našem teoretickém bádání. V samotném závěru potom navrhnu další možnosti testování našich hypotéz. Ještě předtím se ale pokusím spojit ekologické a makroevoluční implikace teorie zamrzlé plasticity a načrtnout velký, i když samozřejmě zatím pouze hypotetický, rozvrh událostí, které mohly vést ke vzniku komplexních organismů a pozemské biosféry ve stavu, který známe dnes.

2 TEORIE ZAMRZLÉ PLASTICITY

Teorii zamrzlé plasticity formulovanou Jaroslavem Flegrem (1998, 2006, 2008, 2010, 2015) můžeme zařadit mezi punktuacionalistické teorie adaptivní evoluce. Stejně jako řada dalších konceptů, které obsáhle shrnul Flegr (2013, 2015, str. 278-286), totiž vychází z předpokladu, že se rychlost a charakter adaptivní evoluce v průběhu existence pravých, tj. pohlavních, druhů výrazně mění.

Po většinu své existence zůstává pohlavní druh ve stavu evoluční stáze. Tlaku usměrněné selekce podléhá jen omezeně a po odeznění selekčního tlaku se jeho fenotyp vrací do původního stavu. Podle Flegra (1998, 2006, 2008, 2010, 2015) jde o důsledek pohlavního rozmnožování, respektive faktu, že noví jedinci v každé generaci nevznikají prostou replikací jedinců starších, ale kombinací genetické výbavy dvou rodičů. U prokaryot, nebo řady druhotně nepohlavních eukaryotických linií (Toman, 2015; Toman & Flegr, 2017a), se genom předává do dalších generací jako ucelená jednotka. Pokud vynecháme různé exotické jevy, jako například horizontální genový transfer, nově vzniklé mutace se u nepohlavních organismů budou v každé generaci nacházet v kontextu stejných alel, tj. na stejném genetickém pozadí. Za každé situace tedy budou mít stejný vliv na biologickou zdatnost svých nositelů a nepohlavní druh bude bez výraznějších omezení podléhat usměrněnému výběru. Pohlavní proces oproti tomu zahrnuje meiózu (tj. proces, při kterém dochází k segregaci chromozomů a intenzivní genetické rekombinaci mezi dvěma kopiemi genetické informace pocházejícími od obou rodičů) a syngamii dvou pohlavních buněk. Potomstvo pohlavních, tj. drtivé většiny eukaryotických, organismů tudíž po genetické stránce není kopií svých předků, ale do velké míry náhodnou kombinací různých alel pocházejících od obou rodičů. Hypotetická nově vzniklá mutace se v důsledku toho dostává v každé generaci na jiné genetické pozadí. Vzhledem k tomu, že různé alely mají často odlišný vliv na fenotyp, může tento jev představovat překážku adaptivní evoluce.

Jak ilustroval Flegr (2005, str. 122-124), alela zvýrazňující druhotný pohlavní znak, podle kterého si samice vybírají samce, se na první pohled jeví univerzálně výhodná. Opravdovou selekční výhodu však přináší pouze těm samcům, které z hlediska ostatních životních funkcí výrazně neomezuje. Pro drobného a slabého samce naopak může být alela zodpovědná například za mimořádný rozvoj paroží vyloženě nevýhodná. Stejně tak bylo například zdokumentováno, že ženy příbuzné po mateřské linii homosexuálním mužům mívají větší množství potomků. Některé alely spoluzodpovědné za homosexualitu u mužů tudíž pravděpodobně výrazně zvyšují plodnost žen (Camperio-Ciani et al., 2004, 2008; tyto studie však byly i kritizovány, viz např. souhrn Baileyho et al. 2016). Také tyto alely tudíž přinášejí výhodu z hlediska (exkluzivní) biologické zdatnosti pouze v určitém kontextu (přítomnost dvou chromozomů X) a naopak ji snižují v kontextu jiném (přítomnost chromozomu Y).

Oba zmíněné systémy jsou samozřejmě v reálném světě výrazně složitější a jejich ultimátní výhodnost či nevýhodnost ovlivňuje řada faktorů. Dobře ale ilustrují fakt, že u pohlavních organismů nemusí mít stejná alela v každé generaci stejný vliv na biologickou zdatnost. Ještě větší problém představuje fakt, že jednotlivé alely neovlivňují fenotyp a potažmo biologickou zdatnost svých nositelů separátně, ale naopak v síti složitých interakcí s alelami dalších genů. U eukaryotických organismů se setkáme jak s pleiotropií, tj. tím, že jeden gen ovlivňuje či spoluvytváří celou řadu znaků, tak s epistází, tj. tím, že je každý znak spoluvytvářen a ovlivňován mnoha různými alelami (viz např. Hansen, 2006). U prokaryotických organismů naopak celý genom vlastně představuje jeden velký gen a podobné problémy u nich za většiny situací vůbec nevyvstávají. Fenotyp pohlavního organismu tudíž vyplývá, pokud necháme stranou vlivy prostředí, ze složité sítě interakcí mezi alelami různých genů. Pleiotropie s epistází tak dále zvyšují dimenzionalitu celého problému s měnícím se genetickým pozadím v průběhu generací. Vlivy různých alel navíc nejsou čistě aditivní. V extrémním případě může docházet až k tzv. znaménkové epistázi, tj. jevu, kdy konkrétní alela na jednom genetickém pozadí mění fenotyp organismu v opačném směru než v přítomnosti jiných genových variant. Extrémní variantou téhož jevu je situace, kdy dvě samostatně výrazně škodlivé mutace zvyšují zdatnost svého nositele, pokud jsou v genomu přítomné obě. Řadu příkladů znaménkové epistáze shrnuli například Weinreich et al. (2005).

Výše zmíněné jevy a jejich problematičnost pro adaptivní evoluci pohlavních organismů reflektovali už někteří dřívější autoři. Za zmínku stojí například Ernst Mayr (1954, 1963), podle kterého nedochází v geograficky rozšířené geneticky polymorfní populaci k selekci alel zvyšujících biologickou zdatnost na daném místě, nýbrž alel-kooperátorů zvyšujících biologickou zdatnost v přítomnosti co největšího spektra ostatních genových variant, Hampton L. Carson (1968) či Alan R. Templeton (1980). Celou řadu dalších podobných konceptů shrnul již zmíněný Flegr (2013, 2015, str. 278-286). Převládá však názor, že kontextový vliv alel a znaků na biologickou zdatnost, pleiotropie a epistáze adaptivní evoluci pohlavních druhů komplikují, ale nikoli znemožňují. Druh, u kterého se tyto jevy uplatňují, sice není působením selekčních tlaků lehce tvárný, při dostatečné síle a trvání selekce se ale nakonec změní.

Jak navíc ve známém myšlenkovém modelu s osmiveslicemi ilustroval Richard Dawkins (2003, str. 29-49), v průběhu času dochází k mezialelické selekci na základě toho, jaké alely spolu dokáží vytvářet zdatná těla. Potenciálně výhodné ale na řadě genetických pozadí škodlivé alely tudíž z genofondu druhu vymizí. Zachovají se jen takové, které za většiny okolností *fitness* svých nositelů zvyšují, nebo alespoň nesnižují. Pokud tuto analogii posuneme na odbornější úroveň, můžeme říct, že v průběhu času nedochází pouze k výběru alel samotných, ale také k přestavbě sítě jejich interakcí, nebo, přesněji, evoluci genetické architektury organismů. Výsledkem je zvýšení pravděpodobnosti, že mutace povedou ke vzniku životaschopného fenotypu s vysokou zdatností, a naopak snížení pravděpodobnosti, že budou škodlivé či letální (viz podkapitola 4.1.2).

Jak však Flegr čím dál intenzivněji akcentuje ve svých novějších dílech (Flegr, 2006, 2008, 2010, 2013, 2015), skutečně zásadní problém pro adaptivní evoluci pohlavních organismů nepředstavují kontextový vliv alel a znaků na biologickou zdatnost, pleiotropie a epistáze samy o sobě, nýbrž ve spojení s negativním frekvenčně závislým vlivem alel a znaků na biologickou zdatnost. Alely vykazující negativní frekvenčně závislou zdatnost, respektive alely podléhající balancující selekci, nejsou běžné. Nejedná se ale ani o žádnou výjimku (Flegr, 2005, str. 105-106, 169-171; Hedrick, 2012; Delph & Kelly, 2014; Key et al., 2014). Dobrým a široce zdokumentovaným příkladem této třídy alel je recesivní alela

HBB pro srpkovitou anémii. Ta vede v recesivně homozygotním stavu k výraznému zdravotnímu postižení až úplné neživotaschopnosti svých nositelů, zatímco v heterozygotním stavu svým nositelům i přes určité fyziologické změny takřka neškodí. Homozygoti i heterozygoti však vykazují zvýšenou odolnost k nákaze malárií, a hlavně jejímu nejnebezpečnějšímu typu způsobovanému krvinkovkou druhu *Plasmodium falciparum.* V malarických oblastech se tudíž alela *HBB* intenzivně šíří, a to až do doby, než její frekvence stoupne natolik, že se začnou disproporčně často vyštěpovat neživotaschopní recesivní homozygoti. Vlivem toho se poměr obou genových variant, tj. původní alely a *HBB*, dlouhodobě ustálí na rovnovážné hodnotě dané rizikem nákazy malárií v dané oblasti (Allison, 1954).

Jak naznačují nedávné výzkumy, zdravotní výhody může v heterozygotním stavu přinášet rovněž negativní alela genu RhD. Zatímco RhD negativní recesivní homozygoti vykazovali relativně nejhorší zdravotní stav, RhD pozitivní heterozygoti na tom byli ze zdravotního hlediska v porovnání se zbytkem populace nejlépe. Právě to je nejspíše důvodem, proč se gen RhD v lidských populacích dlouhodobě udržuje v polymorfním stavu, a to i přesto, že nositelé minoritního fenotypu jsou v trvalé nevýhodě kvůli riziku rozvinutí hemolytické nemoci novorozenců u RhD pozitivních potomků RhD negativních matek (Flegr, 2011, 2016; Flegr et al., 2015). Balancující selekce se ale nemusí uplatňovat pouze ve formě zvýhodnění heterozygotů, nýbrž také mezi alelami různých genů. Na základě nejrůznějších důkazů se soudí, že negativní frekvenčně závislá selekce pomáhá udržovat polymorfismus ve zbarvení kořisti pod vlivem predátorů, polymorfismus barev květů v interakci s opylovači, bohatý repertoár MHC antigenů pod tlakem parazitů (viz např. Flegr, 2005, str. 164-171; Ridley, 2007, str. 58-77; Toman, 2015, str. 119-131), nebo stabilní frekvenci různých potravních (Raffini et al., 2017) či pohlavních morf (Sinervo & Lively, 1996).

Z hlediska teorie zamrzlé plasticity je nejpodstatnější, že alely a potažmo znaky s frekvenčně závislým vlivem na zdatnost zůstávají během existence druhů v trvale polymorfním stavu – nemůže lehce docházet k jejich fixacím ani eliminacím. Vzhledem ke svým pleiotropním a epistatickým vazbám mají navíc potenciál vytvořit síť interakcí, která s nimi funkčně sváže alely dalších genů a úplně nebo takřka úplně znemožní populacím nevratně odpovídat na usměrněnou selekci. Jak píše Flegr (2006, 2008, 2010, 2013, 2015), pohlavní druhy jsou z tohoto důvodu po většinu své existence „evolučně zamrzlé“ a chovají se „elasticky“. Jejich evoluční stáze se neprojevuje statickou neměnností, ale rychlými, omezenými a vratnými reakcemi na změny podmínek. Díky vysokému a dlouhodobě udržovanému genetickému polymorfismu zprvu velmi ochotně reagují na prakticky libovolné změny prostředí. Když ovšem tyto změny odezní, alely podléhající balancující selekci se vrátí do původních frekvencí, což vzhledem k jejich provázání s ostatními alelami vede k návratu fenotypu do původního stavu.

Pokud se selekční tlak stupňuje, nebo trvá delší dobu, přítomný polymorfismus se vyčerpá a evoluční reakce populací zpomalí. Nepohlavnímu druhu by v takové situaci stačilo počkat na vznik a fixování nových mutací. U pohlavních druhů se ale nové mutace (alely) rychle zapojí do stávající sítě mezialelických interakcí, která jejich efektivní fixaci nebo eliminaci brání. V zásadě tak může docházet k fixaci nebo eliminaci pouze těch alel, které jsou do sítě pleiotropních a epistatických interakcí zapojené jen slabě, nebo vůbec. Konkrétně může docházet k odstraňování mutací za všech okolností škodlivých nebo evoluci některých znaků podmíněných jedním až několika málo geny, čemuž odpovídají například antigeny lidského krevního systému AB0 (Yamamoto et al., 1990), nebo (přinejmenším v některých případech) barva srsti (Gratten et al., 2007) či albinismus (Protas et al., 2006). Dokonce i v těch z genetického hlediska nejjednodušších případech však změna příslušných alel ovlivňuje několik znaků – v případě krevního systému AB0 mj. srážlivost krve (O'Donnell & Laffan, 2001), náchylnost k různým typům rakoviny (Xie et al., 2010; Gateset al., 2011) či citlivost k různým druhům patogenů (Glass et al., 1985), v případě zbarvení mj. maskování, termoregulaci, mezidruhovou či vnitrodruhovou signalizaci (viz např. Stuart-Fox & Moussalli, 2009).

I přesto ale někdy mohou podobným stylem, a třeba i sympatricky, vzniknout nové, reprodukčně oddělené, byť fenotypově nepříliš odlišné druhy. Významnější adaptivní evoluce za hranu již přítomného genetického polymorfismu, tj. vnitrodruhové variace mateřského druhu, se však stává velmi obtížnou (Flegr, 2015, str. 154-186, 192-224). V extrémním případě, například pod vlivem lidských šlechtitelů, patrně nakonec může dojít k zafixování většiny stávajících a řady nových genových variant. Jak ale doložil Flegr (2006, 2008, 2013, 2015, str. 145-152, 192-224, 262-269), takřka vždy to bude, přinejmenším v krátkodobém až střednědobém horizontu, na úkor plodnosti či životaschopnosti organismů samotných. V důsledku pleiotropie a epistáze se totiž mohou změny prakticky libovolných znaků projevit zcela nepředvídatelnými důsledky v jiných, předchozí evolucí optimalizovaných, složkách fenotypu.

Pohlavní druhy mohou úspěšně „rozmrznout“ a začít odpovídat na tlaky usměrněné selekce jen za úzce vymezených okolností. Výrazné a nevratné evoluční změny pohlavních organismů jsou podle teorie zamrzlé plasticity omezené na dobu, kdy vznikají nové druhy, respektive na vznik nového druhu peripatrickou speciací (Flegr, 1998, 2006, 2008, 2010, 2013, 2015). První podmínkou evolučního rozmrznutí je oddělení malé části původního druhu. K tomu může dojít například v důsledku náhlého a nevýběrového zmenšení populace, při domestikaci několika jedinců člověkem, nebo kolonizaci nového habitatu. V důsledku efektu zakladatele a průchodu hrdlem lahve nese nová populace jen malou část vzácných alel přítomných v populaci mateřského druhu. Ani to ale samo o sobě ale nestačí k rozvolnění frekvenčně závislých, pleiotropních a epistatických vztahů mezi alelami. Alely vykazující frekvenčně závislý vliv na zdatnost se totiž zpravidla vyskytují v relativně vysokých frekvencích a s velkou pravděpodobností tak přečkají v polymorfním stavu i dramatické změny populační četnosti.

Pokud nová populace narazí na příhodné podmínky a záhy se zvětší, k výraznějšímu rozmrznutí nedojde. Ve větší populaci, pravda, s relativně vysokou frekvencí vznikají nové mutace a roste účinnost přirozeného výběru, takže se nová linie může od mateřského druhu odlišit, a dokonce vyvinout reprodukčně izolační bariéry. Výsledné změny ale patrně nebudou sahat daleko za fenotypovou různorodost mateřského druhu. Častější však je, že nová populace dlouhou dobu živoří v malém počtu jedinců. Právě toto období je pro celý proces evolučního rozmrzání klíčové, neboť v malých populacích neurčuje osud jednotlivých alel přirozený výběr, ale genetický drift. Zcela náhodně tudíž dochází k fixaci a eliminaci zbývajících polymorfních alel, a to včetně těch genových variant, které vykazují negativní frekvenčně závislý vliv na zdatnost. Většina populací patrně při průchodu hrdlem lahve nebo následujícím „bloudění po poušti" vyhyne. Malá část ovšem může přežít až do doby, kdy se podmínky zlepší a umožní populaci zvýšit svou četnost.

Ve velké, nyní již geneticky uniformní, populaci se zvýší účinnost přirozeného výběru. Rovněž v ní s realistickou frekvencí vznikají nové mutace. Všechny nové mutace se zároveň budou nacházet na stejném genetickém pozadí, v důsledku čehož budou mít stejný vliv na biologickou zdatnost. Stejně tak znaky, které kódují, budou vykazovat vysokou dědivost. Populace, respektive nově vznikající druh, se tak dostane do krátkého „plastického" stadia své existence, ve kterém může, podobně jako kdyby byl nepohlavní, klasickým darwinovským způsobem fixovat či eliminovat nové mutace na základě jejich příspěvku k biologické zdatnosti a potažmo podléhat usměrněnému přirozenému výběru. Jak jsme viděli výše a jak do detailu rozvedl Flegr (2015, str. 145-152), je možné, že i v elastické fázi existence druhů mohou z některých populací vnikat odlišné druhy. Ty se však od mateřských druhů nebudou fenotypově příliš odlišovat. Procesem evolučního rozmrznutí oproti tomu vznikají celé nové rody, tj. větve fylogenetického stromu, které se od příbuzných linií liší daleko výrazněji. Celý proces bychom proto mohli nazývat i „rodizací", tj. procesem, při kterém vznikají nové rody (Flegr, 2015, str. 262-269).

Plastická fáze existence druhu však patrně netrvá déle než několik (desítek) tisíc let. Časem totiž nový druh principem třídění alel z hlediska stability (v tomto případě perzistence v genofondu, viz podkapitola 4.2.3) opětovně nashromáždí genetický polymorfismus. To se týká, jak jsme viděli výše, zejména alel vykazujících pleiotropii, epistázi, kontextově a frekvenčně závislý vliv na biologickou zdatnost, které nemůže usměrněný výběr lehce fixovat či eliminovat. Tyto genové varianty a jejich skupiny se tudíž budou pomalu hromadit v genofondu druhu, který v důsledku tohoto procesu přejde do daleko delší elastické fáze své existence.

3 EKOLOGICKÉ IMPLIKACE TEORIE ZAMRZLÉ PLASTICITY

V této sekci rozebereme implikace teorie zamrzlé plasticity týkající se odlišného potenciálu pohlavních a nepohlavních druhů pro život v různých typech prostředí. Po krátkém teoretickém úvodu se budeme věnovat především výsledkům srovnávací studie mezi „starobyle nepohlavními" eukaryotickými klady a jejich pohlavními kontrolami, která měla za úkol otestovat jejich asociaci s prostředími o různé biotické a abiotické heterogenitě. Ve stručnosti si představíme všechny důležité aspekty provedené analýzy a budeme diskutovat její výsledky, přičemž detaily nalezne čtenář v článku „*General environmental heterogeneity as the explanation of sexuality? Comparative study shows that ancient asexual taxa are associated with both biotically and abiotically homogeneous environments*" (Toman & Flegr, 2017a, viz příloha 1 na konci práce). Souvislosti našich objevů s makroevolučními implikacemi teorie zamrzlé plasticity potom budeme diskutovat v samotném závěru práce (viz sekce 5, str. 48-50).

3.1 ODLIŠNÝ CHARAKTER PROSTŘEDÍ POHLAVNÍCH A NEPOHLAVNÍCH ORGANISMŮ

3.1.1 Teoretický úvod

Jak jsme rozebrali v předchozí sekci, podle teorie zamrzlé plasticity nepohlavní organismy odpovídají na tlaky usměrněného výběru „plasticky". Darwinovským způsobem nevratně fixují či eliminují nově vznikající mutace, což po drobných krůčcích vede k postupným změnám fenotypu. V úvodní fázi přizpůsobování může celý proces probíhat poměrně rychle. Dochází totiž ke třídění již přítomné variace, tj. různých evolučních linií na základě selektované vlastnosti (např. odolnosti k antibiotiku). Jakmile se ovšem vyčerpá různorodost na úrovni koexistujících nepohlavních linií, celý proces výrazně zpomalí, protože musí čekat na vznik nových mutací. V důsledku toho jsou nepohlavní druhy schopné sice pomalého, ale stabilního, hlubokého a nevratného přizpůsobování podmínkám prostředí (Flegr, 2006, 2008, 2013, 2015, 2013, 2015; Toman & Flegr, 2017a).

Evoluční reakce pohlavních organismů na usměrněnou selekci jsou oproti tomu do velké míry „elastické". Díky vysokému genetickému polymorfismu populace na selekční tlaky reaguje nejdřív velmi rychle, pouhou změnou v zastoupení již přítomných alel. Jak se ovšem dostávají z rovnovážných frekvencí alely udržované v polymorfním stavu balancující selekcí, *fitness* a potažmo odpověď jedinců na selekční tlak klesají. Pokud není selekční tlak extrémně silný a nepůsobí na populaci velmi dlouhou dobu, přizpůsobování se nakonec zcela zastaví. Řešením přitom nejsou ani nové mutace, protože nemůže docházet k jejich efektivnímu fixování či eliminaci. Po odeznění selekčního tlaku se zastoupení alel s frekvenčně závislým vlivem na zdatnost, stejně jako alel s nimi funkčně svázaných, vrací do původního stavu. To samé platí pro fenotyp dané populace. Pohlavní druhy jsou proto schopné velmi rychlých a vratných reakcí na momentální selekční tlaky, které nedoprovází ztráta genetického polymorfismu. Ze stejného důvodu je pro ně ale po velkou část existence druhu problémem výrazně a nevratně se přizpůsobit novým podmínkám (Flegr, 2006, 2008, 2013, 2015, 2013, 2015; Toman & Flegr, 2017a).

Z odlišného charakteru adaptivní evoluce pohlavních a nepohlavních organismů je zřejmé, že se tyto dva typy organismů mohou podle teorie zamrzlé plasticity lišit i svou úspěšností v různých typech prostředí. Dalo by se čekat, že pohlavnost přinese svým nositelům výhodu v prostorově velmi různorodých, ostrůvkovitých a nepředvídatelných prostředích, jejichž podmínky často fluktuují v opačných směrech. Důležitými zdroji této heterogenity přitom mohou být jak faktory neživého prostředí, tak nerovnoměrně rozdělené zdroje či ostatní koevolvující organismy, tj. konkurenti, paraziti a predátoři. Sníženou schopnost hlubokého a nevratného přizpůsobení zde zastiňuje trvalá schopnost rychle, a přitom vratně reagovat na momentální výkyvy podmínek. Nepohlavní organismy by naopak měly být ve výhodě v prostředích prostorově homogenních a dlouhodobě stabilních, jejichž podmínky se mění jen pomalu a kde se nenachází velké množství koevolvujících organismů. Vysoký genetický polymorfismus a schopnost rychlých vratných reakcí na selekční tlaky zde hrají pouze malou roli. Daleko podstatnější je schopnost nevratně se přizpůsobovat, která svým nositelům umožňuje adaptaci třeba i na velmi extrémní podmínky prostředí.

Jak jsem shrnul už ve své magisterské diplomové práci (Toman, 2013) a navazující monografii (Toman, 2015, str. 106-161), myšlenka odlišných environmentálních preferencí pohlavních a nepohlavních druhů není úplně nová. Stojí v samém jádru některých teorií, které se pokoušejí vysvětlit široké zastoupení pohlavního rozmnožování mezi eukaryotickými organismy navzdory jeho zjevným nevýhodám. Tyto nevýhody shrnuli například Lehtonen et al. (2012) či Toman (2015, str. 36-38), přičemž mezi nejpodstatnějšími můžeme jmenovat časovou a energetickou náročnost meiózy, vyhledávání či lákání partnerů i případného spojení dvou jedinců, složitost, rizikovost a náchylnost těchto procesů ke škodlivým mutacím, rozpad osvědčených kombinací alel (tzv. segregační a rekombinační zátěž), náchylnost na zmenšení populace (tvz. Alleeho efekt), fakt, že pohlavní jedinec předává potomkovi pouze polovinu svých alel (tzv. dvojnásobná cena meiózy), nebo to, že by populace složená z nepohlavních samic mohla růst dvojnásobnou rychlostí (tzv. dvojnásobná cena sexu).

Skupina „ekologických teorií dlouhodobého udržování pohlavního rozmnožování“ předpokládá, že pohlavní rozmnožování přináší svým nositelům zásadní ekologickou výhodu v souboji s nepohlavními druhy. Nejde přitom pouze o souboj s primárně nepohlavními prokaryotickými organismy, jejichž prostředí se od podmínek, ve kterých žije většina eukaryot, výrazně liší. Daleko větší otázkou je, proč nevytlačí pohlavní eukaryotické organismy nepohlavní klony, které ve velké většině pohlavních druhů alespoň občas vznikají a obývají podobná prostředí (Toman, 2015, str. 79-105). Tradičně, snad pod vlivem Ridleyho (2007), se ekologické teorie pohlavního rozmnožování dělí na ty, které zdůrazňují roli abiotického prostředí a ty, které vyzdvihují vlivy ostatních koexistujících a koevolvujících organismů. Ve skutečnosti se však teorie z těchto dvou kategorií vzájemně nevylučují a často se dokonce ve svých vlivech mohou prolínat či doplňovat.

Mezi teorie, které vyzdvihují vliv ostatních organismů, spadá zejména teorie Červené královny akcentující možnost negativní frekvenčně závislé dědičnosti biologické zdatnosti (Hamilton et al., 1990). Paraziti včetně patogenů (ale do jisté míry také konkurenti a predátoři) se v každé generaci přednostně přizpůsobují nejčastějšímu typu hostitele (resp. konkurenta, kořisti). Ve výhodě jsou proto vzácnější jedinci. Ti dají základ další generaci, čímž se ale stanou nejčetnějšími a potažmo nejvyhledávanějšími. Pohlavní rozmnožování umožňuje svým nositelům v každé generaci vyštěpovat vzácné kombinace vlastností, a tak si trvale udržovat náskok před protivníkem. Sexualita však může svým nositelům přinést zásadní výhodu i bez frekvenčně závislé dědičnosti zdatnosti, a to díky zrychlení evolučních reakcí v koevolučních závodech s ostatními organismy (Dawkins & Krebs, 1979). Výhodu pohlavních druhů v souboji s nepohlavními založenou na dlouhodobém udržování vysokého polymorfismu a schopnosti rychle vyštěpit vhodné kombinace alel zdůrazňoval také Maynard Smith (1993, str. 193-215).

Důležitou roli abiotického prostředí při udržování pohlavnosti zdůrazňuje například hypotéza loterie a její speciální případ, hypotéza sisyfovských genotypů (Williams, 1975). Podle těchto konceptů má pohlavní druh výhodu v heterogenním prostředí, protože produkuje různorodé potomstvo. Teoreticky tak může vyštěpit jedince ideálně přizpůsobeného pro každý mikrohabitat. Pokud je prostředí výrazně proměnlivé v čase, může pohlavní druh vyštěpovat vzácné genotypy výborně přizpůsobené momentálním podmínkám, jejichž nositelé dají v extrémním případě základ prakticky celé příští generaci – tzv. sisyfovské genotypy (Williams, 1975) či genetickou elitu (Dobzhansky, 1964). Určitou variací na tyto koncepty je hypotéza vlastního pokoje (Maynard Smith, 1978, str. 89-110), podle které plyne výhoda pohlavních druhů rovněž z produkce různorodého potomstva, v tomto případě ale proto, že si vzájemně nepodobní sourozenci tolik nekonkurují o zdroje a zvyšují tak svou inkluzivní zdatnost. Zásadní výhody ale možná v heterogenním prostředí může přinášet už samotný větší rozptyl ve vlastnostech příslušníků pohlavních populací, díky kterému mají podle hypotézy životem kypícího břehu (Bell, 1982, str. 127-142) pohlavní druhy širší ekologickou niku. V neposlední řadě může přinášet pohlavnost výhodu v prostředí, kde široce fluktuují podmínky abiotického prostředí. Ať už proto, že se jim pohlavní druh dokáže přizpůsobit vyštěpením vhodných kombinací alel (Smith, 1980), nebo proto, že se jim nikdy definitivně nepřizpůsobí, nepřijde o svůj polymorfismus a zachová si schopnost rychlé reakce na další nečekanou změnu (Roughgarden, 1991).

Poslední skupina ekologických teorií pohlavního rozmnožování přiznává důležitou roli jak biotickým, tak abiotickým faktorům. Určitou kombinaci několika ekologických faktorů uvažovala celá řada starších i novějších autorů (viz např. Glesener & Tilman, 1978; Bell, 1982; Roughgarden, 1991; Butlin et al., 1999; Colegrave et al., 2002; Kaltz & Bell, 2002; Renaut et al., 2006; Bluhm et al., 2016; Otto, 2009; Sharp & Otto, 2016). Někteří například rozvinuli základní myšlenku hypotézy životem kypícího břehu v tom smyslu, že výhoda pohlavnosti souvisí hlavně s charakterem faktorů omezujících velikost populace (např. faktorů neživého prostředí, zdrojů, nebo parazitů, predátorů a konkurentů). Pokud tyto faktory závisí na hustotě populace a zastoupení různých genotypů, jsou ve výhodě pohlavní organismy produkující různorodé potomstvo. Pokud naopak tyto faktory na hustotě populace a zastoupení různých genotypů nezávisí, převáží nepohlavní linie (Scheu & Drossel, 2007; Song et al., 2011). Už Williams (1975, str. 145-146, 149-154, 169) také navrhl, že pohlavní rozmnožování může přinášet výhody v obecně fluktuujícím prostředí. Důvodem je paradoxně snížená schopnost nevratně se přizpůsobovat momentálně panujícím podmínkám prostřednictvím fixací a eliminací alel, která chrání pohlavní druhy před tím, aby při každém výraznějším výkyvu podmínek ztratily svůj polymorfismus a následně musely čekat na vznik vzácných mutací. Explicitně ale tuto možnost, jak jsme mohli vidět výše, formuloval až Flegr (2006, 2008, 2013, 2015). Podle teorie zamrzlé plasticity se může jednat o jednu z hlavních výhod pohlavních organismů oproti jejich nepohlavním příbuzným. Dokonce i když vynecháme nespornou výhodu geneticky polymorfních pohlavních druhů plynoucí ze schopnosti rychle a operativně vyštěpovat jedince s vhodnými kombinacemi alel, Flegr a Ponížil (2018) dokázali, že výhodná může být už samotná schopnost nepodléhat selekčním tlakům prostředí příliš ochotně. Za širokého rozmezí proměnlivosti podmínek se totiž v jejich počítačových modelech lépe vedlo druhům, které odpovídaly na selekční tlaky tím méně, čím dále se jejich fenotyp vychýlil od původních hodnot. Z obecného hlediska se navíc zdá, že všechny výše postulované hypotetické výhody pohlavních druhů můžeme převést na společné jmenovatele. Nemusí se tak jednat o separátní konkurenční koncepty, ale spíše různé pohledy na jeden fenomén (viz např. Scheu & Drossel, 2007; Otto, 2009; Song et al., 2011; Toman, 2013, 2015; Sharp & Otto, 2016; Toman & Flegr, 2017a).

Hypotetický rozdíl mezi charakterem prostředí, kde by měly být ve výhodě pohlavní a nepohlavní druhy, nám tedy umožňuje testovat některé základní předpoklady teorie zamrzlé plasticity. První pokus ověřit teorii zamrzlé plasticity na základě literárních dat o ekologii pohlavních a nepohlavních druhů jsem podniknul už ve své magisterské práci (Toman, 2013, viz také Toman, 2015). Za účelem rigoróznější studie jsme však následně vybrali jednu testovanou hypotézu (*nepohlavní druhy převládají v obecně* [tj. časově i prostorově, bioticky i abioticky] *homogenním prostředí*), data doplnili, nově vyhodnotili a výsledky publikovali formou odborného článku (Toman & Flegr, 2017a, viz příloha 1). Pokud by pohlavní druhy převažovaly nad nepohlavními pouze v prostředích s velkým množstvím koevolvujících organismů, výsledky by podporovaly ty ekologické teorie pohlavního rozmnožování, které vyzdvihují roli biotických faktorů při udržování pohlavnosti. Pokud by naopak převažovaly pohlavní druhy jen v abioticky velmi heterogenních a proměnlivých prostředích, nasvědčovalo by to spíše teoriím zdůrazňujícím výkyvy neživého prostředí. Teorii zamrzlé plasticity, respektive konceptům zdůrazňujícím výhodu pohlavního rozmnožování v obecně heterogenním a proměnlivém prostředí, by potom nasvědčovalo zjištění, že pohlavní druhy převažují v prostředích charakteristických jak velkým množstvím různých biologických protivníků, tak abiotickou nestabilitou a různorodostí.

3.1.2 Materiál a metody

Za účelem testování výše uvedené hypotézy jsme uskutečnili srovnávací studii vycházející z literárních dat o způsobech rozmnožování a ekologii eukaryotických organismů. Všechny prokaryotické organismy jsou primárně asexuální (v tom smyslu, že neprodělávají amfimixis). Všechna dnes žijící nám známá eukaryota jsou naopak primárně pohlavní – jejich společný předek byl s největší pravděpodobností pohlavním organismem (Speijer et al., 2015). Přímé srovnání ekologie prokaryot a eukaryot by nicméně naráželo na jen těžko překonatelné překážky vyplývající ze zásadních rozdílů ve velikosti, generační době, buněčné biologii, životních strategiích a řadě dalších faktorů, které by vliv pohlavnosti mohly lehce maskovat. Naštěstí ale existuje řada eukaryotických linií, které buď fakultativně, nebo obligátně přešly k druhotně nepohlavnímu rozmnožování (de Meeus et al., 2007; Van Dijk, 2009; Speijer et al., 2015). Detaily těchto procesů byly rozebrány jinde (viz např. Toman, 2013, 2015), na základě srovnání druhotně nepohlavních eukaryot a jejich pohlavních příbuzných však můžeme testovat různé ekologické teorie pohlavního rozmnožování.

Srovnávací studie podobného typu podnikla řada badatelů už před námi. Jak jsme shrnuli (Toman & Flegr, 2017a), celá řada z nich se týkala (nebo byla později interpretována jako) testování jednotlivých navržených ekologických teorií pohlavního rozmnožování – hypotéz loterie a sisyfovských genotypů (Williams, 1975; Hörandl, 2009), hypotézy vlastního pokoje (Garcia & Toro, 1992; Koella, 1993), teorie Červené královny (Burt & Bell, 1987; Neiman & Koskella, 2009), rychlé odpovědi pohlavních druhů na selekci (Becerra et al., 1999), různých výhod pohlavnosti za fluktuujících podmínek abiotického prostředí (Maynard Smith, 1993; Griffiths & Butlin, 1995; Schön & Martens, 2004; Hörandl, 2009; Vrijenhoek & Parker, 2009), nebo hypotézy životem kypícího břehu (Vrijenhoek, 1984; Burt & Bell, 1987; Griffiths & Butlin, 1995; Domes et al., 2007b; Maraun et al., 2012). Patrně nejobsáhlejší podobné srovnání podnikl Bell (1982, str. 160-392), podle kterého ekologická distribuce pohlavních a nepohlavních skupin mnohobuněčných živočichů (Metazoa) nejvíce nasvědčuje hypotéze životem kypícího břehu.

Všechny výše uvedené analýzy ale trpí zásadními nedostatky a jejich výsledky jsou dosti nejednoznačné. Hlavním problémem je, že většina z nich jsou *de facto* pouhé kazuistiky – popis patrností, které vykazuje náhodně vybraná evoluční linie (často pouhý druh nebo rod) obývající partikulární náhodně vybrané prostředí. Studie, které se zabývaly širším spektrem organismů, zase mezi zkoumané skupiny zahrnuly i relativně mladé nepohlavní linie, které nemusí být zcela reprodukčně izolované od mateřských či příbuzných pohlavních druhů (viz Turgeon & Hebert, 1994; van Raay & Crease, 1995; Butlin et al., 1998b; Mantovani et al., 2001; Bogart et al., 2007) či dlouhodobě evolučně životaschopné (viz Nunney, 1989; Butlin, 2002; Janko et al., 2008; Vrijenhoek & Parker, 2009), nebo dokonce linie, které jsou nepohlavní pouze fakultativně nebo v části jejich geografického rozsahu. Dokonce i obsáhlá Bellova (1982, str. 160-392), srovnávací studie je spíše nevýběrovým přehledem. V neposlední řadě potom vyvolává pochybnosti zaměření drtivé většiny autorů na *pohlavnost*, která ale mezi eukaryoty nepředstavuje výjimku, takže by fenoménem zvlášť hodným zkoumání měla být spíše jejich daleko vzácnější *nepohlavnost*.

Ze všech těchto důvodů jsme výrazně zaostřili náš zájem, a to pouze na jistě, dlouhodobě (> 1 milion let) a obligátně nepohlavní linie eukaryot, které prokázaly svou dlouhodobou evoluční životaschopnost (detaily našeho výběru viz Toman & Flegr, 2017a, příloha 1, a to včetně *online Supporting Information*). Tyto linie bývají nazývány „starobylými asexuály“ (*ancient asexuals*). Na rozdíl od většiny nepohlavních eukaryotických linií, které sestávají pouze z několika mladých druhů nebo maximálně rodů, často vykazují větší diverzitu, ale jsou také daleko vzácnější. Důkladný průzkum související literatury (detaily našeho výběru viz Toman & Flegr, 2017a, příloha 1, a to včetně *online Supporting Information*) ukázal, že z několika desítek navržených kladů dodnes některými autory považovaných za starobyle nepohlavní splňuje naše kritéria pouze 8 skupin: vířníci ze skupiny pijavenek (Bdelloidea), lasturnatky skupiny Darwinulidae, několik linií roztočů skupiny Oribatidae, několik linií roztočů ze skupin Endeostigmata a Trombidiformes, netíkovitá kapradina *Vittaria appalachiana*, tři druhy strašilek (Phasmatodea) rodu *Timema* a několik linií rodu mlžů *Lasaea*.

Následně jsme určili jejich sesterské (nebo, podle možností, alespoň blízce příbuzné) ekologicky srovnatelné pohlavní linie, tj. pohlavní kontroly (detaily našeho výběru viz Toman & Flegr, 2017a, příloha 1, a to včetně *online Supporting Information*). V dalším kroku jsme na základě literárních dat shromáždili informace o charakteru ekologického prostředí studovaných starobyle nepohlavních linií a jejich pohlavních kontrol (detaily našeho výběru viz Toman & Flegr, 2017a, příloha 1, a to včetně *online Supporting Information*). Poté stačilo už jen vyhodnotit tato data a určit, zda se prostředí starobyle nepohlavních linií a jejich pohlavních kontrol liší, respektive zda starobyle nepohlavní linie obývají bioticky a/nebo abioticky homogennější a stabilnější habitaty než jejich pohlavní kontroly.

Určitý problém představoval fakt, že část (5/8) studovaných starobyle nepohlavních skupin byla polyfyletická, tj. sestávala z několika příbuzných nepohlavních linií s různými předky. Tyto polyfyletické skupiny jsme kvůli blízké příbuznosti jejich dílčích monofyletických linií, ekologické podobnosti těchto linií, a tudíž nejspíše i podobnosti faktorů stojících za jejich nepohlavností, do analýzy zahrnuli jako jednotlivá pozorování. Jejich celkové vyznění (*starobyle nepohlavní skupina obývá bioticky/abioticky homogennější/heterogennější prostředí než pohlavní příbuzní*) jsme poté založili na převládajícím směřování vztahů mezi jejich dílčími monofyletickými liniemi a dílčími pohlavními kontrolami (detaily viz Toman & Flegr, 2017a, příloha 1).

Výsledná data jsme analyzovali v programu R v. 3.1.2 prostřednictvím exaktního neparametrického jednostranného binomického testu, který byl také jediným testem, který jsme mohli na data našeho typu (párová a binární) při tak nízkém počtu pozorování použít. Ve dvou případech (*Lasaea* a *Timema*) se nelišil charakter biotického ani abiotického prostředí starobyle nepohlavní skupiny a pohlavní kontroly a v jednom případě (Darwinulidae) se nelišil charakter abiotického prostředí starobyle nepohlavní skupiny a pohlavní kontroly. Vzhledem k tomu, že tento (indiferentní) typ výsledků nedokáže binomický test analyzovat, nejprve jsme tato pozorování vypustili. Ve výsledku jsme tak testovali 6 párů na biotickou heterogenitu, 5 na abiotickou a 6 na oba typy heterogenity prostředí (resp. obývání bioticky nebo abioticky homogennějšího prostředí). S cílem ověřit robustnost výsledků jsme však následně provedli stejný test, jako kdyby indiferentní výsledky ve skutečnosti svědčily proti testované hypotéze (*neprůkazná starobyle nepohlavní skupina ve skutečnosti obývá* *bioticky/abioticky heterogennější prostředí*), a jako kdyby svědčily proti testované hypotéze, jejíž pravděpodobnost ale není 1/2, nýbrž pouze 1/3 (tj. jako kdyby bylo stejně pravděpodobné, že starobyle nepohlavní skupiny budou obývat bioticky/abioticky heterogennější prostředí, homogennější prostředí a že se jimi obývané prostředí nebude lišit, detaily viz Toman a Flegr, 2017a, příloha 1).

3.1.3 Výsledky a diskuse

Jak jsem nastínil už v předchozí podkapitole, naše podmínky pro vymezení starobyle nepohlavních eukaryot splnilo 8 skupin: pijavenky (Bdelloidea), Darwinulidae, několik linií Oribatidae, několik linií Endeostigmata a Trombidiformes, *Vittaria appalachiana*, tři druhy *Timema* a několik linií *Lasaea*. Nedokázali jsme odhalit žádné systematické rozdíly mezi biotickou ani abiotickou heterogenitou starobyle nepohlavních *Lasaea* a *Timema* ve srovnání s jejich pohlavními kontrolami, což platí i pro abiotickou heterogenitu Darwinulidae. Ve všech zbývajících případech však starobyle nepohlavní skupiny obývaly bioticky i abioticky homogennější a stabilnější habitaty (detaily včetně konkrétních hodnocených faktorů viz Toman a Flegr, 2017a, příloha 1).

Výsledky tedy ukázaly, že starobyle nepohlavní skupiny obývají ve srovnání s pohlavními kontrolami statisticky signifikantně bioticky (6 ze 6, p = 0,016) i abioticky (5 z 5, p = 0,031), a tudíž také obecně (6 ze 6, p = 0,016) homogennější prostředí. Pokud by se distribuce starobyle nepohlavních linií obývajících buď bioticky, nebo abioticky stabilní prostředí výrazně lišily, mohlo by to svědčit spíše ve prospěch biotických, nebo abiotických teorií pohlavního rozmnožování. Podobný výsledek, tj. dominantní asociace starobyle nepohlavních skupin s bioticky i abioticky homogennějšími habitaty, však jednoznačně svědčí ve prospěch teorií postulujících výhodu pohlavnosti v obecně heterogenních prostředích. Alternativní možnost, totiž že jsou mezi sebou biotická a abiotická heterogenita ve studovaných prostředích tak silně korelované, že je efektivně nemůžeme rozlišit, vede ke stejnému závěru. Výsledky naší ekologické srovnávací studie jsou tudíž v plné shodě s postulovanými ekologickými implikacemi teorie zamrzlé plasticity.

Pokud zahrneme indiferentní výsledky jakožto pozorování svědčící proti testované hypotéze (tj. starobyle nepohlavní skupiny, jejichž prostředí se svou biotickou/abiotickou heterogenitou neliší od pohlavních kontrol, budeme počítat, jako kdyby obývaly heterogennější prostředí), výsledky se stanou statisticky nesignifikantními (6 z 8, p = 0,145; 5 z 8, p = 0,363; 6 z 8, p = 0,145). Tato nízká robustnost je ale očividně důsledkem nízkého počtu pozorování a celkový trend je zřejmý i v tomto případě. Pokud budeme postupovat stejně, ale pravděpodobnost pozitivního výsledku stanovíme pouze na 1/3 (viz předchozí podkapitola), výsledky se stanou hraničně signifikantními (6 z 8, p = 0,02; 5 z 8, p = 0,088; 6 z 8, p = 0,02). S tak nízkým počtem pozorování bohužel nemůžeme přistoupit k žádným sofistikovanějším statistickým analýzám. Vzhledem k tomu, že signifikantní výsledky vydal exaktní neparametrický binomický, a tudíž nepříliš citlivý, test, stejně jako faktu, že ani jedno pozorování fakticky nesvědčilo proti testované hypotéze, nicméně můžeme uzavřít, že naše data solidně podporují testovanou hypotézu.

Ještě zajímavější a z evolučně-biologického hlediska podstatnější jsou ovšem výsledky explorační části naší studie, ve které jsme se pokusili identifikovat konkrétní organismální adaptace a rysy obývaného prostředí, které jsou charakteristické pro starobyle nepohlavní skupiny (detaily viz Toman & Flegr, 2017a, příloha 1, a to včetně *online Supporting Information*). Celá řada z nich totiž dokresluje závěry našich teoretických studií o makroevolučních implikacích teorie zamrzlé plasticity, kterým se budeme věnovat ve čtvrté sekci práce.

Zaprvé, prostředí starobyle nepohlavních skupin je velmi bioticky i abioticky stabilní nejen ve srovnání s pohlavními kontrolami, ale také obecně. Dále stojí za zmínku, že bioticky i abioticky výrazně homogenní prostředí často obývají nejen studované starobyle nepohlavní skupiny, ale také jejich pohlavní kontroly. Vzhledem k tomu, že řada těchto kontrol představuje mateřské klady studovaných nepohlavních linií a ty zbývající klady blízce příbuzné, můžeme se oprávněně domnívat, že podobná prostředí obývali i společní předkové studovaných dvojic. Asociace s abioticky a bioticky stabilními habitaty tak může představovat jednu z hlavních preadaptací úspěšného a dlouhodobého přechodu k nepohlavnosti. Není bez zajímavosti, že se podobné patrnosti uplatňují také v dalších možných starobyle nepohlavních skupinách, u kterých ale s jistotou nemůžeme potvrdit absenci pohlavního rozmnožování po nejméně jeden milion let.

Co se týče konkrétních adaptací studovaných starobyle nepohlavních skupin, překvapivě jsme nepotvrdili dvě možnosti, o kterých se dlouhodobě spekuluje. Alternativní způsob výměny genetické informace, který bývá často zdůrazňován jako určitá náhražka pohlavních procesů (Butlin et al., 1998a; Gladyshev & Meselson, 2008; Boschetti et al., 2011; Debortoli et al., 2016; Schwander, 2016), například vykazují pouze pijavenky. U některých možných, ale nepotvrzených starobyle nepohlavních skupin se můžeme setkat s parasexuálními procesy. Rozhodně se ale nejedná o faktor, který by mezi nepohlavními eukaryoty dominoval. Většího rozšíření mezi starobyle nepohlavními skupinami nedosahuje ani „domestikovanost“, tj. navázání symbiotického vztahu s jiným organismem, který domestikantovi zajišťuje stabilní podmínky, dostatek zdrojů a zbavuje ho patogenů či parazitů. Typickým příkladem tohoto jevu, samozřejmě kromě lidské domestikace řady hospodářských zvířat a plodin, jsou mravenčí houbové kultivary ze skupin Tricholomataceae a Lepiotaceae (Mueller et al., 1998). U studovaných starobyle nepohlavních skupin se však s tímto vztahem nesetkáme, přičemž se omezuje pouze na několik nepotvrzených starobyle nepohlavních linií.

Široce je mezi starobyle nepohlavními skupinami naopak rozšířená schopnost vytvářet odolná přetrvávající stádia. Typickým příkladem jsou pijavenky, které za krizových podmínek vysychají do soudečkovitých anhydrobiotických stádií (Pilato, 1979; Ricci, 2001). V této formě mohou přečkat až desítky let, dokud se nedostanou do prostředí s dostatkem vody. Bylo ovšem dokázáno, že prostřednictvím stejné strategie mohou unikat také patogenům a parazitům (Wilson, 2011). S podobnými strategiemi se setkáme u všech starobyle nepohlavních skupin, které obývají z našeho pohledu proměnlivá prostředí, stejně jako u několika nepotvrzených starobyle nepohlavních linií. Na první pohled by se zdálo, že organismy, které taková přizpůsobení potřebují, vůbec homogenní prostředí neobývají. Právě tyto strategie však svým nositelům zajišťují, že se pro ně jejich prostředí stává *subjektivně* homogenním. Z hlediska organismů samotných totiž objektivní charakter obývaného prostředí hraje pouze podružnou roli. Důležité je, jak na ně prostředí skutečně působí. Pokud jsou jeho nepříznivé výkyvy schopné přežít v neaktivních stádiích, subjektivně pro ně může být i výrazně homogenním. Dokonce až tak, že se vyhnou většině selekčních tlaků a z makroevolučního hlediska dojdou stavu morfologické stáze (Pilato, 1979). Právě nedocenění *subjektivní homogenity* prostředí patrně zásadně přispělo k neprůkaznosti dřívějších srovnávacích studií testujících předpoklady ekologických teorií pohlavního rozmnožování zmíněných v předchozí podkapitole.

Všechny starobyle nepohlavní skupiny obývající alespoň částečně vodní habitaty jsou dále bentické nebo přisedlé, přičemž je zajímavé, že jejich pohlavní kontroly zahrnují také planktonní druhy či druhy s planktonními stádii. Může se jednat o náhodu. Bylo však pozorováno, že bentické druhy obecně vykazují menší extinkční rychlost, což patrně souvisí s výrazným omezením přenosu parazitů (a tudíž snížením biotické heterogenity prostředí) u přisedlých organismů ve smyslu virové teorie extinkcí (Emiliani, 1993a, b). Teoreticky by se tudíž mohlo jednat o další doklad homogennějšího charakteru prostředí starobyle nepohlavních skupin. Bentická či přisedlá je potom i řada nepotvrzených starobyle nepohlavních skupin.

Další, neméně zajímavou, patrností je nápadně častá asociace starobyle nepohlavních skupin s půdními habitaty a zejména jejich hlubšími horizonty. Některé z těchto skupin, například pijavenky, zde dokonce dominují i nad svou pohlavní kontrolou (Pejler, 1995). Důvodem může být snížené riziko přenosu parazitů (*sensu* Emiliani, 1993a, b), nižší frekvence setkávání s konkurenty, predátory a parazity (Pilato, 1979; Elliott et al., 1980; Murphy & Tate, 1996; Drake et al., 1998; Fischer et al., 2003; Lavelle & Spain, 2003; Paul, 2007) či ochrana před výkyvy abiotických faktorů prostředí (Pilato, 1979; Krivolutsky & Druk, 1986; Siepel, 1994). Výše uvedené samozřejmě nemusí platit vždy a všude. Půda v malých prostorových měřítcích také často představuje relativně ostrůvkovité prostředí (Ettema & Wardle, 2002; Young et al., 2008; Vos et al., 2013). Zdá se ale, že na časoprostorové škále studovaných starobyle nepohlavních skupin představuje půda přinejmenším ve srovnání s povrchem, dnem či vodním sloupcem za většiny okolností bioticky i abioticky relativně homogenní prostředí. Slabšímu působení selekčních tlaků v půdních habitatech ostatně nasvědčuje i morfologická stáze řady jejich obyvatel (Pilato, 1979).

Zcela dominující vlastností všech starobyle nepohlavních skupin je potom absence životních strategií zahrnujících intenzivní antagonistické interakce s jinými organismy. Nenalezneme mezi nimi žádné typické predátory ani parazity. Často se živí autotrofně nebo saprofyticky, v případě predace jde o nespecifické fytofágy či filtrátory. Pravděpodobným vysvětlením je to, že nedokáží v koevolučním závodě držet krok s pohlavními organismy (viz Dawkins a Krebs, 1979).

Sečteno a podtrženo, prostředí asociovaná se starobyle nepohlavními skupinami se mohou svými charakteristikami třeba i výrazně lišit – jedná se o habitaty tak různorodé, jako dočasné vodní plochy, dna vodních nádrží, či hluboké vrstvy půd. V porovnání s prostředími, která obývají pohlavní příbuzní starobyle nepohlavních skupin, jsou však bioticky i abioticky homogennější. Tento rozdíl je přitom i na malém vzorku (8, ale efektivně 6 srovnávaných párů) statisticky signifikantní. Výsledky naší srovnávací studie tudíž podporují, i když samozřejmě nepotvrzují, teorie, podle kterých přináší pohlavnost výhody v celkově různorodých a proměnlivých prostředích, zatímco nepohlavní rozmnožování převažuje ve stabilních a homogenních habitatech. Taková jsou i očekávání teorie zamrzlé plasticity.

Nejdůležitějším bodem celé studie je však poznání, že při vyhodnocování výsledné heterogenity prostředí za účelem testování hypotetických výhod (ne)pohlavního rozmnožování musíme brát v potaz vlastnosti samotných organismů. Důležitá totiž není *objektivní* heterogenita obývaných prostředí, ale heterogenita *subjektivní*, tj. charakter a intenzita selekčních tlaků, které ve výsledku na studované evoluční linie skutečně působí. Mezi tyto vlastnosti náleží především adaptace konkrétních druhů – například výše uvedená schopnost přecházet za nepříznivých podmínek do odolných přetrvávajících stádií. Neméně důležité ale mohou být také inherentní vlastnosti evolučních linií – především řádová velikost a generační doby jejich příslušníků.

Rozdíly ve velikosti a generační době patrně mohou za určitých okolností hrát roli i v našich měřítkách. Bylo například pozorováno, že červci druhu *Nuculaspis californica*, tj. krátkověcí fytoparazité, jsou lépe přizpůsobení starším stromům douglasky tisolisté (*Pseudotsuga menziesii*) než mladším (Edmunds & Alstad, 1978). Pokud ale mezi sebou srovnáváme pouze eukaryotické organismy, nebo dokonce jen jejich mnohobuněčné zástupce, rozdíly ve velikosti či generační době obvykle nejsou radikální a většinou je patrně zastiňují jiné faktory. V opačném případě bychom ostatně pozorovali jasnou závislost mezi velikostí či délkou generační doby a zastoupením pohlavních druhů či frekvencí pohlavního procesu.

Řádově větší rozdíly ve velikosti a generační době mezi typickými eukaryoty a *prokaryoty* (viz např. Carlile, 1982) by nicméně mohly představovat ultimátní vysvětlení, proč mezi eukaryoty pohlavní rozmnožování dominuje. Převážně drobná a krátkověká prokaryota během svého života nenarazí na tolik různých ostrůvků prostředí ani nezažijí příliš zásadních výkyvů podmínek. Řádově větší eukaryota s delšími generačními dobami však (s výjimkou starobyle nepohlavních skupin obývajících výrazně homogenní habitaty) žijí v *subjektivně* daleko heterogennějším prostředí, kde může pohlavnost přinášet zásadní výhody. Pokud se tedy heterogenita nemění v závislosti na škále relativně, ale spíše absolutně, přináší pohlavnost výhody až na větších časoprostorových škálách a nelze dokonce vyloučit, že dlouhodobé udržování vysokého genetického polymorfismu a elastické reakce na selekční tlaky prostředí spojené s pohlavností představovaly nezbytnou podmínku vzniku větších evolučně životaschopných organismů s delšími generačními dobami. Právě tento přechod na vyšší časové a prostorové škály spojený s ustanovením pohlavního rozmnožování přitom mohl, jak uvidíme dále a budeme diskutovat závěru (viz sekce 5), odstartovat celou řadu makroevolučních trendů a v důsledku toho stvořit pozemskou biosféru, jak ji známe dnes.

4 MAKROEVOLUČNÍ IMPLIKACE TEORIE ZAMRZLÉ PLASTICITY

Makroevoluční implikace teorie zamrzlé plasticity, které můžeme shrnout v rámci širší teorie zamrzlé evoluce[1], jsme přezkoumali v sérii teoretických studií. Výsledkem jsou tři odborné články pojednávající o různých aspektech zkoumaného konceptu. Na dalších stránkách postupně představím hlavní zjištění, kterých jsme se spoluautorem dobrali, jejich souvislosti s dalšími publikovanými evolučně-biologickými a teoreticko-biologickými koncepty, specifické předpovědi teorie zamrzlé evoluce a jejich doklady.

Tři následující oddíly přibližně odpovídají jednotlivým článkům, jež jsou přiložené na konci práce ve formě přílohy. Některá témata, která v článcích představujeme z různých úhlů opakovaně, jsem však z důvodu větší přehlednosti shrnul s příslušnými citacemi pouze na jednom místě. Nejprve se budeme věnovat fenoménu „makroevolučního zamrzání" jakožto prvku evoluce evolvability, a to tak, jak jsme toto téma pokryli v článku „*Macroevolutionary Freezing and the Janusian Nature of Evolvability: Is the Evolution (of Profound Biological Novelty) Going to End?*" (Toman & Flegr, 2018a, příloha 2). Následně si představíme proces třídění z hlediska stability, jeho charakteristické rysy, vztah k přirozenému výběru a zejména makroevoluční implikace včetně efektivní nevratnosti makroevolučního zamrzání. Tematicky bude tato kapitola odpovídat článku „*Stability-based sorting: The forgotten process behind (not only) biological evolution*" (Toman & Flegr, 2017c, příloha 3). Nakonec se dotkneme hlavních makroevolučních důsledků makroevolučního zamrzání, mezi které můžeme zařadit mimo jiné zvyšování hierarchické komplexity organismů a jeho doprovodné fenomény, nebo zásadní odlišnost prokaryotické a eukaryotické evoluce. Tyto myšlenky jsme představili v článku „*A Virtue Made of Necessity: Is the Increasing Hierarchical Complexity of Sexual Clades an Inevitable Outcome of Their Declining (Macro)evolutionary Potential?*" (Toman & Flegr, 2018b, příloha 4).

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[1] Terminologická poznámka. Vztah mezi teorií zamrzlé plasticity a teorií zamrzlé evoluce je především z historických důvodů poněkud matoucí. Jak vztah obou konceptů chápu já a jak detailněji vyložím v podkapitole 4.1.1, teorie zamrzlé evoluce částečně vychází z mikroevoluční teorie zamrzlé plasticity a představuje její makroevoluční rozšíření. Zároveň ale jde o širší koncept zastřešující i dříve formulovanou teorii zamrzlé plasticity. Kvůli přehlednosti (název práce koneckonců zní *Makroevoluční a ekologické implikace teorie zamrzlé plasticity*) a také kvůli tomu, že i mikroevoluční koncept sám o sobě vykazuje široké pole souvislostí, však v následujícím textu zachovám jak termín teorie zamrzlé evoluce, tak termín teorie zamrzlé plasticity. Co se týče autora obou konceptů, ten ve svých ranějších dílech mluvil pouze o teorii zamrzlé plasticity a jejích makroevolučních implikacích (Flegr 2006, 2008, 2010, 2013). Později argumentoval, že původní teorie zamrzlé plasticity vlastně představuje konkrétní mikroevoluční model v rámci širšího, makroevolučního, konceptu teorie zamrzlé evoluce (viz např. Flegr 2015, str. 275-278, 283-286). Nejnověji potom, ve své chystané revizi anglického vydání knihy *Zamrzlá evoluce* (Flegr, osobní sdělení), chápe oba koncepty jako více méně nezávislé evoluční teorie spojené klíčovou rolí třídění z hlediska stability (viz kapitola 4.2 a příloha 3). Teorie zamrzlé plasticity je podle něj sice důležitým komponentem teorie zamrzlé evoluce, k základnímu předpokladu teorie zamrzlé evoluce, makroevolučnímu zamrzání, však může docházet i v důsledku jiných procesů než jen těch předpovídaných teorií zamrzlé plasticity (viz podkapitola 4.1.1 a přílohy 2 a 4).

Následující text nemá, stejně jako předchozí sekce, ambice stát se vyčerpávající analýzou. Daleko spíše se jedná o pomocnou nit, která čtenáři představí hlavní body našeho teoretického bádání a jejich souvislosti, přičemž detaily zůstanou k dohledání v přiložených publikacích. Nejširší diskusi našich objevů, a to včetně souvislostí ekologických implikací teorie zamrzlé plasticity s těmi makroevolučními, potom provedeme v závěru práce (viz sekce 5, str. 48-50).

4.1 TEORIE ZAMRZLÉ EVOLUCE JAKO PRVEK EVOLUCE EVOLVABILITY

4.1.1 Makroevoluční zamrzání a teorie zamrzlé evoluce

V druhé sekci práce jsme viděli, že podle teorie zamrzlé plasticity se v průběhu existence druhů postupně hromadí polymorfní alely (Flegr, 2006, 2008, 2010, 2013, 2015). Jedná se zejména o genové varianty vykazující frekvenčně závislý vliv na zdatnost a alely, které jsou s nimi spojené v síti pleiotropních a epistatických interakcí. Vzhledem k tomu, že se do této sítě genových vazeb zachytí také prakticky všechny nově vzniklé alely, nemůže za normálních okolností docházet k efektivní fixaci či eliminaci alel působením usměrněné selekce, a tudíž ani graduálnímu přizpůsobování organismů novým podmínkám za hranice již přítomného genetického polymorfismu. Jediná cesta, jak se může druh vrátit do stavu, kdy bude schopný plasticky odpovídat na tlaky přirozeného výběru, začíná nevýběrovým zmenšením populace spojeným například s peripatrickou speciací. Aby došlo k evolučnímu rozmrznutí, musí následně populace dlouhodobě přežívat v malém počtu jedinců, což vede k vymizení veškerého polymorfismu, a nakonec skokově zvýšit své počty, protože jen ve velké populaci může začít efektivně operovat přirozený výběr.

Zásadním problémem podle teorie zamrzlé plasticity však je, že různé alely rozmrzají s různou obtížností (Flegr, 2006, 2008, 2010, 2013, 2015). Některé polymorfní alely mohou ke své fixaci nebo eliminaci vyžadovat nerealisticky výrazné zmenšení populace, nebo nerealisticky dlouhé přežívání v malém počtu jedinců. Příliš malé populace nemusí být životaschopné. Dokonce ani větší populace ale nemají z dlouhodobého hlediska vyhráno. Při dlouhém přežívání v malém počtu jedinců se totiž vlivem snížené účinnosti výběru nedokáží efektivně přizpůsobovat podmínkám prostředí, nemluvě o hromadění škodlivých mutací působením genetického driftu a efektech inbrední deprese (viz např. Charlesworth & Willis, 2009; Flather et al., 2011). Drtivá většina populací tedy vymře, nebo zvýší své počty dřív, než úplně ztratí veškerý polymorfismus ve všech genech. Nezáleží přitom, jak jsou k rozmrzání odolné nevratně polymorfní alely v absolutním měřítku vzácné. Jakmile se jednou taková alela objeví, proces třídění z hlediska stability, který si ve větším detailu představíme v kapitole 4.2, zajistí, že z genofondu evoluční linie pohlavních organismů už nevymizí. V průběhu existence dané evoluční linie se proto budou podobné alely postupně hromadit.

Podobná pravidla platí i pro celé organismální znaky kódované mnoha různými alelami. Některé, například takové, které kóduje pouze jeden, nebo několik málo genů, patrně mohou podléhat evoluci dokonce i v elastické fázi existence druhu (jak jsme viděli v sekci 2). Dalším ke zplastičtění stačí ztráta genetického polymorfismu v několika málo genech. Občas se ale vyskytnou znaky, které by ke svému zplastičtění vyžadovaly kompletní ztrátu polymorfismu v tolika různých genech, že k tomu za realistických podmínek nemůže nikdy dojít. Podobně jako nevratně polymorfní alely, také tyto makroevolučně zamrzlé znaky v průběhu existence evoluční linie pouze přibývají.

Jak jsme navíc rozvedli v článcích (Toman & Flegr, 2018a, b, přílohy 2, 4), výše uvedený proces patrně není jediný, prostřednictvím kterého může v makroevolučním měřítku docházet k efektivně nevratnému makroevolučnímu zamrzání. Vlivem třídění z hlediska stability se totiž v průběhu existence evolučních linií hromadí všechny geny, jejich funkčně provázané skupiny (moduly) a celé znaky neodpovídající na tlaky přirozeného výběru. Jedná se například o geny, jejichž sebemenší změna by výrazně snížila životaschopnost nebo plodnost organismu, geny, které jsou ve svých účincích složitě pleiotropicky spojené s jinými, nebo geny, které jsou ve svých účincích mnohonásobně zálohované, takže by ke změně jimi kódovaného znaku bylo třeba simultánní změny na mnoha různých místech genomu.

Procesům, které snižují odpověď určitých genů, modulů a znaků na selekci, se věnoval například Rupert Riedl (Riedl, 1977, 1978; Wagner & Laubichler, 2004; Budd, 2006; Schoch, 2010). Podle tohoto autora se procesy a elementy spojené s větším počtem důležitějších znaků funkcí, tj. prvky pro fungování organismu důležitější a pravděpodobně také fylogeneticky starší, v průběhu času stávají čím dál méně proměnlivými. Důvodem je, že jakákoli změna těchto procesů přináší velké riziko nefunkčnosti organismu, které stoupá s tím, jak se okolo těchto procesů a elementů v průběhu evoluce vyvíjejí nové znaky. Toto rostoucí zatížení všech organismálních znaků nazývá Riedl „evoluční zátěží“ (*burden*). William C. Wimsatt (Schank & Wimsatt, 1986; Wimsatt & Schank, 2004; Wimsatt, 2013) v podobném duchu mluví o „vývojovém uzamknutí“ (*generative entrenchment*), které v zásadě odpovídá Riedlově evoluční zátěži, ale je odvozené od načasování v individuálním vývoji a potažmo funkční integrace v systému. Zvyšující se uzamknutí zvyšuje riziko, že změna elementu bude škodlivá a snižuje pravděpodobnost, že zvýší zdatnost svého nositele. K adaptivní evoluci tudíž může efektivně docházet jen na nejméně uzamknutých elementech a, podobně jako u Riedlovy evoluční zátěže, také ve Wimsattově konceptu každé rozšíření vývoje zvyšuje uzamknutí předchozích elementů a procesů.

Jak jsme shrnuli ve větším detailu jinde (Toman a Flegr, 2018b, příloha 4), stejného fenoménu si v minulosti povšimlo i několik dalších autorů. Geny a genové moduly, které se uplatňují brzy v individuální vývoji, které přímo či nepřímo ovlivňují mnoho různých znaků, procesů a funkcí, které spoluvytvářejí znaky a procesy pro fungování organismu důležitější a které spoluvytvářejí znaky a procesy fylogeneticky starší, jež v tomto ohledu porůznu vyzdvihují různí autoři, by si však měly v zásadě odpovídat. Vyplývá to ostatně už z von Baerových vývojových zákonů (viz Schoch, 2010). Typickým příkladem podobných vysoce konzervovaných elementů genetické architektury organismů jsou například geny zajišťující základní buněčný metabolismus, mitózu, meiózu, polarizaci tělní osy na počátku zárodečného vývoje, rozčlenění zárodku na diferenciálně se vyvíjející regiony, nebo organogenezi (Riedl, 1977, 1978; Schank & Wimsatt, 1986; Kirschner & Gerhart, 1998, 2005; Galis &

Metz, 2001; Wimsatt & Schank, 2004; Davidson & Erwin, 2006; Erwin, 2007; Gerhart & Kirschner, 2007; Wimsatt, 2013, 2015; Hu et al., 2017). Pozdější výzkumy sice ukázaly, že nejranější stádia vývoje zárodku mohou podléhat poměrně dynamické evoluci ovlivněné mimo jiné rodičovskými vlivy nebo mírou rodičovské investice do zásobních látek ve vajíčku, o něco pozdější, tzv. fylotypové, stadium však výše uvedeným kritériím odpovídá v plné míře (Galis & Metz, 2001; Irie & Kuratani, 2014; Hu et al., 2017).

Proces hromadění dále neproměnlivých prvků genetické architektury může při makroevolučním zamrzání hrát dokonce důležitější roli než přibývání nevratně polymorfních alel. Není totiž limitován na mikroevoluční úroveň dynamických výkyvů ve frekvencích alel u pohlavních kladů, ale uplatňuje se na všech úrovních organismální organizace (Toman & Flegr, 2018a, b, přílohy 2, 4). Nelze ovšem vyloučit, že spolu oba výše zmíněné procesy efektivně nevratného makroevolučního zamrzání netriviálně souvisí a mohou se dokonce vzájemně posilovat. Bylo například navrženo, že nevratně polymorfní alely vytvářejí jakási dlouhodobě stabilní „krystalizační jádra“, okolo kterých se na základě funkčně propojených genů mohou ustanovovat dále neproměnlivé prvky genetické architektury organismů (Toman & Flegr, 2018a, b, přílohy 2, 4). Nejednalo by se ostatně o nic bezprecedentního, neboť existují srovnatelné modely vzniku modularity na úrovni genomu (viz např. Pepper, 2000; Pigliucci, 2008).

Oba výše zmíněné procesy, tj. hromadění nevratně polymorfních alel i dále neproměnlivých prvků genetické architektury organismů, přispívají k postupnému makroevolučnímu zamrzání celých evolučních linií. Právě myšlenka, že může v průběhu času docházet k hromadění takovýchto ireverzibilně zamrzlých elementů a potažmo snižování proměnlivosti celých evolučních linií, stojí v základu **teorie zamrzlé evoluce** (Flegr, 2008, 2010, 2013, 2015). Tento koncept je tedy částečně makroevoluční implikací teorie zamrzlé plasticity a částečně tuto teorii v obecnějším rámci zastřešuje. Pokud by se alely, geny, genové moduly a znaky dále nepodléhající působení přirozeného výběru v průběhu existence evolučních linií jednoduše hromadily, muselo by postupně docházet ke snižování evoluční proměnlivosti jejich příslušníků. Na počátku existence každé evoluční linie pohlavních organismů by většina znaků zůstávala proměnlivá hodně, pár málo a prakticky žádné vůbec. Nově odštěpené druhy, potenciální zakladatelé nových taxonů, by se mohly odlišovat v celé řadě třeba i velmi důležitých znaků a disparita i diverzita celého kladu by narůstaly. Vlivem přibývání dále neproměnlivých alel, genů, modulů a znaků by se však nově odštěpené druhy mohly proměňovat jen ve stále se zmenšujícím okruhu stále odvozenějších a méně důležitých znaků. Vzhledem k tomu, že v rámci kladu občas dojdou k vymření i vyšší fenotypově výrazně odlišné taxony, jeho disparita by se měla začít časem snižovat, až by z něj nakonec zůstala pouze jedna fenotypově uniformní větev schopná už jen vytváření velmi omezených variací na svůj postupně zamrzající motiv.

K podobnému závěru, stejně jako nutnosti postulovat specifické evoluční procesy schopné překonat snižování evoluční proměnlivosti, historicky dospělo několik autorů (viz Riedl, 1977, 1978; Arthur, 1982, 1984; Schank & Wimsatt, 1986; Wagner & Laubichler, 2004; Wimsatt & Schank, 2004; Budd, 2006; Schoch, 2010; Shcherbakov, 2012, 2013; Wimsatt, 2013), jejichž koncepty ve větším detailu rozebíráme v našich článcích (Toman & Flegr, 2018a, b, přílohy 2, 4). Podle novějších názorů se však zdá, že proces nemusí vést k tak jednoznačným důsledkům. V průběhu času se totiž alely, geny, moduly a znaky odolné k působení selekce jednoduše nehromadí bez ohledu na to, jak ovlivňují další evoluční proměnlivost kladů, nýbrž dochází k přinejmenším částečně adaptivní evoluci genetické architektury organismů. Tato mapa vztahů mezi genotypem a fenotypem následně kanalizuje a do jisté míry optimalizuje další evoluční reakce organismů. V průběhu času tudíž nedochází k prostému snižování evoluční proměnlivosti organismů, ale spíše modulaci tohoto aspektu jejich evoluce v procesu evoluce evolvability (Schoch, 2010; Brigandt, 2015).

4.1.2 Evoluce evolvability

Evolvabilita je klíčovým evolučně-biologickým konceptem s dlouhou historií zkoumání a košatým souborem různých chápání (detailně jsme toto téma rozebrali v Toman & Flegr, 2018a, příloha 2). Na tomto místě můžeme alespoň shrnout, že rozhodně nepředstavuje jednoduše uchopitelný termín. Odborně si evolvabilitu, tj. schopnost podléhat adaptivní evoluci, můžeme definovat například jako „kapacitu organismu vyvářet dědičnou selektovatelnou fenotypovou variaci“ (Kirschner & Gerhart, 1998). Další možné definice uvádíme v již zmíněném článku (Toman & Flegr, 2018a, příloha 2), vesměs se ale jedná o variace na stejné téma. Důležitější je, že evolvabilitu můžeme chápat nejméně na dvou (Wagner & Altenberg, 1996; Wagner, 2005), ale spíše na třech (Pigliucci, 2008) různých úrovních.

Na nejzákladnější úrovni lze evolvabilitu vykládat jako pouhý epifenomén množství různých genových variant a jejich interakcí, respektive množství přítomné genetické variace a kovariace na úrovni genofondu populace. V takovémto pojetí se evolvabilita v zásadě rovná schopnosti odpovídat na působení přirozeného výběru, což ovlivňuje zejména různorodost a dědivost znaků. Takto tradičně chápe evolvabilitu moderní evoluční syntéza, která vesměs neuvažuje o tom, že by vznik nových variant na úrovni genotypu či fenotypu mohl být systematicky vychýlený (viz např. Hansen, 2006; Sniegowski & Murphy, 2006; Pigliucci, 2008).

Evolvabilitu ale můžeme chápat i jako uspořádání vnitřních omezení, například vývojových nebo evolučních *constraints* (zábran či omezení), které určuje, jaká adaptivní fenotypová řešení na úrovni druhu jsou vůbec dosažitelná a jaká ne. V neposlední řadě potom můžeme evolvabilitu vykládat i jako schopnost tato evoluční omezení překonávat a vytvářet zásadní evoluční novinky (viz např. Wagner & Altenberg, 1996; Wagner, 2005; Pigliucci, 2008). V kontrastu k tradičnímu přístupu moderní evoluční syntézy tak můžeme evolvabilitu chápat jako soubor procesů, které na mnoha různých úrovních kanalizují, jak se budou genetické změny projevovat na úrovni fenotypu – od toho, jaké části genomu budou přednostně mutovat a jaké typy mutací zde budou vznikat, přes diferenciální a často dokonce epigenetickou regulaci jednotlivých genů nebo interakce vyvíjejících se buněk, tkání či orgánů až po reakce těchto procesů na změny vnějších podmínek prostřednictvím vývojové plasticity (viz např. Gerhart & Kirschner, 1997; Kirschner & Gerhart, 1998; Hansen, 2003, 2006, 2011, 2016; Rutherford, 2003; West-Eberhard, 2003; Turner, 2007; Pavlicev & Hansen, 2011; Raff, 2012; Flegr, 2015, str. 38-

91). Takto pojatá evolvabilita přitom může sama podléhat evoluci, což je jedním ze základních teoretických kamenů konceptu „rozšířené evoluční syntézy“ (viz Toman & Flegr, 2018a, příloha 2).

Procesy kanalizující vznik fenotypové variace obvykle nazýváme genetickou architekturou organismů, nebo, ještě lépe, genotypovo-fenotypovou mapou. Důvod je ten, že mají mnoho různých úrovní, z nichž některé ovlivňují i jiné typy paměti než genetická – například epigenetická, strukturní, nebo kulturní (Markoš, 2002; Kurismaa, 2018). Genotypovo-fenotypová mapa, stejně jako evolvabilita samotná, v čase prokazatelně podléhají evoluci (Wagner & Altenberg, 1996; Kirschner & Gerhart, 1998; Gerhart & Kirschner, 2007; Pigliucci, 2008; Hansen, 2016). Jedná se o donedávna často opomíjený proces, který zásadně ovlivňuje makroevoluci zvláště mnohobuněčných organismů se složitým individuálním vývojem. Na evoluci evolvability má vliv celá řada procesů, které shrnujeme v našem článku (viz Toman & Flegr, 2018a, příloha 2). V jejím průběhu opravdu může docházet k hromadění vývojových a evolučních *constraints*. Podle řady moderních konceptů však v průběhu evoluce evolvability nedochází k jednosměrnému snižování evolvability (jak zastávaly některé starší koncepty, viz předchozí podkapitola), nýbrž její optimalizaci.

Podle řady autorů (Riedl, 1977, 1978; Wagner & Altenberg, 1996; Kirschner & Gerhart, 1998; Turney, 1999; Pigliucci, 2008; Davies, 2014; Hansen, 2016) se genotypovo-fenotypová mapa vyvíjí tak, aby co nejpřesněji odrážela strukturu fenotypu a selekčních vlivů okolí. Výsledkem je snížení rizika, že náhodná mutace bude škodlivá, zvýšení šance, že bude prospěšná a snížení počtu mutací nutných k vytvoření adaptivního fenotypu. Nelze dokonce vyloučit, že genotypovo-fenotypová mapa, respektive s ní spojená vývojová i environmentální robustnost a *constraints*, je zcela nezbytná k vytvoření jakéhokoli komplexního fenotypu a jeho adaptivní evoluci (Riedl, 1977, 1978; Kirschner & Gerhart, 1998; Wagner & Laubichler, 2004; Wagner, 2005; Budd, 2006; Schoch, 2010; Davies, 2014; Sharov, 2014; Brigandt, 2015). Plně se tato myšlenka rozvinula například v rámci konceptu „usnadněné variace“ (*faciliated variation*) (Kirschner & Gerhart, 2005; Gerhart & Kirschner, 2007;), podle kterého je genotypovo-fenotypová mapa a potažmo charakter evolučních reakcí, prostřednictvím kterých mohou organismy odpovídat na selekční tlaky svého prostředí, optimalizována na základě dřívější evoluční zkušenosti dané linie. Veškerá *constraints* podle tohoto konceptu slouží pouze k výraznějším *deconstraints* na vyšší úrovni. Stejný proces ovšem výrazně omezuje vznik výrazných evolučních novinek. Akumulace *constraints* kanalizuje hloubku a charakter dalších možných evolučních reakcí linií a dalo by se tak říct, že optimalizuje jejich mikroevoluční vyhlídky na úkor makroevolučních. Evolvabilita na nižší úrovni (ve smyslu vytváření adaptivních fenotypů a schopnosti rychle a operativně reagovat na momentální změny podmínek) se zvyšuje na úkor evolvability na vyšší úrovni (ve smyslu makroevolučního potenciálu, respektive vytváření zásadních evolučních inovací) (Wagner & Altenberg, 1996; Kirschner & Gerhart, 1998; Pigliucci, 2008; Sharov, 2014).

Pro teorii zamrzlé evoluce z podobných úvah plyne důležitý poznatek, že v průběhu evoluce evolvability nemusí dlouhodobě docházet k jejímu obecnému snižování, ale pouze poklesu jednoho jejího typu, který se vyznačuje pravděpodobností vzniku zásadních evolučních novinek a kterému v našich článcích říkáme makroevoluční potenciál (viz Toman & Flegr, 2018a, b, přílohy 2, 4). Tento rozdíl mezi různými úrovněmi evolvability se patrně odráží v tzv. paradoxu evolvability, tj. faktu, že i přes jasné důkazy konzervativnosti genetické architektury organismů (Kirschner & Gerhart, 1998; Davidson & Erwin, 2006) nenaznačují hodnoty dědivosti, jiných „nižších“ kvantitativních metrik evolvability, ani mezikladové diverzity zásadním evolučním omezením (Erwin, 2007; Hansen, 2016). Důvod je patrně ten, že výraznější limitace vyvstávají až na vyšších taxonomických úrovních v makroevoluci (Davidson & Erwin, 2006; Erwin, 2007). Rubovou stranou téhož fenoménu je potom pozorování, že mezidruhové a mezikladové rozdíly vyvstávají hlavně ze změn regulačních elementů, zatímco vnitroduhové rozdíly ze změn protein-kódujících sekvencí genů (Stern & Orgogozo, 2008, 2009).

Jak dále shrnujeme v našem článku (viz Toman & Flegr, 2018a, příloha 2), evoluce evolvability, prostřednictvím které se evoluční linie na základě své evoluční zkušenosti *de facto* učí číst charakter svého prostředí, vykazuje nápadnou podobnost individuálnímu učení. Byť k tomuto procesu dochází na základě diferenciálního třídění dílčích evolučních linií, ve výsledku se stejně jako u individuálního učení zvyšuje efektivita evolučních reakcí na změny prostředí (Davies, 2014; Watson et al., 2014, 2016; Lindholm, 2015; Watson & Szathmary, 2016). S trochou nadsázky můžeme označit evoluci za proces, při kterém se biosféra prostřednictvím komplexní mnohoúrovňové evoluce evolvability učí, poznává a buduje okolní svět i samu sebe. Jak argumentujeme dále (viz Toman & Flegr, 2018a, příloha 2), procesy podobného typu můžeme nejefektivněji popsat biosémiotickým přístupem (Markoš & Faltýnek, 2011; Markoš & Cvrčková, 2013; Markoš, 2014, 2015; Markoš & Das, 2016). Sémioze představuje schopnost interpretace na základě paměti, historie, zkušenosti a kontextu (Markoš, 2014). Evoluční reakce linií proto můžeme interpretovat jako výklad podmínek prostředí a jejich změn na základě předchozí zkušenosti s cílem vyprodukovat co nejvýhodnější adaptaci. Celá evoluce evolvability potom v takovémto rozvrhu představuje jeden velký biosémiotický akt a exemplární příklad biosémiotického procesu. S tím souhlasí například fenomény rychlé re-evoluce zdánlivě ztracených, ale momentálně pouze neexprimovaných znaků (např. křídel některých strašilek, Whiting et al., 2003, pohlavnosti roztočů ze skupiny Crotoniidae, Domes et al., 2007a, nebo vajíček jinak živorodých hroznýšů rodu *Eryx*, Lynch & Wagner, 2010), nebo tzv. paralelních fenotypových variací na základě hluboce sdílených vývojových procesů například u rostlin (Vavilov, 1922). Evolvabilitu nicméně ovlivňuje celá řada dílčích biosémiotických procesů (interpretace momentálních podmínek na základě různých typů paměti, individuální učení, transgenerační přenos zkušeností, kulturní evoluce apod.) a to samé platí i naopak, což prozrazuje velmi intimní vztah těchto dvou fenoménů (Shcherbakov, 2012; Hoffmeyer & Stjernfelt, 2016).

Zatím není jasné, zda a do jaké míry představuje evoluce evolvability adaptivní proces, výsledek náhodných dějů, nebo epifenomén jiných evolučních procesů (viz Kirschner & Gerhart, 1998; de Visser et al., 2003; Pigliucci, 2008; Hansen, 2011; Pavlicev & Wagner, 2012; Hansen, 2016). V každém případě ale hraje v evoluci evolvability důležitou roli třídění evolučních linií. Linie s optimální evolvabilitou se vyznačují efektivními reakcemi na změny prostředí, což vede jednak ke snížení pravděpodobnosti extinkce jejich příslušníků, ale rovněž ke zvýšení pravděpodobnosti odštěpení dceřiných linií a obsazení nových ekologických nik. Dlouhodobě tak mohly převážit procesem třídění z hlediska stability, druhového výběru, nebo jiné formy selekce kladů (Waddington, 1957; Alberch, 1991; Dawkins, 1996; Gerhart & Kirschner, 1997; Pigliucci, 2008; Hansen, 2011). Z hlediska teorie zamrzlé evoluce je však nejpodstatnější, že mezi hlavní procesy evoluce evolvability patří třídění z hlediska stability (viz kapitola 4.2), respektive hromadění těch prvků genetické architektury, které odpovídají na selekci jen málo ochotně nebo vůbec (viz Toman & Flegr, 2018a, příloha 2). Tento proces navíc zřejmě dále umocňuje tlak na robustnost individuálního vývoje a potažmo nižší úrovně evolvability (viz Kirschner & Gerhart, 1998, 2005; Wagner, 2005; Gerhart & Kirschner, 2007; Wimsatt, 2013).

I pod vlivem makroevolučního zamrzání však postupně převažují genetické architektury, které zajišťují optimální evolvabilitu. Zdá se, že nejběžnějším způsobem, jak podobných výsledků pozemské evoluční linie dosahují, je uspořádáním genotypovo-fenotypové mapy do dále jen málo proměnlivých kvazinezávislých modulů (Simon, 1962; Lewontin, 1978; Schank & Wimsatt, 1986; Wagner, 1995a; Wagner & Altenberg, 1996; Bonner, 1998; Kirschner & Gerhart, 1998; McShea, 2000; Schlosser, 2002, 2004; Schlosser & Wagner, 2004; Wimsatt & Schank, 2004; Wagner et al., 2005; Callebaut & Rasskin-Gutman, 2005; Davies, 2014; Melo et al., 2016). Odlišitelné znaky za takové situace kódují přirozené skupiny genů silně integrované svými pleiotropními efekty a odlišné od jiných takových skupin (Simon, 1962; Wagner & Altenberg, 1996; Bonner, 1998; McShea, 2000; Schlosser, 2002; Schlosser & Wagner, 2004; Callebaut & Rasskin-Gutman, 2005). Podobná meta-adaptace patrně vede jak k optimalizaci evolvability, tak obnovení makroevolučního potenciálu (viz kapitola 4.3) na vyšší úrovni organizace prostřednictvím nezávislé regulace, kopírování, kombinování, nasazování či odstraňování modulů (Carroll, 2005; Hoekstra & Coyne, 2007; Stern & Orgogozo, 2008, 2009; Marshall & Valentine, 2010; Hu et al., 2017). Toto modulární uspořádání se následně odráží i na vyšších úrovních organismální organizace, viz např. Carroll (2001), nebo kapitola 4.3.

Jak však uvidíme v kapitole 4.2, problémem je, že k třídění z hlediska stability dochází na všech úrovních. Moduly a jejich skupiny se liší ve své proměnlivosti úplně stejně, jako jednotlivé geny a jejich skupiny na úrovni nižší. Obnovení makroevolučního potenciálu únikem na úroveň modulárního uspořádání je tak pouze dočasným řešením, protože i zde se záhy začnou hromadit makroevolučně zamrzlé elementy genetické architektury neodpovídající na tlaky usměrněné selekce. Makroevoluční zamrzání spojené s úbytkem makroevolučního potenciálu tak bude probíhat i na vyšší úrovni, což může vést k další komplikaci genetické architektury. (Ne)vyhnutelnost tohoto zamrzání, navržené cesty, jak jej mohou evoluční linie obejít, ale také řadu zajímavých makroevolučních patrností, které z něj vyplývají, rozebereme v kapitole 4.3.

4.1.3 Doklady snižování makroevolučního potenciálu

Pokud v průběhu makroevoluce opravdu klesá makroevoluční potenciál pohlavních evolučních linií, měl by se tento proces vyznačovat několika specifickými trendy. Zaprvé bychom měli očekávat, že se disparita těchto skupin bude po úvodním nárůstu spojeném se zvýšením druhové bohatosti spíše snižovat. Dále bychom mohli čekat, že se bude snižovat samotný potenciál těchto linií pro vytváření velkých evolučních novinek, jejich proměnlivost a za určitých okolností možná i rychlost evoluce či speciační rychlost (byť, jak jsme viděli v předchozí podkapitole, evolvabilita na nižších úrovních svého chápání klesat nemusí). V neposlední řadě by potom u makroevolučně zamrzajících evolučních linií měla klesat i vnitrodruhová proměnlivost, nebo lépe její měřitelný projev, vnitrodruhová disparita.

Všechny tyto trendy byly v průběhu historie v různých kontextech zkoumány (Riedl, 1977, 1978; Kirschner & Gerhart, 1998; Wagner & Laubichler, 2004; Budd, 2006; Schoch, 2010; Wimsatt, 2013) a nezřídka extenzivně zdokumentovány (viz např. Rosa, 1899; Erwin et al., 1987; Gould, 1989; DiMichele & Bateman, 1996; McShea, 1996; Foote, 1997; Eble, 1998, 1999; Canning et al., 2004; Rasnicyn, 2005; Budd, 2006; Glenner & Hebsgaard, 2006; Erwin, 2007; Webster, 2007; Hughes et al., 2013; Lee et al., 2013). Mezidruhová disparita, zdá se, v souladu s očekáváními zamrzlé evoluce nejčastěji na počátku existence evolučních linií explozivně narůstá (Yochelson, 1979; Knoll et al., 1984; Saunders & Swan, 1984; Swan & Saunders, 1987; Gould, 1989; Hughes, 1991; Briggs et al., 1992; Carlson, 1992; Foote, 1992, 1994, 1995, 1996, 1997, 1999; Foote & Gould, 1992; Lee, 1992; Erwin, 1994; Wills et al., 1994; Anstey & Pachut, 1995; McGhee, 1995; Wagner, 1995b, 1997; Fortey et al., 1996; Jernvall et al., 1996; Miller & Foote, 1996; Saunders & Work, 1996, 1997; Sims, 1996, 2000; Lupia, 1999; Thomas et al., 2000), v některých případech s „čekací dobou“ několika milionů let (Sepkoski, 1979; Tiffney, 1981; Knoll et al., 1984; Marx & Fordyce, 2015). Následně disparita celého kladu nejčastěji dlouhodobě stagnuje či osciluje kolem nejvyšší dosažené hodnoty (Carlson, 1992; Lee, 1992; Wills et al., 1994; McGhee, 1995; Wagner, 1995b; Fortey et al., 1996; Foote, 1997, 1999; Wills, 1998a, b; Lupia, 1999; Smith & Bunje, 1999; Wills & Fortey, 2000; Ciampaglio, 2002, 2004; Labandeira & Eble, 2007; Erwin, 2011). Podobná patrnost odpovídá předpovědím teorie zamrzlé evoluce jen zčásti, určité studie ale nasvědčují i tomu, že u některých kladů docházelo po rychlém dosažení vrcholné disparity už jen k jejímu snižování (Gould, 1989; Foote, 1992, 1993, 1994, 1999; Valentine, 1995; Kirschner & Gerhart, 1998; Lofgren et al., 2003; Hughes, 2007; Marx & Fordyce, 2015; Oyston, et al. 2015; Hopkins, 2017). Podle rozsáhlejších srovnání Goulda et al. (1987), Hughese et al. (2013) a Oystona et al. (2018) je navíc tento průběh charakteristický pro fanerozoické klady mnohobuněčných živočichů, byť různé klady vykazují velmi různorodé průběhy disparity a není vůbec jasné, jaký proces by za statisticky pozorovanými patrnostmi mohl stát. Z uvedeného trendu ale samozřejmě nalezneme i výjimky – několik kladů například vykazuje poměrně komplikovaný průběh vývoje disparity (Foote, 1993; Labandeira & Sepkoski, 1993; Dommergues et al., 1996; Wills, 1998a; Oyston et al., 2015; Stubbs & Benton, 2016).

Pozorované patrnosti ve vývoji mezidruhové disparity mohou mít dvě různá vysvětlení (Erwin, 1993, 2007; Valentine, 1995; Ciampaglio, 2002, 2004; Wagner, 2010). Podle tzv. vývojových (nebo genetických) teorií, mezi které v tomto ohledu spadá i teorie zamrzlé evoluce, stojí za stagnací a snižováním disparity kladů jejich klesající schopnost vytvářet zásadní evoluční novinky vyplývající z jejich vnitřního ustrojení a trendů, v jejichž směru se toto ustrojení mění (tj. z evoluce evolvability). Podle tzv. ekoprostorových teorií stojí za zpomalováním nárůstu disparity, její stagnací, nebo dokonce snižováním ekologické důvody, konkrétně klesající množství volných ekologických nik dostupných pro obsazení. Problémem je, že se obě vysvětlení nemusí vzájemně vylučovat (Valentine et al., 1996; Erwin, 2007; Oyston et al., 2018). I tak bychom ale na základě specifických makroevolučních patrností měli být schopní rozhodnout, který z výše zmíněných procesů hrál v historii života na Zemi důležitější roli.

Spíše vývojovým teoriím nahrává například pozorování, že po hromadných vymíráních, která doprovázela i velká uvolnění ekologických nik, málokdy docházelo k výraznějšímu nárůstu disparity stávajících kladů (Hughes et al., 2013). Stejné závěry podporují také pozorování, že v průběhu existence kladů dochází ke snižování jejich fenotypové proměnlivosti. První čtyřnožci (Tetrapoda) měli například na rozdíl od pozdějších velmi variabilní počet prstů (Coates & Clack, 1990; Clack, 2006). Moderní savci (Mammalia) mají ve srovnání s jinými obratlovci vesměs stabilizovaný počet krčních obratlů (Galis, 1999; Oyston et al., 2018). Podobně konzervovaná je ve srovnání s ranými zástupci vlastní skupiny také stavba hlavy a ústního ústrojí různých dnešních vysokých taxonů členovců (Arthropoda) (Gould, 1989; Wills et al., 1995; Wills & Fortey, 2000). Srovnatelné trendy klesající proměnlivosti můžeme podle Vermeijho (2015) vysledovat rovněž u počtu hrudních článků raně kambrických trilobitů (Trilobita) (Hughes, 1991; Webster, 2007), počtu a pozici plátů raných přisedlých a stélkatých ostnokožců (Guensburg & Sprinkle, 2001, 2009; Deline & Ausich, 2011) či rozložení žilek třetího a vyššího řádu v listové žilnatině raných krytosemenných rostlin (Doyle & Hickey, 1976). Webster a Zelditch (2011) pozorovali nápadně nízkou integraci znaků u kambrických trilobitů. Řadu konkrétních příkladů uvádí také Wills a Fortey (2000) a podle McShea (1996), Wagnera (2000) či Oystona et al. (2018) se snižuje v průběhu evoluce i celková proměnlivost, respektive frekvence vniku nových znaků, mnohobuněčných živočichů. S tím souhlasí pozorování, že disparita kladů klesá zpravidla dlouho před diverzitou, která ještě může po nějaký čas narůstat (Smith, 2007; Vermeij, 2015). Wagner (2018) však uzavírá, že celý fenomén není tak jednoduchý a evoluce evolvability vede spíše k ustanovení těžko proměnlivých modulů sestávajících z korelovaných znaků se souvisejícím vlivem na fenotyp než všeobecnému snižování proměnlivosti.

Vývojová vysvětlení podporuje také asymetrický vznik vyšších taxonů v čase – ať už v rámci všech dvoustraně souměrných mnohobuněčných živočichů (Erwin, 2007; Peterson et al., 2009), nebo dílčích kladů mnohobuněčných živočichů a rostlin (Erwin et al., 1987; DiMichele & Bateman, 1996; Eble, 1999). Stejnému závěru nahrávají rovněž analýzy nasvědčující výrazně zvýšené rychlosti molekulární i fenotypové evoluce v raných fázích existence linií (Ruta et al., 2006; Brusatte et al., 2008, 2014; Slater et al., 2010; Lloyd et al., 2012; Lee et al., 2013, 2014; Close et al., 2015; Marx & Fordyce, 2015), byť i zde nalezneme výjimky (Hopkins & Smith, 2015; Slater, 2015; Cooney et al., 2017).

Zmínit můžeme také další fenomén, který nepřímo podporuje hypotézu o snižování makroevolučního potenciálu, a to tzv. efekt entských žen. Podle Quentala a Marshalla (2013), kteří studovali několik vymřelých a vymírajících savčích kladů, hraje při vymírání klíčovou roli snížení speciační rychlosti. Podobný jev u různých kladů přitom pozorovala i řada dalších autorů (viz např. Van Valen, 1973; Marshall & Hecht, 1978; Gilinsky & Bambach, 1987; Bambach et al., 2004; Rabosky & Lovette, 2008). Vzhledem k tomu, že na základě fosilního materiálu pozorujeme spíše celé rody než druhy, je pravděpodobné, že tito badatelé vlastně zdokumentovali pokles frekvence rozmrzání druhů a s tím spojených přechodů do plastické fáze jejich existence. Právě to bychom mohli očekávat, pokud by přibývalo nevratně polymorfních alel a makroevolučně zamrzlých znaků.

Nepřímým dokladem vývojových teorií je rovněž ústup starších taxonů do okrajových prostředí. V moři, například, vznikají evoluční novinky a potažmo vyšší taxony přednostně na (bioticky i abioticky velmi heterogenních) mělčinách (hlavně tropického pásu) a postupně ustupují do hlubin (Jablonski et al., 1983; Bottjer & Jablonski, 1988; Morris, 1989; Jablonski & Bottjer, 1991; McShea, 1994; Jablonski, 2000, 2005; McKinney & Drake, 2001; Zechman et al., 2010). Podobné patrnosti se ale nejspíše projevují také v evoluci rostlin (DiMichele & Aronson, 1992; Wing & Boucher, 1998; Prestianni et al., 2015; Blomenkemper et al., 2018), nebo obecně, a to častějším vznikem novinek a vyšších taxonů v proměnlivém heterogenním prostředí a ústupu linií se sníženým makroevolučním potenciálem do okrajových podmínek (Jablonski, 1993, 2000; Kiessling et al., 2010; Jansson et al., 2013) (viz také kapitola 3.1).

Posledním, ale velmi důležitým, dokladem nasvědčujícím vývojovým teoriím je postupné snižování vnitrodruhové variability zdokumentované u řady evolučních linií. Důvodem je, že vnitrodruhová fenotypová proměnlivost prokazatelně souvisí s mezidruhovou (Webster, 2018). Obecně bývá tento jev nazýván Rosaovým pravidlem (Rosa, 1899; Omodeo, 1992), a kromě anekdotických dokladů (viz např. Rosa, 1899; Monnet et al., 2012; Frey et al., 2016; Schachat & Gibbs, 2016) mu nasvědčuje dlouhá řada různých studií trilobitů a jejich konkrétních znaků (Jaanusson, 1975; Bergström & Levi-Setti, 1978; McNamara, 1986; Ramsköld, 1986, 1991; Hughes, 1991, 2007; Hughes et al., 1999; Wills & Fortey, 2000; Webster, 2015; Daley & Drage, 2016). Jak jsme detailně shrnuli v článku (Toman a Flegr, 2018a, příloha 2), snižování proporce vnitrodruhově polymorfních znaků v průběhu existence kladu nejsolidněji podpořila kvantitativní Websterova (2007) studie trilobitů. Trend samotný v tomto případě plynul hlavně z rozdílů mezi řády. Ty z nich, které se odvětvily dříve, vykazovaly výrazně větší disparitu v rámci svých druhů. Projevil se ale i v rámci těch řádů, které díky své druhové bohatosti podobnou analýzu umožnily. Podobný trend se podle některých autorů mohl projevit také v evoluci švábů (Blattodea), byť zde výsledky zdaleka nejsou tak přesvědčivé (Vrsansky, 2000; Vrsansky et al., 2009, 2017; Liang et al., 2012; Oruzinsky & Vrsansky, 2017), nebo některých znaků ordovických krinoidů (Foote, 1999; Deline, 2009; Pimiento et al., 2018). Srovnatelné patrnosti známe z evoluce parazitů, kde se Rosaovo pravidlo projevuje jako tendence přecházet od generalismu, přes částečnou hostitelskou specializaci až ke specializaci úplné (Eichler, 1948; Klassen, 1992).

Hypotéze dále nahrává fakt, že vnitrodruhově variabilnější klady mají větší naději na přežití, a to zvláště při hromadných vymíráních (Liow, 2007; Kolbe et al., 2011; Webster, 2018). Byť i zde některá pozorování svědčí spíše proti (Wills & Fortey, 2000; Webster, 2007; Hopkins, 2011), patrně se jedná o důsledek toho, že v těchto případech šlo o průběžná vymírání. Alternativně můžeme spekulovat, zda se z hlediska šance na přežití makroevoluční potenciál, vnitrodruhová variabilita a mezidruhová disparita v historii kladů nevyvíjejí od hodnot z makroevolučního hlediska příliš vysokých, přes optimální až po suboptimální. Tato otázka ale zůstává zcela otevřená.

4.2 TŘÍDĚNÍ Z HLEDISKA STABILITY

4.2.1 Přežití stabilnějších

Přirozený výběr, tj. selekce, nepředstavuje pouze nejdůležitější objev Charlese Darwina (Darwin & Wallace, 1858; Darwin, 1859), ale patrně také moderní evoluční biologie vůbec. Samozřejmě je pravda, že průběh evolučních dějů ovlivňuje celá řada dalších faktorů (viz např. Gould, 2002; Mayr, 2003; Pigliucci & Müller, 2010; Flegr, 2015). Přirozený výběr však nabízí dominantní vysvětlení, jak mohou efektivně vznikat a hromadit se účelné vlastnosti, tj. přizpůsobení, organismů. V tomto ohledu je proto zajímavé, že přirozený výběr představuje pouze jednu konkrétní manifestaci daleko obecnější zákonitosti, která se uplatňuje ve všech systémech s evolucí v širším slova smyslu, tj. pamětí či historií. Ať už se jedná o systémy živých nebo neživých, materiálních nebo nemateriálních entit, vždy platí, že stabilnější, tj. méně proměnlivé a dlouhodobě perzistentnější, nebo častěji vznikající varianty se v jejich rámci budou uchovávat a hromadit, zatímco nestabilní, proměnlivé či řídce vznikající varianty budou ubývat.

Této obecné a na první pohled triviální zákonitosti si v různých typech systémů povšimla dlouhá řada badatelů (např. Lotka, 1922a, 1922b; Simon, 1962; Slobodkin & Rapoport, 1974; Wimsatt, 1980; Van Valen, 1989; Rappaport, 1999; Michod, 2000; Grand, 2001; Slotine & Lohmiller, 2001; Dawkins, 2003; Pross, 2003, 2004, 2012; Bouchard, 2008, 2011; Flegr, 2010, 2013; Maynard Smith & Szathmáry, 2010; Wagner & Pross, 2011; Shcherbakov, 2012; Doolittle, 2014, 2017; Pascal & Pross, 2014, 2015, 2016; Bardeen & Cerpa, 2015), které, stejně jako jejich poněkud odlišnou terminologii, zmiňujeme v našem teoretickém článku (Toman & Flegr, 2017c, příloha 3). Nejznámější se patrně stala pasáž v Dawkinsově knize Sobecký gen (Dawkins, 2003, str. 22), kde autor přímo říká, že: „Darwinovo ‚přežití zdatnějšího' je v podstatě speciálním případem obecnějšího pravidla přežití stabilnějšího". Až na světlé výjimky spojené například s teoriemi vzniku života a přeměnou „perzistorů" na replikátory (Bourrat, 2014), úvahami o ustanovení „gaiánských" zpětnovazebně regulovaných celoplanetárních entit (Doolittle, 2014, 2017), nebo pokusy o redefinici biologické zdatnosti (Bouchard, 2008, 2011) se ale této zákonitosti nikdo nevěnoval do větší hloubky ani jí nepřikládal větší evoluční důležitost. Podle většiny evolučních biologů představuje pouze nepříliš zajímavé, nebo dokonce umělé rozšíření pojmu přirozeného výběru mimo systémy živých entit (viz např. Okasha, 2006, str. 214, Godfrey-Smith, 2009, str. 40 a 104).

Jak však argumentujeme v našem článku (Toman & Flegr, 2017c, příloha 3), tento proces ve skutečnosti může hrát v různých vyvíjejících se systémech včetně biologické evoluce klíčovou roli. Vzhledem k jeho značnému konceptuálnímu neukotvení jsme jej navrhli nazvat tříděním z hlediska stability (*stability-based sorting*, SBS). Určitým problémem zůstává otázka, zda třídění z hlediska stability, respektive konstatování, že stabilní přetrvává, zatímco nestabilní mizí, nepředstavuje pouhou tautologii. Tautologií toto konstatování nejspíš opravdu je, protože se jedná o výrok platný za všech okolností (Grand, 2001, str. 34-38, Pross, 2012; Shcherbakov, 2012; Pascal & Pross, 2014, 2015). V jednoduchém, homogenním, systému by byly stejně triviální i důsledky třídění z hlediska stability. Důležité však je, že většina systémů, kterými se různé vědní obory zabývají (vesmír, naše planeta, biologická evoluce, společnost, kulturní evoluce apod.) takto idealizovaná není a nezřídka vykazuje poměrně velkou heterogenitu. Za podmínek, kdy entity tvořící systém složitými způsoby interagují s proměnlivým a různorodým prostředím zahrnujícím mimo jiné ostatní takové entity, se však jejich stabilita, respektive perzistence v systému, stává proměnlivou a kontextově závislou. Třebaže tedy celý systém stále můžeme charakterizovat jeho směřováním k větší stabilitě, konkrétní stavy, kterých v rámci tohoto procesu nabývá, mají k jednoduchosti či triviální předpověditelnosti daleko (Pross, 2003, 2004, 2012; Bardeen, 2009; Wagner & Pross, 2011; Pascal & Pross, 2014, 2015, 2016). Při zkoumání jednotlivých systémů, v našem případě biologické evoluce, jsou to přitom tyto konkrétní stavy, které nás zajímají. Jak tudíž poeticky uzavírá Shcherbakov (2013): „Tento princip – přežití těch, co přežijí – zní jako tautologie, ale je to *velká tautologie*: Vše, co je opravdu nové, vzniká prostřednictvím tohoto principu.“

4.2.2 Vztah třídění z hlediska stability a selekce

Jak podrobněji rozebíráme v článku (Toman & Flegr, 2017c, příloha 3), všechny formy selekce vyžadují, aby entity podléhající tomuto procesu vznikaly množením či kopírováním entit v systému již existujících a vykazovaly alespoň nějakou dědičnost rodičovských vlastností (Lewontin, 1970, 1978; Okasha, 2006, str. 13-18; Godfrey-Smith, 2009, str. 17-40). Třídění z hlediska stability nic takového nevyžaduje. Podléhají mu všechny materiální i nemateriální entity ve všech systémech prodělávajících evoluci bez ohledu na jejich původ. K třídění z hlediska stability dochází u entit, které vznikají jedna z druhé (organismů a jejich částí v průběhu biologické evoluce či individuálního vývoje, příběhů, jazyků, náboženství apod.) i u entit vznikajících zcela nezávisle (sněhových vloček, kosmických těles, vtipů, vzájemně izolovaných ekosystémů či civilizací apod.). Stabilnější varianty se přitom hromadí také v situaci, kdy méně stabilní entity vznikají častěji.

Selekce i třídění z hlediska stability probíhají v uzavřených a co do počtu entit stagnujících i otevřených a rostoucích systémech. Průběh třídění v těchto dvou typech systémů se liší jen tím, že v prvních jmenovaných stabilnější entity (např. vesmírné objekty) méně stabilní varianty nakonec zcela nahradí, zatímco v druhých se dlouhodobě pouze snižuje podíl méně stabilních entit (např. sněhových vloček) na úkor stabilnějších. Jediné systémy, kde již nedochází ke třídění z hlediska stability, jsou uzavřené systémy s maximálním možným počtem entit, kde již doběhlo do konce a úplně zde převládly maximálně stabilní varianty. Rovněž při selekci v otevřených a rostoucích systémech se pouze zvyšuje podíl lépe přizpůsobených individuí na úkor hůře přizpůsobených, druhá jmenovaná ale nikdy zcela nevymizí. V uzavřených systémech oproti tomu lépe přizpůsobené varianty nakonec zcela převládnou (Flegr, 1997). Jak působením třídění, tak působením selekce tudíž bude evoluce rychleji probíhat v uzavřených systémech.

Ve většině systémů dochází pouze k třídění na základě statické stability, tj. nižší pravděpodobnosti zániku entit nebo jejich změny v entity jiné. V systémech, ve kterých vznikají nové entity z entit starších a dědí alespoň do určité míry jejich vlastnosti, se však dominantní silou stává třídění na základě dynamické stability, tj. největšího rozdílu mezi produkcí dceřiných entit a jejich zanikáním (Pross, 2003, 2004, 2012; Wagner & Pross, 2011; Pascal & Pross, 2014, 2015, 2016). I v tomto procesu jde o zachování původní entity (respektive informace k jejímu vytvoření, viz Shcherbakov, 2012). Ne však prostřednictvím statické perzistence, nýbrž kopírování. Darwinův individuální výběr (Darwin & Wallace, 1858; Darwin, 1859), stejně jako Dawkinsův mezialelický výběr (Dawkins, 2003), druhový výběr (Stanley, 1979; Vrba & Gould, 1986; Gould, 2002) i všechny další typy selekce tudíž vlastně představují speciální případy třídění na základě (statické) stability (Dawkins, 2003; Okasha, 2006, str. 214; Godfrey-Smith, 2009, str. 40 a 104; Bouchard, 2011; Bourrat, 2014; Doolittle, 2014). Jak navíc předpokládá Dawkins (2003, str. 22), a namodeloval Bourrat (2014), třídění na základě dynamické stability – dále jen selekce – se z třídění na základě statické stability – dále jen třídění na základě stability – mohlo postupně vyvinout.

Bylo by však chybou předpokládat, podobně jako například Pross se svými kolegy (Wagner & Pross, 2011; Pross, 2012), že v systémech podléhajících selekci nehraje třídění z hlediska stability žádnou roli nebo že pouze určuje hranice, ve kterých může k výběru docházet. Třídění z hlediska stability je ve všech ohledech obecnějším procesem (Dawkins, 2003, str. 13), dochází k němu na všech úrovních a bez ohledu na původ entit v systému. Podle některých autorů dokonce třídění na základě stability v systémech podléhajících evoluci musí zákonitě vést ke stázi (Shcherbakov, 2012, 2013). Zdá se ale, že přinejmenším v reálných systémech podléhajících biologické evoluci, tj. systémech vykazujících výraznou heterogenitu danou mimo jiné interakcemi jednotlivých entit, celý proces obecně nespěje ke statické stabilitě ani maximálnímu zjednodušení entit spojenému s nejvyšší dosažitelnou rychlostí a přesností jejich replikace. Konstantní napětí mezi tlakem ke konzervaci informace „jak vytvořit dceřinou entitu" a adaptací na nové podmínky naopak může vést k otevřenému charakteru biologické evoluce (de Vladar et al., 2017; Toman & Flegr, 2017b).

Původní informace „jak vytvořit dceřinou entitu" se tudíž v průběhu adaptivní evoluce mění, rozvíjí a košatí. Jedním z prvních kroků na této cestě mohlo být vytvoření jednoduchých dawkinsovských interaktorů (Dawkins, 2003, str. 28-67), které následoval vznik sofistikovaných buněk, mnohobuněčných těl a dalších úrovní, na jejichž bázi může docházet k evoluci včetně kontextově závislého výkladu informace samotné (Markoš, 2002; Ostdiek, 2011; Shcherbakov, 2012). Z hlediska třídění je však důležité, že si informace „jak vytvořit dceřinou entitu“ uchovává svou historickou individualitu.

Z hlediska adaptivní evoluce je selekce daleko efektivnější než třídění na základě stability. Díky tomu, že dceřiné entity dědí vlastnosti svých předchůdců a rychlost produkce potomků závisí na počtu výhodných vlastností, zajišťuje selekce postupnou akumulaci a amplifikaci adaptací zvyšujících biologickou zdatnost. Třídění z hlediska stability se naopak (až na výjimky, např. některé memy, viz Blackmore, 2001) účastní pořád stejný počet stabilních a nestabilních entit bez ohledu na předchozí evoluci systému a bez ohledu na momentální stabilitu entit tvořících systém. Postupným hromaděním drobných selekčně výhodných vylepšení tak v průběhu biologické evoluce mohou vznikat neporovnatelně komplexnější znaky než tříděním z hlediska stability. Tříděním z hlediska stability se mohou hromadit pouze náhodné změny zvyšující stabilitu entit. Zatímco výhodné znaky vzniklé působením selekce se rychle rozšíří mezi všechny členy populace, takže další výhodná změna s velkou pravděpodobností zasáhne jedince již nesoucího změnu předchozí, pravděpodobnost, že by se náhodná změna zvyšující stabilitu několikrát objevila u stejné nereplikující se entity, je zanedbatelná. Při hromadění výhodných vlastností je tak třídění z hlediska stability výrazně pomalejší a méně efektivní než selekce (viz např. Bourrat, 2014; Doolittle, 2014).

Přesto je možné, že i v biologické evoluci tříděním z hlediska stability vzniká určitá třída znaků. Jak rozebíráme v našem článku (Toman & Flegr, 2017c, příloha 3), jedná se o znaky založené na jedné či dvou změnách, často vedlejších důsledcích specifických adaptací vzniklých působením selekce. Třídění z hlediska stability v takovém případě funguje jako síto, kterým projdou pouze evoluční linie nesoucí znak zvyšující stabilitu (Doolittle, 2014, 2017). Jedním z těchto znaků by mohlo být pohlavní rozmnožování, které, jak jsme viděli v kapitole 3.1, přináší svým nositelům řadu nevýhod, ale zároveň zajišťuje dlouhodobé udržování genetického polymorfismu spojené se zvýšením dlouhodobé perzistence pohlavních linií v heterogenním a proměnlivém prostředí. Vůbec přitom nezáleží na tom, jaké byly proximální důvody vzniku pohlavnosti. Mohlo se klidně jednat o partikulární selekční tlaky typické pouze pro jedno geologické období (viz např. Toman, 2015, str. 39-64). Vzhledem k přednostnímu přežívání pohlavních organismů v heterogenním prostředí zde ale dnes dlouhodobě úspěšné obligátně nepohlavní linie prakticky nenalezneme. Další organismální vlastnosti, které mohly převládnout kvůli výhodě z hlediska stability, zahrnují některé formy altruistického chování, nebo třeba extrémně konzervovaný genetický kód (Toman & Flegr, 2017c, příloha 3).

Třídění z hlediska stability tudíž v biologické evoluci nedokáže vytvořit tak spektakulární adaptace jako selekce. Za všech okolností má ale poslední slovo (Toman & Flegr, 2017c, příloha 3). Lidský mozek, například, bývá považován za jeden z vrcholů biologické evoluce. Vzhledem k tomu, že náš druh mohou mimořádně rozvinuté kognitivní schopnosti dovést k záhubě – ať už prostřednictvím ničivé nukleární války, nebo třeba vytvoření tak husté populace, že umožní šíření extrémně virulentních patogenů – se však lehce mohou ukázat jako dlouhodobě stabilnější ty druhy a evoluční linie, které rozvinutou nervovou soustavu, například kvůli různým vývojovým *constraints*, vůbec nevytvářejí. Ze stejného důvodu se vlastnosti fixované působením třídění z hlediska stability jeví nápadně „plánované" a jejich vysvětlení působením přirozeného výběru neuspokojivá. Na rozdíl od selekce totiž třídění z hlediska stability projevuje daleko menší míru oportunismu. Jeho působením se nefixují momentálně výhodné adaptace, které ale ve střednědobém až dlouhodobém měřítku mohou *fitness* snižovat nebo dokonce zvyšovat pravděpodobnost vymření kladu, nýbrž vlastnosti výhodné v nejdelším časovém měřítku.

Když se vrátíme k výše zmíněnému příkladu s pohlavností, sobečtí nepohlavní mutanti samozřejmě mohou získat krátkodobou výhodu a v některých pohlavních populacích dokonce i převládnout. Známe ostatně celou řadu druhů a rodů, které druhotně přešly k nepohlavnosti (Butlin, 2002). Podobnému „převratu" přitom nemůže zabránit ani druhový výběr, který je v pohlavních populacích až na určité speciální případy vždy slabší než výběr individuální (Williams, 1966). Působením třídění z hlediska stability však nakonec převládnou ty linie, které vykazují specifické vlastnosti zabraňující ztrátě znaku zvyšujícího jejich stabilitu. Tyto „pojistky" se přitom vyvinuly pod zcela odlišnými selekčními tlaky, představují vedlejší důsledek jiných adaptací, nebo dokonce spandrely (Gould, 2002), tj. nevyhnutelné důsledky topologické, fyzikální či biochemické báze organismů. V případě savců představuje pojistku proti ztrátě pohlavnosti genetický imprinting (Bartolomei & Tilghman, 1997), přičemž podobné vlastnosti nalezneme také u několika dalších skupin (Hurst & Peck, 1996). V případě pohlavního rozmnožování ale mohla roli jakési „měkké pojistky" sehrát už samotná evoluční výhoda pohlavních organismů v heterogenních prostředích (viz kapitola 3.1). Další vlastnosti, které se mohly v biologické evoluci fixovat působením třídění z hlediska stability, stejně jako možné pojistky proti jejich ztrátě, diskutujeme v článku Toman & Flegr (2017c, příloha 3).

4.2.3 Makroevoluční důsledky třídění z hlediska stability

V našem článku (Toman & Flegr, 2017c, příloha 3) jsme detailně rozebrali celou řadu mikroevolučních, makroevolučních, ekologických, geofyziologických a kulturních fenoménů, které můžeme nejefektivněji vysvětlit působením třídění z hlediska stability. Jako hromadění kontextově stabilních genových variant odolávajících eliminaci ostatně můžeme popsat už samotnou akumulaci polymorfních alel, kterou předpokládá teorie zamrzlé plasticity a která souvisí s přechodem druhu do elastické fáze jeho existence (viz sekce 2). Nejzávažnější důsledek třídění z hlediska stability pro biologickou evoluci nicméně představuje již zmíněné makroevoluční zamrzání, tj. hromadění ireverzibilně polymorfních alel a znaků, které tyto alely kódují, spojené s nevratným hromaděním dále neproměnlivých prvků genetické architektury organismů (viz podkapitola 4.1.1).

Jak jsme viděli v předchozí podkapitole, v systémech podléhajících biologické evoluci může efekty třídění z hlediska stability dočasně maskovat spektakulárně se projevující přirozený výběr.

K třídění z hlediska stability ale i tak dochází na všech úrovních všech systémů podléhajících evoluci. Vzhledem k tomu, že má třídění z hlediska stability nad přirozeným výběrem vždy poslední slovo, efektivně se mu nelze nijak vyhnout. Makroevoluční zamrzání v průběhu evoluce evolvability by tak mělo teoreticky postupovat až do doby, kdy se evoluční linie stanou zcela neschopnými produkovat zásadní evoluční inovace a budou vytvářet pouze drobné variace na postupně zamrzající fenotypový motiv, a to i přes určitou optimalizaci evolvability doprovázející evoluci genetické architektury organismů (viz podkapitola 4.1.2).

K podobnému procesu možná došlo u některých dnes druhově chudých a z fenotypového hlediska velmi uniformních linií, jako jsou například dnešní dvojdyšní (Dipnoi) (Lloyd et al., 2012). Samozřejmě je možné, že v nejdelším časovém měřítku dojde působením třídění z hlediska stability k vytřídění linií, které vůbec evolučně nezamrzají, tj. linií nepohlavních. Na Zemi se tak za nějaký čas možná setkáme pouze s primárně nepohlavními prokaryoty a možná několika liniemi druhotně nepohlavních eukaryot. Než však biologická evoluce dospěje do těchto extrémů, je pravděpodobné, že v selekční výhodě budou linie schopné produkovat výrazné evoluční novinky, tj. klady, které si dokázaly zachovat velkou část svého makroevolučního potenciálu či makroevoluční potenciál alespoň částečně obnovit. Příklady různých evolučních procesů, které mohou zpomalit ubývání makroevolučního potenciálu či jej částečně nebo úplně obnovit, stejně jako důsledky těchto procesů pro makroevoluci eukaryot, jsme shrnuli a obšírně diskutovali v článku Toman & Flegr (2018a, příloha 2) a (zejména) Toman & Flegr (2018b, příloha 4). Detailně se jim budeme věnovat v kapitole 4.3. Na tomto místě ale zbývá diskutovat, zda makroevoluční zamrzání nedokáže zastavit druhový výběr.

Linie vykazující vyšší makroevoluční potenciál by si měly uchovávat schopnost produkovat zásadní evoluční novinky. Ze statistického hlediska by proto měly častěji podléhat speciacím a nově odštěpené dceřiné druhy v rámci těchto linií by měly být schopné relativně výraznějších reakcí na změny podmínek, obsazení úplně nových ekologických prostorů či vytváření zcela nových životních strategií. V důsledku toho by příslušníci těchto linií měli vykazovat nižší pravděpodobnost extinkcí a častěji podléhat explozivním radiacím. Čistě teoreticky by proto linie, které z nejrůznějších důvodů vykazují vyšší makroevoluční potenciál, měly převážit v procesu druhového výběru (Stanley, 1979; Vrba & Gould, 1986; Gould, 2002), tj. selekce na co největší rozdíl mezi pravděpodobností vymření a odštěpování nových druhů, a nakonec makroevolučně více zamrzlé linie nahradit. Zejména v eukaryotických populacích však patrně druhový výběr k zastavení makroevolučního zamrzání hned z několika důvodů nestačí (viz Toman & Flegr, 2017c, 2018a, b, přílohy 2, 3, 4).

Hromadění nevratně polymorfních alel a dále neproměnlivých prvků genetické architektury v průběhu evolučního zamrzání má jednosměrný efektivně nevratný charakter. K podobným změnám dochází neustále na všech úrovních u všech evolučních linií, přičemž většina takovýchto změn snižuje makroevoluční potenciál a potažmo pravděpodobnost vytváření výrazných evolučních novinek jen velmi mírně. Z hlediska selekce se tak jeví neutrálně a jejich akumulaci se nelze vyhnout „evolučním průřezem“ (Wimsatt & Schank, 2004). Jedná se vlastně o proces do velké míry analogický akumulaci slabě škodlivých mutací působením Mullerovy rohatky (Muller, 1964). Působením Mullerovy rohatky se v malých a středně velkých populacích hromadí mírně škodlivé mutace, neboť vznikají u všech jedinců a zůstávají pod rozlišovací schopností přirozeného výběru. Působením „makroevoluční rohatky“ (Toman & Flegr, 2018b, příloha 4), se hromadí změny mírně snižující makroevoluční potenciál, neboť vznikají ve všech evolučních liniích a unikají působení druhového výběru.

Akumulaci mírně škodlivých mutací působením Mullerovy rohatky se mohou vyhnout (zejména prokaryotické) organismy vytvářející početné populace, u kterých přirozený výběr zachytí i velmi slabě škodlivé mutace (Lynch et al., 1993). Nepohlavní prokaryotické organismy, u kterých druhový výběr *de facto* odpovídá individuálnímu (každý jedinec zde zakládá svou vlastní evoluční linii) a které tradičně vytvářejí obrovské populace s velkou účinností selekce, v souladu s tím patrně dokážou zachytit a eliminovat také změny, které jen velmi mírně snižují makroevoluční potenciál. U pohlavních eukaryot, a zejména jejich složitých mnohobuněčných zástupců, kteří za normálních okolností vytvářejí daleko menší populace a u kterých představuje druhový výběr daleko slabší faktor, ale patrně většina z těchto změn zůstane pod rozlišovací schopností selekce a bude se akumulovat genetickým driftem. A to jsme zanedbali realistickou možnost, že makroevolučně zamrzlý element může svému nositeli přinášet individuální výhody (například zvýšenou vývojovou robustnost, viz podkapitola 4.1.2). Vzhledem k tomu, že individuální selekce je zpravidla silnější než druhová (Williams, 1966), taková situace může eliminaci makroevolučně zamrzlých prvků dále komplikovat. Jak navíc uvidíme v kapitole 4.3, makroevoluční zamrzání může dále umocňovat postupně se komplikující genetická architektura mnohobuněčných organismů. Makroevoluční zamrzání by tudíž mělo být charakteristické pro pohlavní eukaryotické organismy a mezi nimi zejména pro komplexní mnohobuněčné organismy s mnohoúrovňovou genetickou architekturou.

Hromadění škodlivých mutací prostřednictvím Mullerovy rohatky samozřejmě dokážou organismy zpomalit nebo dokonce zastavit prostřednictvím pohlavního procesu, který v každé generaci obnovuje rozdíly v počtu škodlivých mutací mezi jedinci (Muller, 1964; Kondrashov, 1982). Žádný podobný proces na úrovni celých evolučních linií ovšem neznáme. Vzhledem k tomu, hromadění škodlivých mutací může výrazně snížit životaschopnost populací a v extrémním případě je až dohnat k vymření (viz např. Chao, 1990), nelze vyloučit, že podobně závažné důsledky může mít pro makroevoluční potenciál pohlavních, tj. eukaryotických, evolučních linií a potažmo jejich evoluční životaschopnost nijak nekorigované hromadění makroevolučně zamrzlých elementů.

4.3 DŮSLEDKY MAKROEVOLUČNÍHO ZAMRZÁNÍ

4.3.1 Vyhnutí se makroevolučnímu zamrzání

V minulé kapitole jsme viděli, že makroevoluční zamrzání patrně nemůže v pohlavních populacích eukaryotické velikosti zastavit či efektivně zpomalit ani druhový výběr. Faktu, že podobnému procesu opravdu dochází, ostatně napovídají už pozorování snižování makroevolučního potenciálu, proměnlivosti kladů a mezidruhové i vnitrodruhové disparity, které jsme shrnuli v podkapitole 4.1.3. Přesto je zřejmé, že klady pozemských organismů stále dokáží vytvářet evoluční novinky a přinejmenším zatím tak svedly proces snižování makroevolučního potenciálu korigovat. V tomto ohledu se nabízí několik možností.

Zaprvé je možné, že evoluce evolvability ve skutečnosti nevede (pouze) ke vzniku makroevolučně zamrzající modulární genetické architektury organismů (Toman & Flegr, 2018a, b, přílohy 2, 4). Nelze vyloučit, že dlouhodobě úspěšnější mohou být jiné způsoby organizace genotypovo-fenotypové mapy, například takové, které nepodléhají makroevolučnímu zamrzání v tak vysoké míře. Této možnosti nasvědčuje například pozorování, že genetické architektury s nejvýraznějším modulárním uspořádáním, tj. minimálním počtem pleiotropních interakcí mezi moduly, nemusí nutně oplývat nejvyšší evolvabilitou. Z hlediska evolvability patrně hraje větší roli směřování a struktura těchto interakcí (Hansen, 2003; Rasskin-Gutman, 2005). Podle některých autorů z tohoto důvodu mohou evoluční novinky vznikat i jinak než přestavbou modulárně uspořádaných elementů genetické architektury, například prostřednictvím sekundární fixace adaptivních variant fenotypové plasticity v genotypu, relativně drobných, ale klíčových adaptací, výrazné skokové přestavby individuálního vývoje (*hopefull monsters*), nebo tandemové evoluce volně propojených znaků (*correlated progression*) (Hansen, 2003; Budd, 2006; Kemp, 2007; Sharov, 2014). Prakticky všechna tato „alternativní" řešení ale do určité míry spoléhají na redundanci funkcí, která vyplývá z modulárního uspořádání genotypovo-fenotypové mapy. Také z empirických studií vyplývá, že výrazně modulární uspořádání u komplexních organismů se složitými adaptacemi naprosto převládá. Jak jsme viděli už v podkapitole 4.1.2, důvod je patrně ten, že poskytuje svým nositelům velmi výrazné krátkodobé až střednědobé výhody z hlediska individuálního výběru (např. výraznou robustnost vývoje) i evolvability v jejím nižším pojetí (tj. optimalizace evolvability z krátkodobého až střednědobého hlediska). Vznik složitých adaptací nemodulárním způsobem tak zůstává teoretickou možností, prakticky ale v živé přírodě vždy převáží inherentní výhody modulárního uspořádání.

Další možností, jak mohou evoluční linie částečně obejít makroevoluční zamrzání, je prostřednictvím nové kombinace několika nepříliš proměnlivých do velké míry zamrzlých znaků (Toman & Flegr, 2017c, 2018a, b, přílohy 2, 3, 4). Podobná situace může nastávat relativně často, z dlouhodobého hlediska však má patrně největší šanci na úspěch při vzniku nové ekologické strategie nebo expanzi do nového, dosud neobsazeného, prostředí. Typickým příkladem je masivní rozvoj aktivní predace mnohobuněčných živočichů v kambriu (viz např. Bengtson, 2002), nebo opakované expanze různých skupin na souš (viz např. Selden & Edwards, 1989) či k aktivnímu letu (viz např. Norberg, 2007). „Experimentující" linie jsou totiž v podobné situaci do velké míry chráněné před selekčními tlaky konkurentů, parazitů a predátorů, takže mohou dlouhodobě přežívat a přizpůsobovat se novému prostředí třeba i s fenotypy, které by v původním prostředí byly suboptimální. Podobná situace může vést až k fenoménu mozaikovité evoluce (de Beer, 1954), tj. situaci, kdy do nového prostředí či k nové ekologické strategii expanduje několik linií s různými kombinacemi znaků.

Nemyslitelná není ani situace, že čas od času určitý zdánlivě nevratně zamrzlý element rozmrzne (Toman & Flegr, 2017c, 2018a, b, přílohy 2, 3, 4). Jak jsme viděli výše (viz podkapitola 4.1.1), efektivně nevratně polymorfní alely i ostatní zamrzlé elementy genetické architektury se v pravděpodobnosti, že budou podléhat adaptivní evoluci, mezi sebou liší. S určitou pravděpodobností se může ztratit polymorfismus i v alelách vykazujících velmi silný frekvenčně závislý vliv na zdatnost. Tato pravděpodobnost je pouze limitně nízká (viz podkapitola 4.1.1). Často se také mluví o tom, že určité pozdější adaptace mohou přímo či nepřímo uvolnit selekční tlaky, které držely určitý element genotypovo-fenotypové mapy v zamrzlém stavu (viz např. Wimsatt & Schank, 2004; Budd, 2006; Melo et al., 2016). Tyto faktory, které sahají od prozaického snížení velikosti populace, přes zálohování funkcí až k přítomnosti různých nápravných mechanismů typu chaperonů, jsme vyčerpávajícím způsobem shrnuli v článku (Toman & Flegr, 2018a, příloha 2). Podobné události se mohly uplatnit například na počátku evoluce ptáků (Dececchi & Larsson, 2013) či krytosemenných rostlin (Simonin & Roddy, 2018).

Výraznější evoluční rozmrznutí jsou patrně vázaná na změny individuálního vývoje (Toman & Flegr, 2017c, 2018a, b, přílohy 2, 3, 4). V důsledku heterochronické změny (zejména neotenie) může organismus expandovat do nového prostředí. Rovněž při ní dochází k uvolnění některých vývojových modulů pro nové účely (Raff & Wray, 1989; Budd, 2006). Podobné události mohly sehrát důležitou roli například při diverzifikaci hlavních kladů strunatců (Chordata) (Hu et al., 2017). Změny, při kterých může docházet k hlubokým přestavbám celého tělního plánu, jsou ale patrně velmi vzácné a vázané na radikální zjednodušení individuálního vývoje. Pro tento evoluční fenomén se vžil název *sakulinizace,* a kromě známých kořenohlavců (Rhizocephalia) (Glenner & Hebsgaard, 2006) se s ním můžeme setkat například u výtrusenek (Myxozoa) (Canning et al., 2004) a kousáním či pohlavně přenosných rakovin savců (Murchison, 2008). Tyto z vývojového hlediska radikálně zjednodušené organismy se mohou stát zakladateli nového, zpočátku evolučně velmi plastického, kladu. Vzhledem k tomu, že neznáme žádnou velkou, různorodou a úspěšnou taxonomickou skupinu, která by od konce kambria vznikla v důsledku výrazné změny tělního plánu při sakulinizaci, je ale pravděpodobné, že z makroevolučního hlediska mají tyto události pouze omezenou roli (Toman & Flegr, 2018a, b, přílohy 2 a 4).

Třebaže známe konkrétní příklady všech výše zmíněných procesů, nezdá se, že by některý z nich dokázal kompletně zastavit makroevoluční zamrzání. Všechny dnešní úspěšné klady eukaryotických organismů jsou patrně potomky linií, které prošly některým z nich. I tak se u nich ale ve statistickém měřítku uplatňují výše zmíněné doklady snižování makroevolučního potenciálu (viz podkapitola 4.1.3). Důvod je nasnadě. Třídění z hlediska stability, které hraje při makroevolučním zamrzání hlavní roli, působí stále a na všech úrovních (viz podkapitola 4.2.3). Pravděpodobnost, že zamrzlý element podlehne změně, je přitom vždy nepřímo úměrná míře jeho zamrznutí. Makroevoluční potenciál eukaryotických linií tak může i přes občasná rozmrznutí slaběji zamrzlých elementů pouze klesat. Kombinace několika do velké míry zamrzlých znaků a jednoduché heterochronické změny mají potenciál zvrátit snižování makroevolučního potenciálu pouze velmi lehce a sakulinizace jsou podle všeho velmi vzácné, přičemž navíc nemusí vždy vést ke vzniku velkého kladu s obnoveným makroevolučním potenciálem. Když se ještě jednou vrátíme ke srovnání s Mullerovou rohatkou, výše uvedené procesy *de facto* představují obdobu zpětných mutací v genetickém modelu hromadění slabě škodlivých mutací u nepohlavních organismů (Lynch et al., 1993). Občas k nim samozřejmě může docházet a takové změny mají potenciál napravit funkci mutací poškozeného proteinu. Reálně jsou ale tak vzácné, že z evolučního hlediska hrají pouze malou roli (Toman & Flegr, 2018a, b, přílohy 2 a 4).

4.3.2 Postupy na novou úroveň hierarchické organizace

Jediným způsobem, prostřednictvím kterého může evoluční linie efektivně obnovit svou evolvabilitu, tak patrně zůstává postup na vyšší stupeň hierarchické organizace. K podobné události může dojít hned několika různými cestami. Vždy je ale charakteristická tím, že se v jejím důsledku stává původní entita jen omezeně proměnlivým modulem v rámci vyššího celku vykazujícího obnovený makroevoluční potenciál (McShea, 1996, 2001a, b, 2015; Sterelny, 1999; McShea & Changizi, 2003; Marcot & McShea, 2007).

Přechodům na vyšší úrovně hierarchické organizace jsme se obsáhle věnovali hlavně v článku Toman a Flegr (2018b, příloha 4), ale okrajově také v Toman a Flegr (2018a, příloha 2). Nejpodstatnějším důsledkem těchto událostí je přirozená modularita organismů vyšší úrovně. Tyto organismy sestávají z vnitřně do velké míry zamrzlých a vzájemně kvazinezávislých jednotek (Carroll, 2001), které ale mohou ve své evoluci nezávisle regulovat, zmnožovat, kombinovat, nebo nasazovat na jiných místech těla, v jiných částech individuálního vývoje či v jiných kontextech (Simon, 1962; Lewontin, 1978; Schank & Wimsatt, 1986; Bonner, 1988; Wagner & Altenberg, 1996; McShea, 2000; Schlosser, 2002, 2004; Schlosser & Wagner, 2004; Callebaut & Rasskin-Gutman, 2005; Melo et al., 2016). Právě tato kombinatorika otevírá organismům vyšší úrovně nové evoluční možnosti, díky čemuž vykazují obnovený makroevoluční potenciál.

Z makroevolučního hlediska mohou přechody na vyšší úroveň hierarchické organizace nastávat relativně často. Jednotlivé přechody se mezi sebou ale výrazně liší co do množství inherentních evolučních omezení (Nedelcu & Michod, 2004; Calcott, 2008). I ty nejperspektivnější linie vyšší hierarchické úrovně zpočátku trpí celou řadou problémů, které je mohou zásadně znevýhodňovat v konkurenci organismů původní úrovně (Queller, 2000; Michod, 2000, 2007; McShea, 2001a; Michod & Nedelcu, 2003; Michod & Herron, 2006; Calcott, 2008; Godfrey-Smith, 2009; Queller & Strassmann, 2009; Corning & Szathmary, 2015). Jak uvidíme dále, tato znevýhodnění plynou například z nízké integrace prvků nižší úrovně, rizika jejich sobeckého jednání, nebo přílišné podobnosti. Jisté je, že dlouhodobě úspěšné přechody na vyšší úroveň hierarchického uspořádání jsou v historii pozemského života poměrně vzácné (viz např. Novák, 1982; Szathmáry & Maynard Smith, 1995; McShea, 1996, 2001a, b, 2015; Pettersson, 1996; Knoll & Bambach, 2000; Michod, 2000; Calcott & Sterelny, 2001; McShea & Simpson, 2001; McShea & Changizi, 2003; Jablonka & Lamb, 2006; Okasha, 2006; Marcot & McShea, 2007; Maynard Smith & Szathmáry, 2010; Bouchard & Huneman, 2013; Buss, 2014;

Corning & Szathmary, 2015; Szathmáry, 2015). Snižování makroevolučního potenciálu na jedné úrovni však stále výrazněji zvýhodňuje entity, které tento faktor dokáží obnovit. Díky tomu mohou nakonec uspět a rozvinout se třeba i zpočátku značně suboptimální řešení postupu na vyšší úroveň hierarchické organizace.

Zásadním makroevolučním problémem však je, že makroevoluční zamrzání vlivem třídění z hlediska stability pokračuje i na nové, hierarchicky vyšší, úrovni (Toman & Flegr, 2018b, příloha 4). Samozřejmě platí, že akumulace nevratně polymorfních alel a jejich skupin, které jsme se blíže dotkli v podkapitole 4.1.1, probíhá pouze na úrovni populace pohlavních organismů. Ke hromadění dále neproměnlivých elementů genetické architektury však dochází na všech úrovních. Tento proces se projevuje postupnou integrací kompozitního organismu vyšší úrovně. Původně jasně modulární stavba zaniká, dochází ke vzniku nových pleiotropních vazeb, prvky se specializují, rostou jejich vzájemné rozdíly, vznikají mezi nimi nové vazby a nové společné způsoby regulace (Lewontin, 1978; Bonner, 1988, 1998; Wagner & Altenberg, 1996; McShea, 2000, 2002, 2015; Schlosser & Wagner, 2004; Callebaut & Rasskin-Gutman, 2005; McShea & Anderson, 2005). Typickým příkladem tohoto jevu jsou evoluční proměny buněk zelenivek (Chlorophyceae) ze skupiny Volvocales (Nedelcu & Michod, 2004), nebo tělních přívěsků členovců (Shubin et al., 1997).

Dále neproměnlivé vazby a prvky se, podobně jako předtím na nižší úrovni, hromadí procesem třídění z hlediska stability a spolu s tím klesá i makroevoluční potenciál evoluční linie. Nakonec organismus vyšší hierarchické úrovně sám makroevolučně zamrzá a jedinou efektivní cestou z této „slepé uličky“ se stává další postup na ještě vyšší úroveň hierarchické organizace. Na tento proces, který je charakteristický tříděním z hlediska stability, má přitom vliv jak selekce na různých úrovních, tak neutrální mechanismy typu *Zero Force Evolutionary Law* (McShea & Brandon, 2010). Dokonce je možné, že rostoucí komplexita genetické architektury pohlavních eukaryotických organismů makroevoluční zamrzání na každé další úrovni ještě umocňuje (viz podkapitola 4.3.3). Zatím nevíme, jestli existuje nějaký horní práh, za kterým již bude další zvyšování hierarchické úrovně nemožné. V historii pozemského života se nicméně tento fenomén mnohokrát opakoval, a to i ve stejných evolučních liniích (McShea, 2001b).

Různým typům přechodů na vyšší úroveň se obsáhle věnujeme v článku Toman & Flegr (2018b, příloha 4). Stručně však můžeme shrnout, že prvním typem postupu na vyšší úroveň hierarchické komplexity je vnitřní modularizace organismální struktury a fungování. Na nejnižší úrovni se vnitřní modularizace projevuje jako ustanovení genetických, vnitřně silně propojených ale vzájemně kvazinezávislých modulů zodpovědných za vývoj, stavbu a fungování organismu. Celou řadu genově regulačních (např. regulace transkripce), signálních (např. dráhy hedgehog, TGFβ, Wnt, RTK či Notch) či pozičních (např. *Hox* či *Pax* geny) modulů přehledně shrnuje například Schlosser (2004). Na vyšších úrovních organizace se potom může jednat o buňky, tkáně, orgány, celé tělní články, nebo dokonce systémové moduly typu hormonálního řízení vývoje (Schlosser, 2004).

Tento proces je přirozenou součástí evoluce evolvability, respektive formování genotypovo-fenotypové mapy, a tak jsme jej *de facto* již popsali v podkapitole 4.1.2. Na počátku každé vnitřní modularizace patrně stojí parcelace, respektive multiplikace již existujícího modulu či modulů dané úrovně (genů, fyziologických či vývojových drah, buněk, tělních článků apod.) (Wagner, 1989a, b; Wagner & Altenberg, 1996). V průběhu další evoluce dochází k integraci modulů, modulární charakter na dané úrovni se stírá a ustanovují se modulární celky stále vyšší úrovně (McShea, 2002, 2015; McShea & Anderson, 2005). Procesy parcelace a integrace se tak na následujících úrovních jakoby střídají (Wagner & Altenberg, 1996; Kirschner & Gerhart, 1998; Eble, 2005). Výsledkem je, že se dnes, zejména u mnohobuněčných organismů se složitým individuálním vývojem, můžeme setkat s komplexní mnohoúrovňovou genotypovo-fenotypovou mapou sestávající z různých vývojových, morfologických a funkčních modulů (viz např. Callebaut, 2005; Callebaut & Rasskin-Gutman, 2005; Wagner et al., 2005; Lorenz et al., 2011). Ta se projevuje jak genetickou modularitou, tak modulárním uspořádáním tělní stavby (např. segmentací) a fungování.

Extrémním případem stejného fenoménu jsou i duplikace celého genomu, ke kterým v některých liniích dochází relativně běžně a které patrně hrály důležitou roli v počátcích evoluce obratlovců (Vertabrata) nebo paprskoploutvých ryb (Actinopterygii) (Meyer & Van de Peer, 2005). V neposlední řadě bychom mohli do stejné kategorie bychom zařadit i vznik nových způsobů dědičnosti, tj. uložení, přenosu a (re)interpretace informace – od editace genů, přes vznik chromozomů a buněk prokaryotického či eukaryotického typu, strukturní a epigenetické dědičnosti nebo zárodečného vývoje mnohobuněčných organismů až po individuální učení a složité vzorce chování (Szathmáry & Maynard Smith, 1995; Markoš, 2002; Maynard Smith & Szathmáry, 2010; Szathmáry, 2015; Kurismaa, 2018).

Druhou cestou, jak mohou organismy přejít na vyšší úroveň hierarchické komplexity, je spojením několika původně nezávislých entit nižší úrovně. Jak jsme shrnuli (Toman & Flegr, 2018b, příloha 4), Queller (Queller, 1997, 2000) nazval tyto procesy fraterálními a egalitářskými přechody v individualitě. Fraternální přechody se vyznačují tím, že se při nich spojují v entitu vyšší hierarchické úrovně identičtí nebo vzájemně blízce příbuzní jedinci. Často jde o klony, nebo potomky jednoho individua. Podobným způsobem nejspíše vznikly buněčné kompartmenty sestávající ze stejných molekul, kolonie jednobuněčných prokaryot a eukaryot, mnohobuněčné organismy, nebo kolonie mnohobuněčných organismů včetně organismů eusociálních. Exemplárním příkladem fraternálního přechodu v individualitě je vznik koloniálních trubének (Choanoflagellata) a evoluce jedné jejich linie v mnohobuněčné živočichy (Budd & Jensen, 2017).

Egalitářské přechody na vyšší úroveň hierarchické organizace jsou charakteristické tím, že se při nich spojují dvě nebo více vzájemně nepříbuzných entit nižší úrovně. Konkrétně se tak jedná o nejrůznější symbiotické vztahy a symbiogenetické události sahající od soužití hub s rostlinami (ať už ve formě mykorhizy nebo lišejníků) či mravenčími (Formicidae), termitími (Isoptera) a kůrovčími (Scolytinae) pěstiteli, přes spolupráci jednobuněčných organismů s termity, přežvýkavci (Ruminantia), krvesajným a mízosajným hmyzem či ostatními mnohobuněčnými organismy ve formě střevní mikroflóry, symbiózu obrněnek (Dinoflagelalta) s korálnatci (Anthozoa) a kvetoucích rostlin s opylovači až po symbiózy jednobuněčných organismů či vznik endosymbiotických organel typu mitochondrií a plastidů. Procesy podobného typu ale mohly sehrát důležitou roli také při formování buněčných kompartmentů sestávajících z různých molekul či vzniku chromozomu spojením různých genů. Exemplárním příkladem podobného procesu je pohlcení α-proteobakteriálního předka dnešní mitochondrie organismem z příbuzenstva archeí (Archea), které dalo základ moderní eukaryotické buňce (Martin et al., 2015).

Oba typy přechodů v individualitě vykazují z hlediska selekce a evoluční životaschopnosti výsledných organismů specifické výhody a rizika. U fraternálních přechodů například tolik nehrozí rozpad kompozitní entity v důsledku sobeckého jednání jednotlivých konstitutivních entit, původních samostatných organismů (viz např. Michod, 2000, 2007; Queller, 2000; Michod & Nedelcu, 2003; Michod & Herron, 2006; Calcott, 2008; Godfrey-Smith, 2009; Queller & Strassmann, 2009; Corning & Szathmary, 2015). Ty totiž v tomto případě sdílí většinu genetické informace. Ze stejných důvodů se ale počáteční výhody fraternálně vzniklých entit vyšší úrovně omezují pouze na zvětšení objemu a s tím související fyziologické či metabolické výhody (Bonner, 1988, 1998; Queller, 1997; Calcott, 2008). Všechny další adaptace jsou až druhotné a vyplývají z eventuální specializace konstitutivních entit (viz např. Bonner, 1988, 1998, 2003; Szathmáry & Maynard Smith, 1995; Queller, 1997; Calcott, 2008; Maynard Smith & Szathmáry, 2010; Simpson, 2012; Corning & Szathmary, 2015; Szathmáry, 2015).

Výhody a nevýhody egalitářských entit jsou zrcadlově obrácené. V důsledku vzájemné nepříbuznosti konstitutivních entit jin neustále hrozí vnitřní konflikt plynoucí ze sobeckého jednání jednotlivých elementů nižší hierarchické úrovně. Ze stejných důvodů může být výrazně obtížnější a časově náročnější jejich vzájemná integrace, kterou podmiňuje spravedlivá alokace zdrojů a vzájemná existenční závislost entit (viz např. Szathmáry & Maynard Smith, 1995; Michod, 2000, 2007; Queller, 2000; Michod & Nedelcu, 2003; Michod & Herron, 2006; Calcott, 2008; Godfrey-Smith, 2009; Queller & Strassmann, 2009; Maynard Smith & Szathmáry, 2010; Corning & Szathmary, 2015; Szathmáry, 2015). Spojení nepodobných, ale funkčně komplementárních entit nicméně od počátku vykazuje zásadní synergické výhody, které se v průběhu další evoluce mohou dále rozvíjet.

4.3.3 Makroevoluční souvislosti teorie zamrzlé evoluce

V předchozí podkapitole jsme viděli, že makroevoluční zamrzání může zásadně ovlivňovat průběh makroevoluce. Na tomto místě shrneme široké spektrum dosud záhadných makroevolučních fenoménů a patrností, pro které teorie zamrzlé evoluce nabízí koherentní vysvětlení (detaily viz Toman & Flegr, 2018b, příloha 4).

Jak jsme zmínili už výše, samotný fenomén makroevolučního zamrzání dokáže vysvětlit pozorované trendy snižování makroevolučního potenciálu, proměnlivosti kladů i mezidruhové a vnitrodruhové disparity (viz podkapitola 4.1.3). Myšlence, že v průběhu evoluce evolvability mohou přibývat evoluční omezení snižující potenciál evolučních linií pro vytváření zásadních evolučních novinek, se věnovala řada autorů (viz podkapitola 4.1.1). Jediný, kdo před námi uvažoval o možnosti úplného vyčerpání makroevolučního potenciálu a řešení této situace postupem na vyšší úroveň hierarchické komplexity, byl však patrně Wimsatt (2013).

Nejnápadnější implikací teorie zamrzlé evoluce je makroevoluční trend zvyšování hierarchické komplexity organismů. Jak rozebíráme v článku (Toman & Flegr, 2018b, příloha 4), trendy v komplexitě je poněkud obtížné přesně specifikovat. I tak je ovšem zřejmé, že se komplexita organismů přinejmenším v některých vymezeních historicky zvyšovala. Nejprůkaznější je právě zvyšování hierarchické komplexity, tj. nárůst maximální dosažené hierarchické úrovně organismů prostřednictvím modulárního zahnízdění jednotek nižší úrovně v jednotce úrovně vyšší (McShea, 1996, 2001a, b, 2015; Sterelny, 1999; McShea & Changizi, 2003; Marcot & McShea, 2007). Tento trend historicky komentovala řada autorů (viz např. Novák, 1982; McShea, 1991, 1994, 1996, 2001a, b; Szathmáry & Maynard Smith, 1995; Pettersson, 1996; Knoll & Bambach, 2000; Michod, 2000; Calcott & Sterelny, 2001; Jablonka & Lamb, 2006; Okasha, 2006; Marcot & McShea, 2007; Maynard Smith & Szathmáry, 2010; Bouchard & Huneman, 2013; Buss, 2014; Corning & Szathmary, 2015; Szathmáry, 2015). Nejznámějším konceptem v této oblasti je patrně koncept velkých evolučních přechodů (*major transitions in evolution*) (Szathmáry & Maynard Smith, 1995; Calcott & Sterelny, 2001; Maynard Smith & Szathmáry, 2010; Corning & Szathmary, 2015; Szathmáry, 2015). Nalezneme ale i řadu alternativních přístupů (McShea, 1991, 1994, 2001a, b; Pettersson, 1996; Knoll & Bambach, 2000; Michod, 2000; McShea & Simpson, 2001; Jablonka & Lamb, 2006; Buss, 2014; Corning & Szathmary, 2015), mezi kterými není bez zajímavosti teorie sociogeneze českého evolučního biologa Vladimíra J. A. Nováka (1982).

V průběhu času byla navržena celá řada vysvětlení trendu zvyšování (hierarchické) komplexity organismů (viz např. McShea, 1991; McShea & Simpson, 2001; Marcot & McShea, 2007; Corning & Szathmary, 2015). Tato vysvětlení můžeme rozlišit na (1) nehnané, (2) externalistické (darwinovské) a (3) internalistické (nedarwinovské) koncepty (McShea, 1991; Corning & Szathmary, 2015). Podle nehnaných vysvětlení je trend *de facto* výsledkem náhody, a to buď prostých náhodných změn komplexity organismů v evoluci, nebo difuze této vlastnosti během evoluce v přítomnosti dolní neprostupné hranice komplexity (tento model zpopularizoval Gould, 1996, jakožto „efekt zdi“). Podle externalistických vysvětlení je postup na vyšší úroveň hierarchické komplexity výhodný z hlediska některé formy selekce. Podle internalistických vysvětlení jsou postupy na vyšší úrovně hierarchické organizace důsledkem vnitřního ustrojení organismů, například jejich vývojových mechanismů a souvisejících vývojových a potažmo evolučních omezení.

Teorie zamrzlé evoluce zcela nezapadá ani do jedné z těchto kategorií. Přechod na vyšší úroveň hierarchické komplexity je sice podle našeho konceptu selekčně výhodný, nejedná se ale o okamžitou individuální výhodu, nýbrž dlouhodobou výhodu celé linie v druhovém výběru plynoucí z obnovení makroevolučního potenciálu. Zároveň ale můžeme koncept označit i za internalistický, neboť motorem postupů na vyšší hierarchické úrovně jsou změny vnitřního ustrojení organismů, konkrétně makroevoluční zamrzání evolučních linií. V každém případě se trend podle teorie zamrzlé evoluce jeví po většinu času nehnaný. Pouze v situaci, kdy poklesne makroevoluční potenciál na dané úrovni pod kritickou mez, dramaticky stoupá šance, že entita vyšší hierarchické úrovně s obnoveným makroevolučním potenciálem bude evolučně životaschopná a založí nový velký úspěšný klad. V globálním McSheaově (McShea 1994, 1998; Marcot & McShea, 2007) rozvrhu bychom tudíž trend zvyšování hierarchické komplexity zapříčiněný tříděním z hlediska stability a souvisejícím makroevolučním zamrzáním mohli označit za hnaný ve velkém měřítku (*driven at the large scale*).

Některá z navržených vysvětlení trendu se teorii zamrzlé evoluce blíží. Za zmínku stojí zejména historické koncepty Edwarda D. Copeho a Williama K. Gregoryho (které shrnuje např. Daniel W. McShea, 1991), kteří zdůrazňovali roli multiplikace a diverzifikace modulárních celků v evoluci, nebo Saunderse a Ho (1976, 1981), podle kterých může být zdrojem trendu asymetrie mezi snadným přidáváním komponent a jejich obtížným odebíráním kvůli jejich integraci v rámci celku. Našli se i autoři, kteří trend pokládali za důsledek druhového výběru (Wagner, 1996; McShea & Changizi, 2003; Marcot & McShea, 2007). Nikdo z nich jej ovšem nespojil s klesající evolvabilitou či makroevolučním potenciálem. Již zmiňovaný Wimsatt (2013) sice uvažoval o možném úniku z pasti snižování evolvability na vyšší hierarchickou úroveň, v rámci svého obecného konceptu se však vůbec nevěnoval myšlence, že by se tento proces mohl opakovat, vést k celému makroevolučnímu trendu či některým dalším makroevolučním fenoménům. Není přitom bez zajímavosti, že podle teorie zamrzlé evoluce vede evoluce evolvability explicitně k modulární stavbě a fungování organismů. To podle řady ostatních konceptů zdaleka nemusí být samozřejmé.

S makroevolučním trendem zvyšování hierarchické komplexity organismů se navíc volně pojí několik záhadných makroevolučních fenoménů. V první řadě jde o rozrůznění a specializaci jednotek nižší úrovně, které zpravidla následují postup na vyšší úroveň. To se zpočátku projevuje zvýšením počtu různých částí na bezprostředně nižší úrovni a rozdílů mezi nimi. Stejné procesy ale v průběhu času vedou ke zjednodušování elementů na nižších úrovních organizace, ztrátě jejich komplexity a stupňů volnosti až do zcela neproměnlivého, strojového, stavu. Nejhlubší elementy genetické architektury v důsledku toho mohou reagovat na selekční tlaky zpravidla jen velmi omezeně či v předem kanalizovaném směru (Schank & Wimsatt, 1986; McShea, 2002, 2015; McShea & Anderson, 2005). Speciální případ téhož jevu, konkrétně postupná redukce počtu seriálně se opakujících částí těla, jejich specializace a integrace, byl už dříve popsán jako tzv. Willistonovo pravidlo (Gregory et al., 1935). Tyto dva fenomény se ke zvyšování hierarchické komplexity pojí tak silně, že je McShea (2015) označil za „evoluční syndrom“ – makroevoluční patrnost, která si eminentně žádá společné vysvětlení.

Právě toto vysvětlení přitom nabízí teorie zamrzlé evoluce, ze které existence McSheaova evolučního syndromu vyplývá vlastně samozřejmě. Snižování makroevolučního potenciálu vlivem třídění z hlediska stability na každé úrovni hierarchické komplexity vede k rostoucímu tlaku na další postupy. V důsledku těchto postupů dochází ke zmnožování entit bezprostředně nižší úrovně. I na nové úrovni nicméně dochází v průběhu evoluce evolvability k třídění z hlediska stability. To má nejprve formu rozrůzňování, specializace a ztrát redundantních funkcí u entit na této úrovni a později stírání modularity, integrace, zjednodušování a „strojovatění“ entit na této úrovni a úrovních nižších (Toman & Flegr, 2018b, příloha 4). Rubovou stranou stejného procesu je střídání procesů parcelace a integrace na sousedních hierarchických úrovních zmíněné v předchozí podkapitole. Třebaže si různí autoři tohoto fenoménu všimli (Wagner & Altenberg, 1996; Kirschner & Gerhart, 1998; Eble, 2005), až teorie zamrzlé evoluce pro něj nabízí přirozené vysvětlení. Postup na vyšší úroveň má vždy za následek vznik modulárního celku parcelací. Jeho části se ale na této úrovni specializují, integrují a ztrácí svůj modulární charakter, což následuje další zvýšení hierarchické komplexity.

Další zajímavou patrností je, že se frekvence přechodů na vyšší úrovně komplexity v historii pozemského života postupně zrychluje (McShea, 2001a, b, 2015; McShea & Changizi, 2003). Zvlášť markantní jsou dvě skoková zrychlení před asi 1,2 miliardou let, tj. v neoproterozoiku, a 540 miliony let, tj. v kambriu (Carroll, 2001; McShea & Changizi, 2003; McShea, 2015). Trend se navíc podle dostupných údajů nejvýrazněji projevoval u pohlavních eukaryotických organismů a zejména jejich komplexních mnohobuněčných zástupců. Ani tyto fenomény by nás podle teorie zamrzlé evoluce neměly překvapovat (Toman & Flegr, 2018a, b, přílohy 2 a 4). Po skokovém úvodním nárůstu spojeném se vznikem prokaryotické buňky maximální dosažená úroveň hierarchické komplexity více méně stagnovala. Jak jsme viděli v podkapitole 4.2.3, prokaryotické organismy dokáží díky svým velkým populacím, ve kterých hraje velkou roli selekce včetně selekce na makroevoluční potenciál, makroevolučnímu zamrzání efektivně vzdorovat. Občas sice vytvářejí komplexnější formy (McInerney et al., 2011) nebo kolonie a jednoduché mnohobuněčné útvary (Claessen et al., 2014), absence tlaku k postupům na vyšší úrovně hierarchické komplexity však vede k tomu, že má jejich evoluce spíše „dvourozměrný“, tj. v nepřítomnosti silných selekčních tlaků pomalý a stabilizující, charakter (McShea, 2001a, b, 2015; McShea & Changizi, 2003; Marcot & McShea, 2007).

Trend zvyšování hierarchické komplexity proto výrazně zrychlil až se vznikem pohlavního rozmnožování v průběhu eukaryogeneze, který můžeme datovat s největší pravděpodobností právě do období neoproterozoika (Carroll, 2001; McShea & Changizi, 2003; McShea, 2015). Pohlavnost umožňuje akumulaci efektivně nevratně polymorfních alel. Menší velikost eukaryotických populací spojená s nižší účinností selekce, stejně jako omezení kompetice mezi evolučními liniemi na základě zbývajícího makroevolučního potenciálu na relativně slabý druhový výběr, navíc (možná synergisticky, viz podkapitola 4.1.1) usnadnily hromadění dále neproměnlivých elementů genetické architektury a vydláždily tak cestu makroevolučnímu zamrzání. Ultimátním výsledkem těchto změn se stal „trojrozměrný“ charakter eukaryotické evoluce, která se oproti prokaryotické vyznačuje výrazně odlišnou dynamikou, trendem zvyšování hierarchické komplexity a výše uvedenými doprovodnými makroevolučními fenomény (Knoll & Bambach, 2000; Carroll, 2001; Butterfield, 2007; Toman & Flegr, 2017a, příloha 1).

Druhé zrychlení trendu je potom nejspíše spojené se vznikem složitého individuálního vývoje mnohobuněčných organismů, jejichž vznik těsně předcházel kambriu (McShea, 2001a, b; Davidson &

Erwin, 2006). Komplexifikace genotypovo-fenotypové mapy totiž zvyšuje evoluční zátěž a vývojové uzamknutí nižších úrovní (viz podkapitola 4.1.1), přičemž evoluční zamrzání může podporovat i rostoucí počet interakcí a sdílených regulací na dané úrovni organizace i mezi úrovněmi (viz např. Thomas, 2005). To vše může dále umocňovat selekce na vyšší robustnost vývoje (Kirschner & Gerhart, 1998; Von Dassow & Meir, 2004; Schoch, 2010; Wimsatt, 2013; Brigandt, 2015) a integraci bránící sobeckému jednání kvazinezávislých konstitutivních elementů (Szathmáry & Maynard Smith, 1995; Michod, 2000; McShea, 2001a, b; Michod & Herron, 2006). Stejné procesy by mohly stát i za pozorovaným průběžným zrychlováním trendu v průběhu evoluce (McShea, 2001a, b, 2015; McShea & Changizi, 2003). Celá výše popsaná patrnost se potom odráží i v zásadním rozdílu mezi „dvojdimenzionálním“ charakterem pre-neoproterozoické (a hlavně prekambrické) a „trojdimenzionálním“ charakterem fanerozoické evoluce (Knoll & Bambach, 2000; Carroll, 2001; Butterfield, 2007; Toman & Flegr, 2017a).

5 ZÁVĚR

V druhé sekci práce jsme si stručně představili teorii zamrzlé plasticity. Podle tohoto konceptu se v evoluci pohlavních druhů střídají dlouhá období stáze, během kterých reagují populace na selekční tlaky pouze elastickou změnou ve frekvenci již přítomných alel, s krátkými obdobími plastické evoluce, během kterých může docházet k fixaci a eliminaci alel působením usměrněného výběru. Nepohlavní druhy by si podle tohoto konceptu sice neměly dlouhodobě udržovat tak vysoký genetický polymorfismus, zase by ale měly vykazovat potenciál plasticky reagovat na selekční tlaky v průběhu celé své existence.

Z těchto rozdílů mezi pohlavními a nepohlavními druhy vyplývá možnost odlišných environmentálních preferencí obou skupin. Zatímco nepohlavní druhy by měly mít výhodu v bioticky i abioticky velmi stabilním a homogenním prostředí, evoluční elasticita pohlavních druhů by jim měla přinášet výhodu v bioticky i abioticky heterogenních a proměnlivých habitatech. Nelze dokonce vyloučit, že tento faktor stojí za dlouhodobým udržováním pohlavního rozmnožování u eukaryot i navzdory jeho zjevným nevýhodám. Jak jsem shrnul v třetí sekci věnované ekologickým implikacím teorie zamrzlé evoluce, tuto hypotézu jsme testovali na základě literárních dat prostřednictvím srovnávací studie prostředí obývaných starobyle nepohlavními liniemi eukaryot a jejich příbuznými pohlavními kontrolami. Výsledky publikované studie (Toman & Flegr, 2017a, příloha 1) tuto hypotézu statisticky významně podpořily (biotická heterogenita p = 0,016, abiotická heterogenita p = 0,031, obecná heterogenita p = 0,016). Jako zásadní se přitom ukázalo vycházet z heterogenity prostředí, kterou organismy skutečně zažívají v aktivním stavu, nikoli například ve formě klidových či dormantních stádií, tj. heterogenity *subjektivní*. Kromě toho se nám podařilo vytipovat několik konkrétních adaptací a environmentálních preferencí, které starobyle nepohlavním organismům umožňují subjektivní heterogenitu prostředí snižovat.

Ve čtvrté sekci práce, která vychází z našich teoretických studií (Toman & Flegr, 2017c, 2018a, b, přílohy 2, 3, 4), jsme se věnovali makroevolučním implikacím teorie zamrzlé plasticity. Jedná se především o fenomén makroevolučního zamrzání, tj. postupného snižování makroevolučního potenciálu pohlavních linií. Makroevoluční zamrzání může mít řadu příčin. Především ale vyplývá z hromadění efektivně nevratně polymorfních alel, které nejsou schopné přejít do plastického stavu za žádných realistických okolností, a hromadění dále neproměnlivých prvků genotypovo-fenotypové mapy v průběhu evoluce evolvability jednotlivých linií. Jednotlivé příčiny se navíc mohou za určitých okolností synergisticky podporovat.

V souladu s tím jsem se nejprve v kapitole 4.1 věnoval naší studii (Toman & Flegr, 2018a, příloha 2) pojednávající o fenoménu evoluce evolvability a společných rysech genetické architektury (genotypovo-fenotypové mapy) různých organismů. Viděli jsme, že evoluce evolvability je v zásadě biosémiotický proces, který kanalizuje evoluční změny a usnadňuje adaptaci evolučních linií. Společnými atraktory evoluce evolvability jsou robustnost a modularita, přičemž evolvabilita se vyvíjí v závislosti na evoluční zkušenosti dané linie. Vedlejším důsledkem stejného kanalizačního procesu je však vznik a hromadění evolučních *constraints*, které mohou vést až k úplnému vyčerpání makroevolučního potenciálu, tj. schopnosti vytvářet výrazné evoluční novinky. Tento fenomén přitom není čistě teoretický – jak jsme doložili, projevoval se v historii života mj. snižováním proměnlivosti evolučních linií nebo jejich mezidruhové a vnitrodruhové disparity.

Klíčovým, ale doposud značně opomíjeným, procesem evoluce evolvability je třídění z hlediska stability. Popisu tohoto fenoménu, jeho specifik, vztahu k přirozenému výběru a (makro)evolučních důsledků jsme se věnovali v následující kapitole 4.2 vycházející ze studie (Toman & Flegr, 2017c, příloha 3). Z hlediska makroevolučních implikací teorie zamrzlé plasticity je nejpodstatnější, že se vlivem třídění z hlediska stability na všech úrovních biologické evoluce neustále hromadí stabilnější prvky, tj. prvky, které vykazují menší pravděpodobnost svého zániku nebo změny v prvky jiné.

Evoluční linie s vyšším makroevolučním potenciálem mají větší pravděpodobnost odštěpení zásadně odlišných dceřiných druhů, odstartování adaptivních radiací či osídlení nových prostředí. Makroevoluční zamrzání by tudíž teoreticky mohl zastavit druhový výběr. Prokaryotické organismy s velkými populacemi, kde řídí selekce osud změn i jen velmi lehce postihujících makroevoluční potenciál, každý jedinec zakládá vlastní evoluční linii a u kterých druhový výběr na základě makroevolučního potenciálu v zásadě odpovídá individuální selekci, nejspíše na tomto základě opravdu dokáží makroevoluční zamrzání efektivně zpomalit. U pohlavních organismů, které mají zpravidla daleko menší populace, druhovým výběrem jsou ovlivňovány jen slabě a drobná snížení makroevolučního potenciálu hromadí pod rozlišovací schopností selekce, však makroevoluční zamrzání nejspíše představuje efektivně nevratný „rohatkovitý“ proces a pokračuje v plné síle.

Jak jsme rozebrali dále v kapitole 4.3 podle článku Toman a Flegr (2018b, příloha 4), alternativy zamrzající modulární genetické architektury jsou sice představitelné, kvůli jejím přirozeném výhodám se ale v reálném světě prakticky nevyskytují. Ani jiné relativně jednoduché cesty, jak se vyhnout makroevolučnímu zamrzání či obnovit makroevoluční potenciál, patrně v evoluci nehrají zásadní roli. Za určitých okolností může docházet k perspektivní kombinaci několika do velké míry zamrzlých elementů tělní stavby či fungování, nebo rozmrzání některých takovýchto komponentů. Další možností, která může vést k dílčímu obnovení makroevolučního potenciálu, jsou heterochronické změny vývoje a zejména jeho radikální zjednodušení. Žádný z těchto procesů však nejspíše v dlouhém časovém měřítku nedokáže makroevoluční zamrzání zastavit.

Jedinou efektivní cestou ze „slepé uličky“ tak patrně zůstává postup na vyšší úroveň hierarchické organizace. Ten může mít podobu vnitřní modularizace organismální stavby či fungování včetně vzniku nového způsobu dědičnosti, nebo fraternálního či egalitářského přechodu v individualitě. Přirozeně modulární organismus vyšší úrovně oplývá obnoveným makroevolučním potenciálem. Třídění z hlediska stability však účinkuje i na této úrovni, a tak pomalu dochází ke specializaci jeho konstitutivních elementů a jejich integraci doprovázené ubýváním makroevolučního potenciálu a rostoucím tlakem na další postup na ještě vyšší úroveň hierarchické komplexity. Výsledkem tohoto procesu je podle teorie zamrzlé evoluce známý makroevoluční trend zvyšování hierarchické komplexity v historii pozemského života. Stejné vysvětlení ale patrně může mít i řada jeho doprovodných fenoménů včetně McSheaova evolučního syndromu, modulárního charakteru organismů, postupného zrychlování trendu se dvěma velkými skoky v neoproterozoiku a kambriu, jeho typičnosti pro eukaryota a zejména jejich komplexní zástupce, odlišnosti pre-neoproterozoické (a hlavně prekambrické) evoluce od post-neoproterozoické (a hlavně fanerozoické), nebo odlišného charakteru evoluce prokaryot a eukaryot. Žádný jiný koncept přitom nenabízí koherentní vysvětlení pro tak široké spektrum dosud spolehlivě nevysvětlených makroevolučních fenoménů.

Z předchozích řádků vyplývá, že teorie zamrzlé plasticity, respektive její zastřešující koncept, teorie zamrzlé evoluce, dokáží koherentně vysvětlit řadu záhadných ekologických a makroevolučních fenoménů sahajících od udržování sexuality až po trendy v evolvabilitě a hierarchické komplexitě. Když se navíc s ohledem na makroevoluční implikace teorie zamrzlé plasticity vrátíme k výsledkům naší první, ekologické, studie (Toman & Flegr, 2017a, příloha 1), začíná se rýsovat dosud neodhalený komplexní obrázek evolučních dějů, které v období proterozoika mohly vést k zásadní změně evoluční dynamiky a vzniku moderní formy pozemské biosféry.

Eukaryotické organismy se od svých prokaryotických předků liší v bezpočtu různých ohledů. Základní rozdíl nicméně spočívá v odlišné životní strategii těchto dvou skupin pozemského života (Carlile, 1982; Ward & Brownlee, 2000, str. 83-112, Cohan & Koeppel, 2008; Schulze-Makuch & Irwin, 2008, str. 43-64). Bez ohledu na nezřídka velké vnitroskupinové rozdíly, typická eukaryotická buňka je zhruba desetkrát delší než prokaryotická, což znamená zhruba tisícinásobný objemový rozdíl (Carlile, 1982). Také generační doby prokaryot bývají výrazně kratší. Byť výjimečně nalezneme i populace, ve kterých dosahují desítek až stovek let (viz např. Kuhn et al., 2014), výjimkou nejsou generační doby okolo dvaceti minut. Ty umožňuje menší velikost buněk, která neklade tak velké časové nároky na difuzi metabolitů. Výsledkem je kapacita pro výrazně vyšší intenzitu metabolismu, růstovou a reprodukční rychlost prokaryotických organismů ve srovnání s eukaryotickými (Carlile, 1982). Nejkratší mitóza oproti tomu eukaryotům trvá kolem hodiny (Carlile, 1982) a meióza okolo deseti hodin (Flegr, 2005, str. 243). Prokaryota jsou tudíž ve své podstatě typickými r-stratégy uzpůsobenými na život v prostředí s nerovnoměrným přísunem zdrojů, kde jsou ve výhodě linie schopné nejrychlejšího množení. Eukaryota jsou oproti tomu přirozenými K-stratégy uzpůsobenými na život v bioticky a abioticky proměnlivém a heterogenním prostředí s malým konstantním objemem strukturovaných zdrojů (Carlile, 1982).

S prostorovou a časovou škálou se patrně zvyšuje heterogenita prostředí. Celá tato obecná problematika na pomezí teoretické ekologie a evoluční biologie by si zasloužila větší pozornost badatelů. I tak nicméně můžeme shrnout, že se prostorová a časová heterogenita v tomto ohledu poněkud liší. Z prostorového hlediska může panovat vysoká heterogenita prostředí na velkých i malých škálách. Půda (Ettema & Wardle, 2002; Lavelle & Spain, 2003; Paul, 2007; Young et al., 2008; Vos et al., 2013), povrch (Jiang, 2015), nebo dokonce vodní sloupec (Stocker, 2012) mohou být například velmi ostrůvkovité i ve velmi malém měřítku. Rozsáhlejší srovnání prostorové heterogenity sahající přes několik úrovní jsou však vzácná a zůstává tak otázkou, nakolik je podobně fraktální charakter prostředí typický. Prodloužení generační doby oproti tomu musí nutně vést k *subjektivnímu* zvýšení temporální heterogenity, tj. zažívané proměnlivosti, prostředí – dlouhověké organismy se během vlastního života vždy setkají s více výkyvy podmínek. To se navíc může zpětně promítat do *subjektivní* prostorové heterogenity, protože takové organismy mají potenciál během svého života narazit na větší množství různých ostrůvků prostředí. Nepřímým dokladem výše uvedených skutečností je například fakt, že prokaryotické organismy vykazují jen slabé nebo žádné biogeografické patrnosti, zatímco tento faktor hraje důležitou roli u eukaryotických, a především mnohobuněčných eukaryotických, organismů (Ragon et al., 2012).

Bez ohledu na to, z jakých proximálních důvodů eukaryotické organismy dosáhly větších tělesných velikostí a delších generačních dob, je tedy takřka jisté, že právě tato obecná změna vedla k výraznému zvýšení *subjektivní heterogenity* jejich prostředí. Pro život v heterogenním prostředí je však klíčová schopnost rychlých, a přitom vratných reakcí na různorodé a neustále se měnící podmínky. Obývání větších časových a prostorových škál tak vytvořilo tlak na dlouhodobé udržování genetického polymorfismu. Právě tuto vlastnost má, jak jsme viděli v kapitole 3.1, pohlavnost. Sexualita se tudíž mohla bez ohledu na proximální důvody svého vzniku stát ideální preadaptací na život ve vyšších časových a prostorových škálách a postupně se u eukaryot fixovat jako nezbytná metaadptace. Tomu mohla dále napomoci i tendence eukaryotických organismů vstupovat do bioticky intenzivních interakcí typu predace a parazitace (Carlile, 1982). Dominantní zastoupení pohlavních zástupců mezi eukaryotickými organismy, třebaže je ve většině skupin druhotný přechod k nepohlavnosti možný (Toman, 2015, str. 79-105), tuto hypotézu jen podporuje.

Stejné procesy, tj. pohlavnost, prodloužení generační doby, zvětšení velikosti a zmenšení populačních četností nicméně v delším časovém měřítku vydláždily cestu makroevolučnímu zamrzání, které nepohlavní prokaryotické organismy s obrovskými populacemi pod silným vlivem selekce tolik nepostihuje (viz podkapitola 4.2.3). Výsledkem byl jednak tlak na komplikaci, a zejména modularizaci, genotypovo-fenotypové mapy (viz podkapitola 4.1.2), v delším časovém měřítku ale hlavně k přechodům na vyšší úrovně hierarchické komplexity s obnoveným makroevolučním potenciálem (viz podkapitola 4.3.2). Vzhledem k tomu, že makroevoluční zamrzání probíhá na všech úrovních a s komplikací genotypovo-fenotypové mapy možná ještě zrychluje, výsledkem se stal trend zvyšování hierarchické komplexity organismů výrazně akcelerující od neoproterozoika až kambria. Vedlejšími důsledky stejného procesu je několik makroevolučních fenoménů, z nichž některé McShea shrnul pod názvem makroevoluční syndrom (viz podkapitola 4.3.3).

Zvyšování hierarchické komplexity organismů přitom v dlouhém časovém měřítku přímo (vlivem vytváření nových životních strategií, obsazování nových prostředí apod.) i nepřímo (prostřednictvím koevoluce s organismy nižších úrovní, spoluvytváření nových prostředí a ovlivňování ekologických podmínek) vedlo k zásadnímu přebudování ekologického prostoru naší planety, radikální změně dynamiky evoluce a dramatické změně biosféry (Knoll & Bambach, 2000; Carroll, 2001; Butterfield, 2007; Toman & Flegr, 2017a). Zdánlivě triviální zvětšení tělesné velikosti a prodloužení generační doby u prvních eukaryot tak mohlo spustit celé domino vedlejších efektů, které vedly až ke vzniku pozemské biosféry, jak ji známe dnes.

Celou tuto hypotézu je třeba zatím brát s rezervou. Ne všechny organismy například pasují do poněkud zjednodušené ekologicko-evoluční dichotomie mezi prokaryoty a eukaryoty uvedené výše. Rovněž je jasné, že prokaryotické organismy prodělaly po vzniku eukaryot stejně intenzivní evoluci jako eukaryota samotná. Při našich úvahách tudíž musíme vycházet z ekologie a životních strategií eukaryot co nejpodobnějších neoproterozoickým zástupcům. Pokud ale bude postulovaný rozvrh částečně, nebo úplně podpořen, může mít závažné implikace hned pro několik oborů.

Žádné doposud provedené počítačové simulace ani laboratorní experimenty otevřené evoluce například dosud bez silného tlaku umělého výběru nereplikovaly růst (hierarchické) komplexity organismů. Pro tyto neúspěchy byla samozřejmě navržena řada vysvětlení, nelze ale vyloučit, že růstu (hierarchické) komplexity tyto zjednodušené modely dosáhnou až když inkorporují faktor makroevolučního zamrzání a obnovy makroevolučního potenciálu postupem na nové úrovně hierarchické organizace (Toman & Flegr, 2017b, 2018b, příloha 4). Teorie zamrzlé evoluce také může výrazně usměrnit naše očekávání ohledně fosilního záznamu. Pokud je trend zvyšování (hierarchické) komplexity charakteristický pouze pro pohlavní organismy, nemáme žádný důvod očekávat komplexnější organismy ve vrstvách z doby před vznikem eukaryot. Zároveň se nemusíme podivovat, proč s výjimkou eukaryot prokaryotické organismy nikdy nevytvořily hierarchicky komplexnější těla organizovaná na mnoha různých úrovních. Může se totiž jednat o specifický vedlejší produkt evoluce pohlavních makroevolučně zamrzajících linií.

Ještě závažnější jsou potom astrobiologické implikace našeho konceptu. Evoluce evolvability, stejně jako třídění z hlediska stability, představují fenomény, kterým musí nutně podléhat všechny živé systémy. Pokud tedy představoval vznik velkých eukaryotických buněk s dlouhou generační dobou, které kvůli životu v heterogenním prostředí větších časových a prostorových škál potřebují udržovat vysoký genetický polymorfismus prostřednictvím pohlavního rozmnožování, výjimku, nebo pokud existují nějaké jiné procesy, které velkým a dlouhověkým organismům umožní dlouhodobě přežívat i bez makroevolučního zamrzání, nemáme žádný důvod očekávat ve vesmíru velké zastoupení komplexních forem života. Samozřejmě zatím můžeme vycházet pouze ze vzorku naší Země. Fakt, že zde život vznikl záhy po zformování planety (před asi 4 miliardami let), zatímco trend zvyšování hierarchické komplexity organismů efektivně odstartoval až zhruba o 2,8 miliardy let později, nicméně nenasvědčuje, že by vznik velkých a dlouhověkých eukaryotických organismů eukaryotického typu byl zákonitý. Není přitom bez zajímavosti, že ke stejnému závěru ohledně frekvence komplexního života ve vesmíru dospěli také Ward a Brownlee (2000).

Úplným závěrem můžeme zmínit několik možností dalšího testování našich teoretických konceptů. Řadu z nich jsme nastínili už v našich publikacích (Toman, 2015; Toman & Flegr, 2017a, b, c; 2018a, b, přílohy 1, 2, 3, 4). Jako první se nabízí testování reálné existence, síly a rozšíření prezentovaných makroevolučních trendů – trendu snižování makroevolučního potenciálu, fenotypové proměnlivosti v rámci kladů, mezidruhové a vnitrodruhové disparity, nebo zvyšování hierarchické komplexity organismů v evoluci. Jak jsme viděli v podkapitolách 4.1.3 a 4.3.3, podpora těchto trendů v provedených studiích rozhodně není stoprocentní. Případné detailní charakteristiky těchto trendů nás navíc mohou nasměrovat při dalším bádání. To samé se týká procesů stojících za evolucí evolvability, kterým se věnuje hlavně obor evoluční a vývojové biologie (Evo-Devo). Proti našemu konceptu by například svědčilo, pokud by evoluce evolvability u různých kladů nevykazovala žádné společné patrnosti, nebo kdyby rané fáze (nikoli však úplně nejrannější, viz Galis & Metz, 2001; Irie & Kuratani, 2014; Hu et al., 2017) individuálního vývoje nebyly konzervovanější než ty pozdní.

V úvahu připadají i pozitivní testy našeho konceptu. Ten je příliš rozsáhlý, než aby ho bylo možné testovat jako celek. Můžeme se ale zaměřit na jednotlivé hypotézy. Rozhodně by bylo možné, například prostřednictvím počítačového modelu, ověřit, zda a za jakých okolností může třídění elementů tělní stavby či fungování z hlediska stability na jedné úrovni vést ke zvyšování hierarchické komplexity. V obecnější rovině by potom bylo přínosné simulovat evoluci evolvability při zahrnutí námi postulovaných fenoménů včetně třídění z hlediska stability. V neposlední řadě by šlo prostřednictvím numerického modelu přezkoumat rozmezí podmínek – populačních četností, síly druhového výběru, frekvence pohlavního rozmnožování apod. – za kterých operuje makroevoluční zamrzání principem „makroevoluční rohatky".

Kromě toho by bylo zajímavé porovnat evoluční dynamiku pohlavních a nepohlavních linií. Podle teorií zamrzlé plasticity a zamrzlé evoluce by se evoluce pohlavních organismů měla vymykat svým elastickým charakterem, tendencí k makroevolučním zamrzání, růstem hierarchické komplexity a dalšími výše zmíněnými charakteristikami. Prvním pokusem v tomto směru vlastně byla už ekologická srovnávací studie (Toman & Flegr, 2017a, příloha 1) popsaná v kapitole 3.1. Kromě toho bychom však mohli srovnávat například mezidruhovou disparitu (starobyle) nepohlavních skupin oproti jejich příbuzným pohlavním kontrolám. Podle teorie zamrzlé evoluce bychom mohli očekávat, že nepohlavní linie, a zvláště dlouhodobě úspěšné a rozrůzněné klady starobyle nepohlavních organismů, budou díky permanentně plastickému charakteru své evoluce prostému makroevolučního zamrzání vykazovat větší proměnlivost a potažmo rozptyl měřených vlastností, tj. mezidruhovou disparitu. O podobné srovnání na základě literárních dat jsem se již pokusil (Toman, 2013). Konkrétně jsem se zaměřil na rozmezí teplotních mezí aktivity starobyle nepohlavních eukaryotických kladů a jejich pohlavních kontrol. Kvůli malému množství spolehlivě identifikovatelných starobyle nepohlavních kladů, jejich poměrně obskurnímu charakteru a malé probádanosti jsem však bohužel nedošel k žádným statisticky významným výsledkům. Experimentální měření tolerancí různých faktorů prostředí mezi příslušníky pohlavního a nepohlavního kladu by však mohlo představovat nadějnější přístup.

Přínosná by mohla být také kvantitativní studie zaměřená na identifikaci makroevolučních jevů postulovaných teorií zamrzlé evoluce. Podle našeho konceptu bychom měli v každém časovém řezu nalézt silně zamrzlé a nepříliš proměnlivé evoluční linie s nízkou disparitou, stejně jako linie, které nedávno svůj makroevoluční potenciál obnovily a vykazují velkou proměnlivost i disparitu. První jmenované klady by mohly v průběhu geologického času svůj makroevoluční potenciál vzácně obnovovat, zatímco druhé by jej za průběžného snižování své disparity měly ztrácet. Výsledné patrnosti v disparitě a potažmo diverzitě by mělo být možné odhalit a studovat na základě paleontologických či fylogenetických dat.

Neméně zajímavé se jeví srovnání primárně pohlavních eukaryotických druhů s primárně nepohlavními druhy prokaryotickými. Podobná studie by samozřejmě byla snížená tím, že u prokaryot nenalezneme žádné blízce příbuzné pohlavní druhy. Případné rozdíly mezi oběma velkými skupinami tak mohou jít na vrub jiným faktorům než přítomnosti nebo nepřítomnosti pohlavního rozmnožování. Na druhou stranu jsou ale prokaryota, na rozdíl od mladých druhotně nepohlavních eukaryotických linií, nepohlavnímu způsobu života dokonale přizpůsobená a evolučně životaschopná. Nejproveditelnější by patrně bylo srovnání subjektivní heterogenity prokaryotického a eukaryotického prostředí podobné studii Toman & Flegr (2017a, příloha 1). Podle našeho konceptu by se mělo prostředí pohlavních eukaryotických druhů obecně vyznačovat větší relativní časovou a prostorovou heterogenitou. Zásadní otázkou také je, jak se prostorová a časová heterogenita prostředí mění s měřítkem, a to zejména na mikroskopických škálách. V tomto ohledu ale samozřejmě musíme počítat i s adaptacemi samotných organismů, tj. zkoumat subjektivní a nikoli objektivní heterogenitu jejich prostředí.

V neposlední řadě potom můžeme získat zajímavé vhledy do evoluční dynamiky různých živých systémů studiem jiných systémů podléhajících evoluci – například kultury, nebo jejích konkrétních aspektů jako jsou technologie, společnosti, instituce, jazyky či nauky. Také tyto systémy hromadí ve své historii prvky tříděním z hlediska stability, což se může (samozřejmě s nutnými specifiky) projevovat různými variacemi na optimalizaci jejich evolvability včetně vnitřní modularizace (jazykových prvků, institucí apod.) za současného snižování pravděpodobnosti zásadních změn. Také v těchto případech může být radikální změna možná pouze po výrazném zjednodušení celého systému. O podobné vhledy jsme se pokusili v našich článcích (Toman & Flegr, 2017c, 2018a, b, přílohy 2, 3, 4).

Teorie zamrzlé plasticity se týká samotných základů biologické evoluce. Její ekologické a makroevoluční implikace dokáží koherentně vysvětlit bezprecedentně dlouhou řadu záhadných evolučních fenoménů. Z konceptuálního hlediska navíc propojuje mikroevoluční ekologicko-genetické bádání ve stylu moderní evoluční syntézy s makroevolučně-paleontologickými úvahami o evoluci evolvability charakteristickými spíše pro evoluční a vývojovou biologii či rozšířenou evoluční syntézu. Kromě toho má silnou návaznost na biosémiotiku a další hraniční evolučně-biologické koncepty. V budoucnu by tak mohla posloužit jako svorník těchto nezřídka protichůdných ale nikoli nekompatibilních přístupů a odrazový můstek pro další bádání na poli evoluce evolvability.

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7 PŘÍLOHY

7.1 PŘÍLOHA 1

Toman J, Flegr J. 2017a. General environmental heterogeneity as the explanation of sexuality? Comparative study shows that ancient asexual taxa are associated with both biotically and abiotically homogeneous environments. *Ecology and Evolution* **8:** 973-991.

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ORIGINAL RESEARCH

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General environmental heterogeneity as the explanation of sexuality? Comparative study shows that ancient asexual taxa are associated with both biotically and abiotically homogeneous environments

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Abstract

Ecological theories of sexual reproduction assume that sexuality is advantageous in certain conditions, for example, in biotically or abiotically more heterogeneous environments. Such theories thus could be tested by comparative studies. However, the published results of these studies are rather unconvincing. Here, we present the results of a new comparative study based exclusively on the ancient asexual clades. The association with biotically or abiotically homogeneous environments in these asexual clades was compared with the same association in their sister, or closely related, sexual clades. Using the conservative definition of ancient asexuals (i.e., age >1 million years), we found eight pairs of taxa of sexual and asexual species, six differing in the heterogeneity of their inhabited environment on the basis of available data. The difference between the environmental type associated with the sexual and asexual species was then compared in an exact binomial test. The results showed that the majority of ancient asexual clades tend to be associated with biotically, abiotically, or both biotically and abiotically more homogeneous environments than their sexual controls. In the exploratory part of the study, we found that the ancient asexuals often have durable resting stages, enabling life in subjectively homogeneous environments, live in the absence of intense biotic interactions, and are very often sedentary, inhabiting benthos, and soil. The consequences of these findings for the ecological theories of sexual reproduction are discussed.

KEYWORDS
ancient asexuals, asexual reproduction, Frozen evolution theory, habitat heterogeneity, sexual reproduction

1 | INTRODUCTION

1.1 | Paradox of sexual reproduction

Sexual reproduction (sensu amphimixis, the alternation of meiosis and syngamy) is one of the most enigmatic phenomena in evolutionary biology (see, e.g., Bell, 1982; Maynard Smith, 1978; Meirmans & Strand, 2010; Williams, 1975), mainly because it brings many obvious disadvantages in comparison with asexual reproduction—the well-known twofold cost of sex being only the first and most obvious one (see, e.g., Lehtonen, Jennions, & Kokko, 2012). None of these disadvantages apply to all sexual species because of the highly variable nature of their reproduction. However, under many circumstances, the disadvantages apply profoundly (Lehtonen et al., 2012). Thus, sexual reproduction, its overwhelming predominance, and its long-term maintenance in eukaryotes remain an enigma that call for explanation.

Many main concepts and their countless variants were proposed to explain the paradox of sexual reproduction (reviewed, e.g., in Bell, 1982, 1985; Kondrashov, 1993; Maynard Smith, 1978; Meirmans & Strand, 2010; Otto, 2009; Sharp & Otto, 2016; Williams, 1975). The genetic advantages of sex for sexually reproducing populations or individuals are highlighted by concepts such as the Weismann's idea of sex generating variability, later delimited as the hypothesis of Vicar of Bray (Bell, 1982), Fisher–Muller's accelerated evolution of sexual species (Fisher, 2003; Muller, 1932), breaking free of neighboring deleterious mutations (Crow, 1970), reduction of the spread of genomic parasites (Sterrer, 2002), advantage of diploidy (Lewis & Wolpert, 1979), repair of DNA (Bernstein & Bernstein, 2013), restoration of epigenetic signals (Gorelick & Carpinone, 2009), eventually stochastic and deterministic variants of Muller's ratchet hypothesis (Kondrashov, 1982; Muller, 1964). These concepts are not mutually exclusive and underwent their own evolution during the last decades, leading to some convincing scenarios of the spread of sexuality and its long-term predominance (see, e.g., Keightley & Otto, 2006; Otto, 2009; Otto & Lenormand, 2002; Sharp & Otto, 2016).

Ecological theories of sexual reproduction, on the other hand, stress the assumption that sex provides some ecological advantage to sexual species. Certain trends can be clearly found in the geographic distribution of sexual reproduction, as was recently summarized by Hörandl (2006, 2009) or Vrijenhoek and Parker (2009). Moreover, primarily asexual prokaryotes are abundant and, as will be shown later in this study, clear examples of short-term and long-term secondarily asexual eukaryotic taxa have been identified. Sex is obviously not universally advantageous. It was also suggested that some advantages of sexual reproduction postulated by "genetic theories" could be achieved by automixis (Gorelick & Carpinone, 2009; Neiman & Schwander, 2011; but see also Keightley & Otto, 2006; Otto, 2009; Otto & Lenormand, 2002; Sharp & Otto, 2016).

However, ecological theories of sexual reproduction need not contradict the benefits of sex identified by "genetic theories." In fact, "genetic theories" that consider adaptiveness are necessarily related to ecological phenomena, and most "ecological theories" have important genetic components as well (see Otto, 2009; Otto & Lenormand, 2002; Sharp & Otto, 2016). The difference lies mainly in their target of interest. "Ecological theories" focus on the direct, ecological, conditions that facilitate the evolution, spread, and long-term predominance of sex. Therefore, it might be more correct to designate them as ecology-dependent (in contrast to ecology-independent theories mentioned above). In any case, the final answer to the "greatest paradox of evolutionary biology" probably lies in the group of ecological theories of sexual reproduction, respectively, in some form of theoretical synthesis that incorporates the assumptions of both genetic and ecological theories of sex (Otto, 2009; Otto & Lenormand, 2002; Scheu & Drossel, 2007; Sharp & Otto, 2016; Song, Drossel, & Scheu, 2011; West, Lively, & Read, 1999).

1.2 | Ecological theories of sexual reproduction and their predictions

"Ecological theories" such as the Red Queen theory (Hamilton, Axelrod, & Tanese, 1990), the evolutionary arm-races hypothesis (Dawkins & Krebs, 1979), and the fast-sexual-response hypothesis of Maynard Smith (1993) emphasize the sexually reproducing organisms' advantage when interacting with other organisms that are able to dynamically react in a coevolutionary manner. According to these "biotic heterogeneity advantage" theories (see Table 1), sexual species should prosper in spatially and temporally biotically heterogeneous environments, that is, environments with many biotic interactions from competitors, predators, and parasites (see Table 2). In the presence of such intensive biotic interactions, sexual species are expected to be especially favored because they maintain high-genetic polymorphism and could quickly react to the counter-adaptations of their evolutionary opponents by a simple change of allele frequencies in the

TABLE 1 Ecological theories of sexual reproduction

"Biotic heterogeneity advantage" theories	E.g. Red Queen theory (Hamilton, et al. 1990), evolutionary arm-races hypothesis (Dawkins & Krebs, 1979), fast-sexual-response hypothesis (Maynard Smith, 1993)
"Abiotic heterogeneity advantage" theories	E.g. Lottery and Sisyphean genotypes hypothesis (Williams, 1975), elbow room hypothesis (Maynard Smith, 1978), tangled bank hypothesis (Bell, 1982), hypothesis of fluctuating selection (Smith, 1980), hypothesis of reduced response to fluctuating selection (Roughgarden, 1991)
"Overall heterogeneity advantage" theories	E.g. hypothesis of genetic polymorphism in fluctuating environments (Williams, 1975), frozen plasticity theory (Flegr, 2013), concept of density-dependent–independent population regulation (Scheu & Drossel, 2007; Song, et al. 2011)

A classification of ecological theories of the maintenance of sexual reproduction presented in this paper. Given the extraordinary plethora of proposed concepts, this summary cannot be exhaustive nor complete. Only the major concepts as they were originally proposed are included.

TABLE 2 Biotically and abiotically heterogeneous environments

	Biotically heterogeneous environments	*Abiotically heterogeneous environments*
Characteristics	Environments with numerous and/or intensive biotic interactions among competitors and hosts and their predators/parasites that are characteristic by dynamic coevolutionary reactions	Spatiotemporally abiotically very variable environments, i.e. patchy, diverse, changeable, unpredictable, and with unequally distributed resources
Examples	Tropical rainforests, low-latitude coral reefs, ancient lakes, habitats with climax communities or generally with species-rich complex ecosystems	Temporary, ephemeral or exposed habitats, dynamically changing freshwater environments, coastal habitats, biomes of high latitudes and/or altitudes

Main characteristics of biotically and abiotically heterogeneous environments in the optics of ecological theories of sexual reproduction and examples of habitats that are characteristic by strong biotic and abiotic heterogeneity.

population. The speed, not the depth, of adaptation is more important in these environments (Maynard Smith, 1993).

Another group of ecological theories of sexual reproduction comprises, for example, the lottery and Sisyphean genotypes hypothesis (Williams, 1975), elbow room hypothesis (Maynard Smith, 1978), tangled bank hypothesis (Bell, 1982), hypothesis of fluctuating selection (Smith, 1980), and hypothesis of reduced response to fluctuating selection (Roughgarden, 1991). These "abiotic heterogeneity advantage" theories (see Table 1) see the main advantage of sexual reproduction in the higher fitness that sexual individuals or species achieve in abiotically heterogeneous environments—environments that are abiotically variable in space and/or time, that is, diverse, unpredictable, and with unequally distributed resources (see Table 2). An abiotic environment does not co-evolutionarily react to the evolutionary moves of its inhabitants, potentially allowing them to deeply adapt to it under certain circumstances, for example, under conditions of slow, long-term changes. Under these circumstances, the asexual species might have an advantage because, for example, they do not suffer from segregation and recombination loads (Crow, 1970). However, the spatial and temporal heterogeneity of an environment is expected to usually ensure the advantage of sexual species.

The heterogeneity of the environment, both biotic and abiotic, can be comprehended as the sum of heterogeneity in space (in the sense of variability, e.g., patchiness) and time (in the sense of instability, especially when the change is unpredictable). Both spatial and temporal heterogeneity could be the consequences of both biotic and abiotic factors (Li & Reynolds, 1995). The temporal and spatial aspects of heterogeneity, even though differing substantially at first sight, could act remarkably similarly in terms of favoring sexual species (Kondrashov, 1993; Neiman & Schwander, 2011; Otto, 2009; Otto & Lenormand, 2002; Scheu & Drossel, 2007; Sharp & Otto, 2016; Song et al., 2011). In principle, the most important factor is always whether the environment inhabited by the offspring differs in its character (i.e., selective pressures) from the environment inhabited by their parents.

The "biotic" and "abiotic" theories of sexual reproduction mentioned above have different predictions regarding the character of the environment that will be advantageous for sexual and asexual species. According to the major source of the environmental heterogeneity, it is therefore essentially possible to differentiate between these two groups of ecological theories of sexual reproduction. However, the predictions of different theories are not absolutely disparate—one could easily devise examples of environments suitable for asexual species according to both groups of theories, for example, stable extreme environments. Similarly, the individual theories of sexual reproduction are far from being disparate; they are usually interconnected in their basic principles, they intermingle and complement each other (Meirmans & Strand, 2010; Otto, 2009; Otto & Lenormand, 2002; Scheu & Drossel, 2007; Sharp & Otto, 2016; Song et al., 2011). Moreover, biotic and abiotic parts of the environmental heterogeneity, as well as other factors, are usually interconnected and influence and complement each other in their effects on the advantage of sexual or asexual reproduction (Glesener & Tilman, 1978; see also Otto & Lenormand, 2002; Otto, 2009; Sharp & Otto, 2016). It is therefore possible that the differentiation of "biotic" and "abiotic" ecological theories of sex is important in theory, but not important in the real world, and that sexual organisms do have an advantage in environments that are both biotically and abiotically relatively heterogeneous (i.e., overall heterogeneous environments, see Table 1 and Figure 1).

The fitness values of alleles of sexual species are often frequency- and contextually dependent (on other alleles of the same gene, alleles of other genes, or particular traits). Such alleles (as well as alleles that are pleiotropically or epistatically interconnected with them) are not easily fixated or eliminated. Therefore, sexual species usually maintain high-genetic polymorphism that enables them to readily react to momentary changes of environment (by the changes in the frequency of already present alleles). However, the same factor (frequency- and contextually dependent fitness values of alleles) is expected to slow-down or, eventually, stop this response as soon as the frequency of present alleles significantly change. Therefore, it is possible that sexual species, in contrast to asexual ones, are usually not able to fully adapt to transient environmental changes; they mostly retain some genetic polymorphism that helps them escape extinction when the conditions

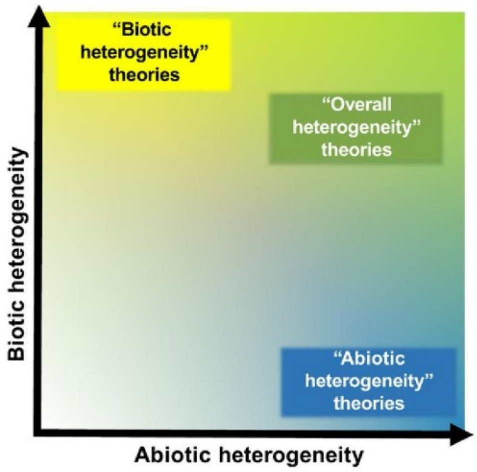

FIGURE 1 Ecological theories of sexual reproduction and their predictions regarding environmental heterogeneity. Diagram illustrating predictions of ecological theories of sexual reproduction regarding environmental heterogeneity. "Biotic" theories consider highly biotically heterogeneous environments (y axis, yellow) to be those that promote sexuality over asexual reproduction. "Abiotic" theories, on the other hand, highlight abiotically heterogeneous environments (x axis, blue) in this regard. Excluding more complicated models, abiotic heterogeneity has no role in "biotic" theories and *vice versa*. This is in stark contrast with several concepts that consider both kinds of environmental heterogeneity important for promoting sexual reproduction (green). Color saturation indicates hypothetical advantage of sexual organisms over asexuals in given conditions according to each group of theories

quickly return to normal. It was suggested by Williams (1975 pp. 145–146, 149–154, 169) and explicitly discussed by Flegr (2008, 2010, 2013) that the resulting lower ability of sexual species to fully adapt to transient environmental changes may bring them, paradoxically, a major advantage in randomly fluctuating environments, that is, in environments expressing large (biotic or abiotic) heterogeneity in time.

According to this (meta-)hypothesis (see Table 1 and Figure 1), asexuals would prevail in stable or predictively slowly changing, possibly extreme, environments of low-temporal heterogeneity (Flegr, 2013). Given the similarities between the effect of temporal and spatial heterogeneity mentioned above, this notion can be readily extended to encompass both temporal and spatial heterogeneity. Similar remarks were made, for example, by Williams (1975, p. 153) and Roughgarden (1991), while a combination of several aspects of heterogeneity was implicitly also proposed as the explanation of the presence of sexual reproduction by Glesener and Tilman (1978) and some interpreters of the Red Queen theory (e.g., Butlin, Schön, & Martens, 1999) or the tangled bank hypothesis (e.g., Bell, 1982; Scheu & Drossel, 2007; Song et al., 2011).

Otto (2009) and Sharp and Otto (2016) identified a plethora of factors that enable the spread and long-term predominance of sex in computer simulations, spatiotemporal heterogeneity, and varying selection pressures being among the most important. Moreover, the assumption of Flegr (2008, 2010, 2013) that the contextually dependent fitness value of alleles is a major factor in maintaining high long-term genetic variability of sexual populations seems to be empirically supported (see Otto, 2009). This hypothesis was also supported by the results of certain experimental studies, for example, long-term patterns of fitness and genetic variability (Renaut, Replansky, Heppleston, & Bell, 2006) or dynamics of adaptation (Colegrave, Kaltz, & Bell, 2002; Kaltz & Bell, 2002) in sexually and asexually reproducing *Chlamydomonas*. Furthermore, it is in accordance with theoretical modeling (Scheu & Drossel, 2007; Song et al., 2011) and empirical testing (e.g., Bluhm, Scheu, & Maraun, 2016) of concepts that consider density-dependent and independent population regulating factors as the main factors favoring sexual or asexual reproduction.

1.3 | Comparing the ecology of sexual and asexual groups

Most of the organisms that live on Earth, Archaea and Bacteria, are primarily asexual. The primary asexuality is a plesiomorphic trait and therefore does not need any special explanation. In contrast, most of the known species, eukaryotes, are primarily sexual (Speijer, Lukes, & Elias, 2015) while only some eukaryotic lineages switched to secondary asexual reproduction (de Meeus, Prugnolle, & Agnew, 2007; Speijer et al., 2015; Van Dijk, 2009). It is therefore possible to compare the environmental biotic heterogeneity and abiotic heterogeneity of such secondary asexual clades with that of their sexual relatives to test particular ecological hypotheses of sexual reproduction.

Most studies aimed at testing and discriminating between individual ecological theories of sexual reproduction on the basis of their predictions about the environmental correlates of sexual and asexual lineages showed largely inconclusive results. Often their aim was to test particular theoretical concepts: lottery hypothesis and Sisyphean genotypes hypothesis (Hörandl, 2009; Williams, 1975), elbow room hypothesis (Garcia & Toro, 1992; Koella, 1993), Red Queen theory (Burt & Bell, 1987; Neiman & Koskella, 2009), fast-sexual-response hypothesis (Becerra, Brichette, & Garcia, 1999), hypothesis of optimal responsibility to fluctuating selection (Griffiths & Butlin, 1995; Schön & Martens, 2004), hypothesis of prevention of loss of genetic variability under fluctuating selection (Hörandl, 2009; Maynard Smith, 1993; Vrijenhoek & Parker, 2009), or tangled bank hypothesis (Burt & Bell, 1987; Domes, Scheu, & Maraun, 2007; Griffiths & Butlin, 1995; Maraun, Norton, Ehnes, Scheu, & Erdmann, 2012; Vrijenhoek, 1984); or at least they were later interpreted as such. The most extensive comparison not focused on testing one particular theoretical concept was performed by Bell (1982) on multicellular animals (Metazoa). It mostly supported the tangled bank hypothesis. Experiments aimed at discriminating the selective pressures of biotically (see, e.g., Fischer & Schmid-Hempel, 2005) or abiotically (see, e.g., Becks & Agrawal, 2010) heterogeneous and homogeneous environments were also performed, mostly pointing to the conclusion that heterogeneous environments select higher rates of recombination or sexual reproduction. However, particular mechanisms that favor higher levels of sex are hard to determine in these cases that are, moreover, often based on facultatively sexual organisms.

The main problem of the comparative studies mentioned above may be the inclusion of both old and young asexual taxa. Most secondary asexual groups probably are not evolutionarily viable in the long term, as could be deduced from the distribution of asexual lineages on the "tree of life." With the exception of several ancient asexuals (AAs), they form only the terminal twigs—species and genera (Butlin, 2002). This pattern is probably the consequence of the opportunistic nature of their transition to asexual reproduction and subsequent failure in species selection (Nunney, 1989), or the higher persistence of sexual lineages in the process of stability-based sorting (Toman & Flegr, 2017). Moreover, at least some young asexual lineages could, in fact, consist of short-lived clones continuously cleaved from maternal sexual population (Janko, Drozd, Flegr, & Pannell, 2008; Vrijenhoek & Parker, 2009). Alternatively, they could be sustained by an occasional hybridization with related sexual lineages (Butlin, Schön, & Martens, 1998; van Raay & Crease, 1995; Turgeon & Hebert, 1994) or an infrequent transfer of genetic material from "host species" in hybridogenetic and gynogenetic lineages (Bogart, Bi, Fu, Noble, & Niedzwiecki, 2007; Mantovani, Passamonti, & Scali, 2001). In sum, young asexuals do not have to exhibit the properties that would allow them to survive in the long term, the reasons of their temporary success might, in contrast to the AA lineages, differ from case to case, and, contrary to the mainstream view, they could in fact bring a significant noise into the studies of long-term maintenance of sexual (and secondary asexual) reproduction.

1.4 | Aims of the study

The main aim of this study was to map the environmental heterogeneity of well-supported AA groups and identifies possible trends in its differences from the environmental heterogeneity of their closely related sexual clades. In the first part of the study, we compiled data on the environmental heterogeneity of AAs and their sexual controls. In the second, analytical, part of the study, we used the data to test whether AAs more often inhabit (1) generally less heterogeneous environments, (2) less biotically heterogeneous environments, or (3) less abiotically heterogeneous environments. To this end, we used paired exact tests to compare the ecological demands of sexual species and AA species within unrelated clades of eukaryotic organisms. In the third, exploratory, part of the study, we searched for particular environmental properties and organismal adaptations that are common among the AA members of the pairs.

As we outlined in the previous section, the phenomenon of asexual "terminal twigs contra ancient asexuals" is still somewhat controversial, and its real existence is being discussed (see, e.g., Janko, Drozd, & Eisner, 2011; Neiman, Meirmans, Meirmans, Schlichting, & Mousseau, 2009; Schön, Martens, & Rossi, 1996; Schwander & Crespi, 2009). Regardless of these discussions, it is obvious that out of all the secondary asexual clades only the AAs have been able to survive or even diversify in an asexual state for millions of years (Judson & Normark, 1996; Neiman et al., 2009; Normark, Judson, & Moran, 2003; Schurko, Neiman, & Logsdon, 2009; Schwander & Crespi, 2009). This is the main reason that our study is based exclusively on AAs as they already proven to be evolutionarily viable in the long term.

However, it is worth mentioning that the focus on AAs puts forward another serious difficulty: These clades were separated from their sister sexual lineages a long time ago (at least 1 million years ago, see Materials and Methods), and both sexual and asexual lineages thus underwent considerable time periods of independent evolution. Therefore, both lineages independently acquired numerous adaptations that distinguished them but need not be related to the mode of their reproduction. Singular case studies comparing AAs and their sexual sister lineage thus are not expected to have a strong predictive value in the long-term maintenance of asexual reproduction. On the other hand, a comparative study enables us to compare several such pairs of AAs and sexual controls and reveal possible common adaptations of AAs related to their long-term survival in an asexual state.

2 | MATERIALS AND METHODS

2.1 | Identification of ancient asexuals and their sexual controls

2.1.1 | Ancient asexual groups

The definition of the "ancient asexual group" is rather vague. Some researchers consider a lineage to be AA if it reproduces obligately asexually for at least 50,000 generations or 0.5 million years (Law & Crespi, 2002a); some prefer one million generations (Schwander, Henry, & Crespi, 2011), yet others just speak about "millions of years" (Judson & Normark, 1996; Normark et al., 2003). It was even suggested that AAs are not substantially different from other asexuals and their delimitation is more or less arbitrary (Neiman et al., 2009). It is not the aim of this study to argue for the substantial difference of AAs from other asexuals or against it. We focus only on groups that were proven to survive exclusively in an asexual state for a considerable amount of time. Thus, regardless of the discussion on the fundamental distinction of young and old asexual taxa, in the current study we defined AAs conservatively as those secondary asexual eukaryotic lineages that reproduce obligately asexually with a great deal of certainty for at least one million years (see Table S1 for details).

At the beginning, we identified well-supported AA groups with the help of literary sources. We started with published secondary literature such as Judson and Normark (1996), Normark et al. (2003), Neiman et al. (2009), Schurko et al. (2009), Schwander and Crespi (2009), and Speijer et al. (2015), investigated cited primary literature and other novel primary literal sources concerning putative AA groups. We also investigated other possible AAs proposed in the primary literature and some lineages traditionally believed to be long-term asexual. The evidence for confirmation or rejection of putative AAs included organismal, life history, palaeontological, biogeographical, molecular, individual genetic, and population genetic data and also other indices of ancient asexuality proposed in the AA literature listed above. The list of supported and contested AA candidates, as well as reasons for our decision, is summarized in Table S1. Only well-supported AA groups were included in our comparative study.

2.1.2 | Sexual controls

In the next step, we identified ecologically comparable sexual sister lineages for the eight AA groups using literary sources. In those individual cases in which the phylogenetic relations between the sexual and asexual lineages were not entirely clear, we used the closest possible comparable clades (see Table S2 for details). Three of the AA groups were monophyletic (Bdelloidea, Darwinulidae, and *Vittaria*). The remaining AA groups were polyphyletic, that is, they included several related monophyletic asexual sublineages with interstitial sexual lineages. We treated each of these groups as single unit in the analysis. In these cases, we compared every individual AA lineage with its sexual control in the monophyletic subtaxa of the polyphyletic AA group and based our conclusions on the prevailing trend (i.e., over 50% of the cases; however, all actual trends were much more convincing, see Table 3) in the whole polyphyletic group. With the exception of *Timema*, the internal phylogenetic relationships of the studied polyphyletic AA groups were more or less unclear. Where possible, we proceeded using the most probable relationships (Bdelloidea, Darwinulidae, Oribatidae, Nematalycidae and Proteonematalycidae, Grandjeanicidae, and Oehserchestidae, see Table S2). In the cases with several equally probable alternative phylogenetic relationships of AA and sexual lineages (both in monophyletic/*Vittaria*/, and polyphyletic/*Alicorhagia* and *Stigmalychus*, Pomerantziidae, *Vittaria*, *Lasaea*/AA taxa), we compared AA lineages with alternative sexual controls to determine the consistency of the trend in the association of AA lineages or sexual controls with biotically and/or abiotically more heterogeneous environments (all trends were consistent over all alternative sexual controls, see Table 3).

2.2 | Determination of environmental heterogeneity

Using relevant literary resources, we collected and analyzed data on the (biotically or abiotically more heterogeneous or homogeneous) character of environments inhabited by the studied groups (the data are summarized in Table 3). Biotic and abiotic environmental heterogeneity clearly have a nontrivial relationship to each other (see Discussion), but it is essentially possible to distinguish them.

It is also worth mentioning that an environmental heterogeneity, both biotic and abiotic, is an emergent property stemming from different factors and different adaptations in various AAs. An environmental heterogeneity of microscopic and macroscopic organisms, or more generally organisms living on different spatiotemporal scales, eventually organisms with completely different ecological strategies (terrestrial, benthic, planktonic, parasitic etc.), could not be quantified and rated on a single universal scale. However, individual AAs and their ecologically comparable sexual controls can be compared on the basis of particular factors that indicate a higher or a lower biotic or abiotic environmental heterogeneity of their particular environment. These factors are summarized in Table 4 (see Supporting information Materials and Methods for details). Resulting binary data were possible to analyze statistically.

2.3 | Statistics

Collected data were analyzed using the R v. 3.1.2 software environment (R_Core_Team, 2014). We used an exact test suggested by R. A. Fisher, specifically a one-tailed binomial test, the only statistical technique which has a sufficiently high statistical power able to reject null hypothesis when we have extremely low N (theoretically a minimum of five). Using this technique, we tested three hypotheses: In case, the heterogeneity of habitats of AAs and their sexual controls differ, then asexual members of the pairs inhabit predominantly (1) biotically or abiotically, (2) biotically, and (3) abiotically more homogeneous environments.

Only in two AA groups (*Lasaea*, *Timema*), we were unable to identify any consistent differences in the heterogeneity of the environments inhabited by their sexual and asexual lineages. The most probable explanation of the absence of such a difference is a lack of empirical data. As the tested hypothesis makes predictions only about those pairs of species that differ in the heterogeneity of their habitats (and the binomial test analyses only binary variables, i.e., "less vs. more heterogeneous group," not "equally heterogeneous groups," see, e.g., McDonald, 2014), *Lasaea* and *Timema* were not included in the first round of our statistical analysis. The same applies for the abiotic heterogeneity of the environment of Darwinulidae.

To test the robustness of our results, we also ran more conservative second and third rounds of statistical analysis, including pairs with no reported difference in heterogeneity of habitats (1) as if they differed in the opposite direction than was predicted by our hypotheses and (2) as if they differed in the opposite direction but with only a 1/3 probability of positive outcome, that is, assuming a 2/3 probability of negative or indifferent result. The ecology, relevant adaptations, and environmental correlates of all eight pairs of AAs and their sexual controls were thoroughly examined in the exploratory part of the study, see Discussion.

3 | RESULTS

We conclude that eight of the putative AA groups do fulfill our strict criteria of ancient asexuality: bdelloid rotifers (Bdelloidea), darwinulid ostracods (Darwinulidae), several lineages of oribatid mites (Oribatidae), several lineages of mites from the suborder Endeostigmata and order Trombidiformes, shoestring fern *Vittaria appalachiana* (Farrar & Mickel), three species of stick insects from the genus *Timema*, and several lineages of the bivalve genus *Lasaea*; see Table S1. Their sister or closely related ecologically comparable sexual groups were identified consequently with the help of relevant literature; see Table S2.

The comparison of the character of environments inhabited by the AAs and their sexual controls in the cases that differed in this factor showed that AAs inhabit biotically or abiotically (six of six, $p = .016$),

TABLE 3 The heterogeneity of an environment of studied taxa

Ancient asexual taxon	Sexual control	Abiotically more homogenous than control	Biotically more homogenous than control
Bdelloidea	Monogononta	Yes Tend to be associated with marginal habitats and predominate there over sexual control (Pejler, 1995; Ricci, 1987; Ricci & Balsamo, 2000; Welch, Ricci, & Meselson, 2009), predominate over sexual control in polar habitats (Dartnall, 1983; Janiec, 1996; Jungblut, Vincent, & Lovejoy, 2012; Pejler, 1995; Sohlenius & Bostrom, 2005) + anhydrobiosis (Pilato, 1979; Ricci, 2001); predominate over sexual control in soil (Devetter & Scholl, 2014; Donner, 1975; Pejler, 1995; Scholl & Devetter, 2013); predominate over sexual control in hot springs at temperatures above 40°C (Issel, 1900, 1901; McDermott & Skorupa, 2011; Pax & Wulfert, 1941)	Yes Tend to be associated with marginal habitats and predominate there over sexual control (Pejler, 1995; Ricci, 1987; Ricci & Balsamo, 2000; Welch et al., 2009); aquatic representatives are exclusively benthic and sedentary in contrast to sexual control (Koste & Shiel, 1986; Ricci & Balsamo, 2000); predominate over sexual control in soil (Devetter & Scholl, 2014; Donner, 1975; Pejler, 1995; Scholl & Devetter, 2013); predominate over sexual control in polar habitats (Dartnall, 1983; Janiec, 1996; Jungblut et al., 2012; Pejler, 1995; Sohlenius & Bostrom, 2005); predominate over sexual control in hot springs at temperatures above 40°C (Issel, 1900, 1901; McDermott & Skorupa, 2011; Pax & Wulfert, 1941); absent in ancient lakes in contrast to sexual control (Martens & Schön, 2000; Schön & Martens, 2004); no typical predators and parasites (filtration, grazing etc.) in comparison with the sexual control (Ricci & Balsamo, 2000); getting rid of parasites (Wilson, 2011; Wilson & Sherman, 2010) and escaping from competitors, predators and parasites (Ladle, Johnstone, & Judson, 1993) via Bdelloidea-specific anhydrobiosis; high tolerance to irradiation (Gladyshev & Meselson, 2008) and starving (Ricci & Perletti, 2006) because of Bdelloidea-specific anhydrobiosis
Darwinuloidea	Cypridoidea	No Difference Tend to be associated with marginal habitats, springs and interstitial (Pieri, Martens, Stoch, & Rossetti, 2009; Pinto, Rocha, & Martens, 2005; Schön, et al. 1998; Schön, et al. 2009) + torpor (Carbonel, et al. 1988; Delorme & Donald, 1969; Retrum, Hasiotis, & Kaesler, 2011), but the same applies to some degree also to the sexual control; Darwinuloidea does not dominate in hot springs over its sexual control (Brues, 1932; Jana & Sarkar, 1971; Klie, 1939; Külköylüoğlu, Meisch, & Rust, 2003; Moniez, 1893; Wickstrom & Castenholz, 1985)	Yes Tend to be associated with marginal habitats, springs and interstitial, but the same applies to some degree also to the sexual control (Pieri et al., 2009; Pinto et al., 2005; Schön et al., 1998, 2009); no typical predators and parasites (filtration) in comparison with the sexual control (Dole-Olivier, et al. 2000); able to escape from competitors, predators and parasites because of torpor, but the same applies also to the sexual control (Carbonel et al., 1988; Delorme & Donald, 1969; Retrum et al., 2011); little parasitized, but the same applies to some degree also to the sexual control (Bruvo et al., 2011; Schön et al., 2009); aquatic representatives are exclusively benthic and sedentary in contrast to sexual control (Dole-Olivier et al., 2000; Pokorný, 1965; Rossetti, Pinto, & Martens, 2011; Schön et al., 2009); riverine and lacustrine representatives predominantly inhabit hypoxic depths with few competitors, predators and parasites (Rossi, Todeschi, Gandolfi, Invidia, & Menozzi, 2002; Schön et al., 2009; Smith, Kamiya, & Horne, 2006); little predated (Ranta, 1979); highly tolerant to starving (Rossi et al., 2002); absent in ancient lakes with numerous competitors, predators and parasites in contrast to sexual control (Martens, 1998; Schön & Martens, 2004); does not dominate in extremely cold (Bunbury & Gajewski, 2009; Külköylüoğlu & Vinyard, 2000; McLay, 1978; Tudorancea, Green, & Huebner, 1979) or hot (Brues, 1932; Jana & Sarkar, 1971; Klie, 1939; Külköylüoğlu et al., 2003; Moniez, 1893; Wickstrom & Castenholz, 1985) environments in comparison with sexual control
Ancient asexual Oribatidae	Compared sexual Oribatidae	Yes Tend to be associated with soil in contrast to sexual controls and their predominance rises with the depth of soil horizon (Devetter & Scholl, 2014; Karasawa & Hijii, 2008; Krivolutsky & Druk, 1986; Maraun et al., 2009; Norton & Palmer, 1991); only few arboreal representatives in comparison with sexual controls (Karasawa & Hijii, 2008; Maraun et al., 2009); predominantly inhabit abiotically more stable forest soils in comparison with meadows (Krivolutsky & Druk, 1986; Siepel, 1994), but see also Devetter and Scholl (2014)	Yes Tend to be associated with soil in contrast to sexual controls and their predominance rises with the depth of soil horizon (Karasawa & Hijii, 2008; Maraun et al., 2009; Norton & Palmer, 1991); only few arboreal representatives (Karasawa & Hijii, 2008; Maraun et al., 2009); dominantly not typical predators and parasites (decomposition, fungivory, lichens, microorganisms), but the same applies also to the sexual controls (Norton & Behan-Pelletier, 2009); predominantly inhabit stable environments with unstructured resources (Domes, et al. 2007; Maraun, et al. 2012); but do not prevail in the environment with less parasites and predators (Cianciolo & Norton, 2006)

(Continues)

TABLE 3 (Continued)

Ancient asexual taxon	Sexual control	Abiotically more homogenous than control	Biotically more homogenous than control
Ancient asexual Endeostigmata	Compared sexual Endeostigmata	Yes Tend to be associated with soil, and, in contrast to sexual controls, especially its deep horizons (Darby, Neher, Housman, & Belnap, 2011; Neher, Lewins, Weicht, & Darby, 2009; Norton & Behan-Pelletier, 2009; Norton et al. 1993; Oconnor, 2009; Walter, 2001, 2009); all hypothetical sister sexual lineages of *Alicorhagia* + *Stigmalychus* are much more ecologically disparate, including life in abiotically changeable environments (Darby et al., 2011; Neher et al., 2009; Norton & Behan-Pelletier, 2009; Norton et al., 1993; Oconnor, 2009; Walter, 2001, 2009); ecological patterns analogical to Oribatidae but poorly explored (Norton & Behan-Pelletier, 2009; Norton et al., 1993; Walter, 2009)	Yes Tend to be associated with soil, and, in contrast to sexual controls, especially its deep horizons (Darby et al., 2011; Neher et al., 2009; Norton & Behan-Pelletier, 2009; Norton et al., 1993; Oconnor, 2009; Walter, 2001, 2009); dominantly not typical predators and parasites (decomposition, fungivory, microorganisms), but the same applies also to the sexual controls internal to the clade Endeostigmata (Walter, 2009); all hypothetical sister sexual lineages of *Alicorhagia* + *Stigmalychus* are much more ecologically disparate, including strategies with high degree of interspecific interactions (predators, parasites etc.) (Darby et al., 2011; Neher et al., 2009; Norton & Behan-Pelletier, 2009; Norton et al., 1993; Oconnor, 2009; Walter, 2001, 2009); ecological patterns analogical to Oribatidae but poorly explored (Norton & Behan-Pelletier, 2009; Norton et al., 1993; Walter, 2009)
Ancient asexual Trombidiformes	Compared sexual Trombidiformes	Yes Tend to be associated with soil, and, in contrast to sexual controls, especially its deep horizons (Bochkov & Walter, 2007; Darby et al., 2011; Kethley, 1989; Neher et al., 2009; Walter et al. 2009); all hypothetical sister sexual lineages are much more ecologically disparate, including life in abiotically changeable environments (Darby et al., 2011; Neher et al., 2009; Norton et al., 1993; Walter et al., 2009); ecological patterns analogical to Oribatidae but poorly explored (Norton & Behan-Pelletier, 2009; Norton et al., 1993; Walter et al., 2009)	Yes Tend to be associated with soil, and, in contrast to sexual controls, especially its deep horizons (Bochkov & Walter, 2007; Darby et al., 2011; Kethley, 1989; Neher et al., 2009; Walter et al., 2009); no typical predators and parasites (decomposition, fungivory, microorganisms) in comparison with sexual controls (Darby et al., 2011; Neher et al., 2009; Norton et al., 1993; Walter et al., 2009); all hypothetical sister sexual lineages are much more ecologically disparate, including strategies with high degree of interspecific interactions (predators, parasites etc.) (Darby et al., 2011; Neher et al., 2009; Norton et al., 1993; Walter et al., 2009); ecological patterns analogical to Oribatidae but poorly explored (Norton & Behan-Pelletier, 2009; Norton et al., 1993; Walter et al., 2009)
Vittaria appalachiana	Related sexual species	Yes Distributed in higher latitude in comparison with sexual controls (Farrar, 1978, 1998), but associated exclusively with geologically and ecologically highly stable habitats (caves, excesses etc.) in contrast to sexual controls (Farrar, 1978, 1990, 1998); sexual controls are associated with exposed habitats (epiphytic on trees or decomposing wood) (Farrar, 1978, 1990; Farrar & Mickel, 1991)	Yes Associated with habitats characterized by minimal competition due to low light levels in contrast to sexual controls (Farrar, 1978, 1998); distributed in higher latitude in comparison with sexual controls (Farrar, 1978, 1998); highly vulnerable to parasitization and competition (Caponetti, Whitten, & Beck, 1982)
Ancient asexual *Timema*	Sister sexual species	No Difference No difference in their phenotype in comparison with sexual controls (Sandoval, Carmean, & Crespi, 1998); areas of 2/3 AA species extend to higher latitudes than their sexual controls (Law & Crespi, 2002a,b), but other species of the genus (including short-term asexual and sexual species) have even northern distribution (Law & Crespi, 2002b)	No Difference 2/3 AA species have narrower food niche in comparison with sexual controls (Law & Crespi, 2002b); 2/3 AA species has separate areas from remaining species (Law & Crespi, 2002b; Sandoval et al., 1998) in contrast with sexual and short-term asexual representatives of the genus (Law & Crespi, 2002b), but see Law and Crespi (2002a); areas of 2/3 AA species extend to higher latitudes than their sexual controls (Law & Crespi, 2002a,b), but other species of the genus (including short-term asexual and sexual species) have even more northern distribution (Law & Crespi, 2002b)

(Continues)

TABLE 3 (Continued)

Ancient asexual taxon	Sexual control	Abiotically more homogenous than control	Biotically more homogenous than control
Ancient asexual *Lasaea*	Sexual *Lasaea*	No Difference Ancient asexual representatives have global distribution including high latitudes, whereas the distribution of sexual species is limited to the shores of Australia and Tasmania (Ó Foighil & Smith, 1995; Ó Foighil & Thiriot-Quievreux, 1999; Taylor & Ó Foighil, 2000); associated with tidal zone, but the same applies both to AA and sexual *Lasaea* lineages (Morton et al. 1957); the ability to slow down metabolism and survive up to 12 days outside water, but the same applies both to AA and sexual *Lasaea* lineages (Morton et al., 1957)	No Difference Ancient asexual representatives have global distribution including high latitudes, whereas the distribution of sexual species is limited to the shores of Australia and Tasmania (Ó Foighil & Smith, 1995; Ó Foighil & Thiriot-Quievreux, 1999; Taylor & Ó Foighil, 2000); all AA representatives (but also one of two sexual species in the genus, *Lasaea colmani*) are exclusively benthic and directly developing without the presence of ancestral planktonic larva (Ó Foighil, 1989; Ó Foighil & Eernisse, 1988; Rosewater, 1975); associated with diverse community of invertebrates, cyanophyta and algae including algal species directly eroding Lasaea's shell, but the same applies both to AA and sexual *Lasaea* lineages (Morton et al., 1957); not typical predator or parasite (filtration), but the same applies both to AA and sexual *Lasaea* lineages (Morton et al., 1957)

Comparison of the biotic and abiotic heterogeneity of an environment inhabited by the studied ancient asexuals and their sexual controls. Detailed evaluation of the habitat heterogeneity is given in each pair to support our decision of which member of the pair inhabits a biotically or abiotically more heterogeneous environment.

biotically (six of six, $p = .016$), and abiotically (five of five, $p = .031$) more homogeneous environments. All these results are statistically significant. In cases in which the indifferent pairs were included in the analysis as negative observations, results became statistically insignificant (six of eight, $p = .145$; six of eight, $p = .145$; respectively, five of eight, $p = .363$). However, in cases in which the probability of positive result was set on 1/3 (leaving 2/3 probability of negative or indifferent result, however, see Discussion), results became marginally significant (six of eight, $p = .02$; six of eight, $p = .02$; respectively, five of eight, $p = .088$). Details of the results are summarized in Table 3 and the Supporting information Review of AA ecology.

In the exploratory part of the study, we searched for the traits that could be typical for ancient asexual organisms. We identified several properties and adaptations that are common to a considerable number of studied AAs, see Table 5. The most notable are durable resting stages, life in benthos and soil, and life in the absence of intense biotic interactions. On the other hand, widely discussed alternative means of genetic exchange and association with other species in a "domesticated" state were not found to be very frequent among putative AAs.

4 | DISCUSSION

In contrast with other comparative studies in the field, the presented one is based exclusively on the AA taxa. Moreover, biotic and abiotic environmental heterogeneity have been distinguished. We conclude that all six of the six AA groups that meet inclusion criteria of our initial statistical analysis (i.e., age >1 million years, reported differences in a heterogeneity of a habitat of AA and its sexual control) inhabit biotically more homogeneous environments and all five of the five-ones inhabit abiotically more homogeneous environments when compared with their sexual controls. No AA group lives in an environment abiotically or biotically more heterogeneous than its sexual control.

In the cases excluded from the initial analysis (abiotic heterogeneity in Darwinulidae and both biotic and abiotic heterogeneity in *Timema* and *Lasaea*), it was not possible to distinguish whether the heterogeneity is lower in the AA group or in the sexual control. As expected, the observed results are not very robust due to an extremely low number of pairs of species for which the reliable ecological data are available (six). In the case of paired of species with no reported differences in heterogeneity of habitats were added to the analysis as negative observations, results became insignificant. Setting the probability of positive result to 1/3 (i.e., simulating 2/3 probability of negative or insignificant result) led to marginally significant results in the same case. However, this last test of the robustness of our results should be taken only as tentative because the direct assessment of the probability of indifferent result was beyond the possibilities of today's comparative studies. Nevertheless, even stepping aside from *p*-values, our results show a clear trend of AA association with biotically and abiotically homogeneous environments, both in general and in comparison with their sexual controls.

The associations with biotically and abiotically more homogeneous environments overlap almost perfectly. Thus, the results of the comparative analysis clearly indicate that either the AA groups tend to be associated with overall (both biotically and abiotically) homogeneous environments or that these two types of heterogeneity are so strongly correlated that it is impossible to decide in favor of theories of sexual reproduction that stress the key role of biotic or abiotic heterogeneity. In general, our results obtained on AAs support, but of course do not prove, the hypotheses that consider both biotic and abiotic heterogeneities acting as one factor in their effect on organisms (Flegr, 2010, 2013; Roughgarden, 1991; Scheu & Drossel, 2007; Song et al., 2011; Williams, 1975 pp. 145–146, 149–154, 169).

Despite the widespread apprehension that the long independent evolution of AAs and their sexual controls would hamper any ecological comparative analysis of the type presented here

TABLE 4 Factors determining biotic and abiotic environmental heterogeneity

Biotic heterogeneity		
Higher	**Lower**	**References**
Complex ecosystems with high degree of competition, predation, and parasitism; e.g. ancient lakes	Simple ecosystems low degree of competition, predation, and parasitism; for example, ephemeral, marginal, extreme habitats	Martens (1998); Martens and Schön (2000); Schön and Martens (2004) versus Bell (1982); Tobler, Schlupp, de Leon, Glaubrecht, and Plath (2007)
Unpredictable changes (predator-prey cycles etc.)	Predictable changes (predator–prey cycles etc.)	Dawkins and Krebs (1979); Tokeshi (1999)
Tight and specific association with prey or host; e.g. predatory or parasitic lifestyle	Loose association with prey or host; for example, filtering or micropredatory lifestyle	Dawkins and Krebs (1979)
No adaptations to avoid competition, predation, and parasitism; e.g. durable resting stages	Adaptations to avoid competition, predation, and parasitism; for example, durable resting stages	Dawkins and Krebs (1979); Wilson (2011)
Planktonic or nektonic lifestyle	Benthic or sedentary lifestyle	Emiliani (1982, 1993a,b); Suttle, Chan, and Cottrell (1990); Bratbak, Egge, and Heldal (1993); Fuhrman (1999); Wommack and Colwell (2000); Fisher, Wieltschnig, Kirschner, and Velimirov (2003); Bettarel, Bouvy, Dumont, and Sime-Ngando (2006); Filippini, Buesing, Bettarel, Sime-Ngando, and Gessner (2006); Suttle (2005), Suttle (2007)
Not inhabiting soil, or only shallow soil horizons	Inhabitancy of soil, especially deep soil horizons	Wallwork (1970); Elliott, Anderson, Coleman, and Cole (1980); Murphy and Tate (1996); Drake, Choi, Haskell, and Dobbs (1998); Fisher et al. (2003); Lavelle and Spain (2003); Paul (2007)
Lower latitudes	Higher latitudes	Rohde (1986); Rohde and Heap (1998); Tokeshi (1999)
Shallower parts of water column	Deeper parts of water column	Etter, Rex, Chase, and Quattro (2005)
Abiotic heterogeneity		
Temporally changeable (on ecological timescales), spatially very heterogeneous, diverse and unstable habitats with unequally distributed resources; e.g. ephemeral and marginal habitats	Temporally stable, spatially homogeneous habitats with equally distributed resources; for example, caves, ground water reservoirs or soil environment (especially deeper soil horizons or soils of certain biomes)	Wallwork (1970); Farrar (1978); Farrar (1990); Farrar (1998); Krivolutsky and Druk (1986); Siepel (1994),; Siepel (1996); Pejler (1995); Lavelle and Spain (2003); Coleman, Crossley, and Hendrix (2004); Quesada et al. (2004); Paul (2007); Devetter and Scholl (2014)
Unpredictable changes	Predictable changes (e.g., cyclical)	Tokeshi (1999)
No adaptations to avoid temporary adverse abiotic conditions or enable migration; e.g. durable resting stages	Adaptations to avoid temporary adverse abiotic conditions or enable migration; for example, durable resting stages	Wilson (2011)
Extreme yet spatiotemporally changeable habitats; for example, nunataqs, desiccating ponds, bark surface	Temporally stable extreme habitats; e.g. hot springs or subsurface cavities	Bell (1982)
Lower latitudes and altitudes	Higher latitudes and altitudes	Hörandl (2006, 2009); Vrijenhoek and Parker (2009)
Freshwater habitats and coastal areas	Deeper parts of water column	Etter et al. (2005); Sheldon (1996)

Summary of factors that were evaluated to determine a higher or a lower environmental heterogeneity of AAs in comparison with their sexual controls. Note that the factors are not universal (a terrestrial organism cannot be benthic/nektonic etc.) and cannot be compared across all studies organisms. See Supporting information Materials and Methods for commentary and detailed description on how we determined biotic and abiotic environmental heterogeneity.

(leading to the preference of studying young asexual lineages, see Introduction), we found that both groups usually inhabit quite similar and considerably homogeneous environments. This can, in fact, complicate analyses in the opposite way by making the determination of differences in a habitat heterogeneity impossible (as was the case of *Timema* and *Lasaea*, see Table 3). On the other hand, their common ancestor's association with the homogeneous environments could have been a preadaptation to the successful and long-term transfer to asexual reproduction in the AAs. This tendency is obvious especially in Darwinuloidea–Cypridoidea, but it can also be

TABLE 5 Specific ecological properties and adaptations of AA taxa

	Alternative exchange of genetic information	Durable resting stages	Sedentary life and life in benthos	Life in the soil	Absence of life strategies with intensive biotic interactions
Bdelloidea	X	X	X	X	X
Darwinuloidea		X	X	X	X
Ancient asexual Oribatidae				X	X
Ancient asexual Endeostigmata				X	X
Ancient asexual Trombidiformes				X	X
Vittaria appalachiana					X
Ancient asexual *Timema*					X
Ancient asexual *Lasaea*		?	X		X

The distribution of specific environmental properties and organismal adaptations associated with studied AA taxa. Significance of these findings is discussed below.

seen in Bdelloidea-Monogononta, Oribatidae, and Endeostigmata (see Table 3).

It is interesting in this regard that many contested AAs (see Table S1) also inhabit considerably homogeneous environments—for example,. arbuscular mycorrhizal fungi of the order Glomales (Croll & Sanders, 2009), tardigrades (Mobjerg et al., 2011; Pilato, 1979), nematode genus *Meloidogyne* (Castagnonesereno et al., 1993), ostracods *Heterocypris incongruens* (Ramdohr) and *Eucypris virens* (Jurine) (Butlin et al., 1998; Martens, 1998), bristle fern *Trichomanes intricatum* (Farrar) (Farrar, 1992), basidiomycete fungal families Lepiotaceae and Tricholomataceae (Currie, Mueller, & Malloch, 1999; Currie, Scott, Summerbell, & Malloch, 1999), ambrosia fungi Ophiostomatales (Farrell et al., 2001), or brine shrimp "*Artemia parthenogenetica*" (Bowen & Sterling) (Vanhaecke, Siddall, & Sorgeloos, 1984)—and their adaptations are similar to those of the AAs included in this study (see below).

4.1 | What environmental properties and organismal adaptations are associated with AA taxa?

Besides the tendency to inhabit biotically and abiotically homogeneous environments, we discovered several properties and adaptations that are common to a considerable number of studied AAs, occur in AAs more often than in their sexual controls, and could be the particular adaptations enabling their long-term survival in the environments mentioned above (see Table 5). The occurrence of these properties can, of course, be of little significance as we did not study their distribution throughout the near phylogeny. It is, however, interesting to mention them for the purposes of further research as universally distributed adaptations potentially connected to the mode of reproduction was not expected to be found in our sample because of markedly different ecological strategies of the studied AAs.

4.1.1 | Alternative exchange of genetic information

Alternative ways of exchange of genetic information could theoretically substitute sexual reproduction and thus were repeatedly proposed as the key adaptation to asexuality (Boschetti, Pouchkina-Stantcheva, Hoffmann, & Tunnacliffe, 2011; Butlin, Schön, & Griffiths, 1998; Debortoli et al., 2016; Gladyshev & Meselson, 2008; Schwander, 2016). However, we identified this factor only once in the AAs included in our study (i.e., in one of eight cases), namely in Bdelloidea that experience intensive horizontal gene transfer (Boschetti et al., 2011; Debortoli et al., 2016; Gladyshev & Meselson, 2008). Another mechanism of genetic exchange, parasexuality (sensu Pontecorvo, 1954), was proposed in some contested ancient asexuals—Glomales (Croll & Sanders, 2009), Tricholomataceae and Lepiotaceae (Mikheyev, Mueller, & Abbot, 2006), and certain protists (Birky, 2009). However, considering only the well-supported AAs, these mechanisms have limited distribution.

4.1.2 | Durable resting stages and subjectively homogeneous environment

The character of the environment is probably subjectively experienced rather differently by its inhabitants with their specific adaptations and by a human observer. In case that a particular organism reacts to the adverse change of environmental conditions by entrenching itself in the resting or durable persistent stages (e.g., anabiosis), then, as a result, it de facto does not subjectively experience the unfavorable conditions at all. Its objectively heterogeneous environment becomes subjectively much more homogeneous. It was even proposed that the presence of durable resting stages may, because of the reduced strength of selective pressures affecting these organisms in the long term, lead to an evolutionary stasis (Pilato, 1979).

This subjectivity of experienced environment probably addresses especially its abiotic factors, for example desiccation, which is survived in the anabiotic stages by Bdelloidea (Pilato, 1979; Ricci, 2001), or freeze and desiccation, which is survived in a state of torpor by Darwinulidae and some of their sexual relatives (Carbonel, Colin, Danielopol, Loffler, & Neustrueva, 1988). Similar durable stages could also be found in some contested AAs, namely "*Artemia parthenogenetica*" (Vanhaecke et al., 1984) and tardigrades (Mobjerg et al., 2011). Moreover, AA *Lasaea* is able to become mostly inactive and rests during the adverse conditions for some time as well (Morton, Boney, & Corner, 1957). On the other hand, at least in Bdelloidea, the anhydrobiosis may serve as the escape from biotic stresses too—especially parasites, both directly (the individual gets rid of parasites during desiccation) and indirectly (by enabling the escape from parasites in space and time), as was proposed by Wilson (2011). The distribution of durable resting stages among well-supported AAs looks rather scarce (three of eight cases). However, these 2–3 groups comprise all studied AAs associated with significantly (objectively) abiotically heterogeneous habitats.

An underestimation of this phenomenon might be another reason why most researchers did not come to unambiguous conclusions in their comparative analyses of the ecology of sexual and asexual organisms. For example, many "extreme" environments may not be abiotically very homogeneous, whereas some environments that were designated as abiotically heterogeneous, for example, in the famous Bell's (1982) study (periodical ponds, dendrotelms etc.), could be very subjectively homogeneous for local inhabitants (e.g., anhydrobiotic Bdelloidea). After all, the heterogeneity of the environment depends on the adaptation of the observer, including the presence or absence of the durable stages.

4.1.3 | Sedentary life and life in benthos

At least three well-supported AA groups (Bdelloidea, Darwinulidae, and *Lasaea*) are exclusively benthic or sessile in contrast to their sexual relatives (Dole-Olivier, Galassi, Marmonier, & Des Chatelliers, 2000; Ó Foighil, 1989; Ricci & Balsamo, 2000). Some species of rotifer group Monogononta (sexual control for Bdelloidea) (Pejler, 1995) and ostracod group Cypridoidea (sexual control for Darwinulidae) (Martens, Schön, Meisch, & Horne, 2008) are planktonic; one of the two sexual lineages in genus *Lasaea* has planktonic larvae (Ó Foighil, 1988).

It was proposed that benthic or sessile life may significantly reduce the biotic heterogeneity of an environment affecting such organisms by effectively hampering and reducing the spread of parasites (Emiliani, 1993a,b), which is often considered to be one of the most dynamic and influential components of the organisms' environment. It is true that, somehow paradoxically, paleontological studies (Jablonski, 1986) show increased extinction rates of species without planktonic larvae. However, the main reason for this is probably better colonizing abilities that are usually, but not always, associated with indirect development (Ó Foighil, 1989).

In a similar way to resting stages, the distribution of benthic or sedentary lifestyle among well-supported AAs looks rather scarce on the first sight (three of eight cases). However, these three groups comprise all studied AAs that are (at least partially) associated with aquatic habitats. Moreover, it is interesting that numerous contested aquatic AAs are also exclusively benthic: flatworm *Schmidtea polychroa* (Schmidt) (Pongratz, Storhas, Carranza, & Michiels, 2003), New Zealand mudsnail *Potamopyrgus antipodarum* (Gray) (Neiman, Jokela, & Lively, 2005), and ostracods *Heterocypris incongruens* (Ramdohr) and *Eucypris virens* (Jurine) (Butlin et al., 1998; Martens, 1998).

4.1.4 | Life in the soil

Another adaptation widely distributed among AA groups is the inhabitancy of soil, especially deeper parts of the soil horizon. This tendency can be seen mainly in the AA mites from groups Oribatidae, Endeostigmata, and Trombidiformes, although their sexual relatives have some soil representatives too (Karasawa & Hijii, 2008; Maraun et al., 2009; Walter, 2009). Bdelloidea and Darwinuloidea tend to be associated with semiterrestrial habitats (Schön, Rossetti, & Martens, 2009). Moreover, AA Bdelloidea dominate among the soil rotifers above any of their sexual relatives (Pejler, 1995). Most representatives of Darwinulidae inhabit soil (respectively interstitial) too, although this applies also to some of their sexual relatives (Schön et al., 2009). Taken together, five of eight studied AA groups have numerous soil-inhabiting representatives and show a tendency to inhabit soil.

Living in soil may, in a similar way to life in benthos, reduce the capacity of parasites to spread (sensu Emiliani, 1993a,b). The soil environment is three-dimensional in its nature. Environments of surface organisms usually have some vertical dimension as well; however, this feature is pronounced much stronger in soil. Especially on smaller spatial scales characteristic for rotifers, ostracods, mites, fungi, and other putative AAs, the environment of soil organisms consists of tortuous system of pores and crevices. The shortest way from point A to point B in soil is only rarely a straight line. Under normal circumstances (i.e., population densities comparable to surface environments), this feature probably reduces any interactions of soil organisms and thus negatively affect parasitization, predation, and competition (Drake, Choi, Haskell, & Dobbs, 1998; Elliott, Anderson, Coleman, & Cole, 1980; Fisher, Wieltschnig, Kirschner, & Velimirov, 2003; Lavelle & Spain, 2003; Murphy & Tate, 1996; Paul, 2007; Pilato, 1979). However, it should be noted that this may change under high population densities (especially in surface layers of the soil or during some special occasions, such as periodic inflow of resources, and swarming) and therefore should be subject of further research. Besides, soil is an abiotically very stable environment shielding its inhabitants from fluctuations in temperature and humidity, as well as from UV radiation, and could be very favorable for asexuals also for this reason (Krivolutsky & Druk, 1986; Pilato, 1979; Siepel, 1994). In sum, the inhabitancy of soil habitats may eventually erase many of the hypothetical evolutionary advantages of sexuality and enable its inhabitants, or at least those who are not blocked to do so by some evolutionary constraints, to change their mode of reproduction to asexual. This, however, remains a speculation until a more extensive survey of soil organisms' mode of reproduction is made.

Other explanations have also been proposed for the asexuals' association with soil habitats. Oribatidae could suffer less intense selective pressures in the soil than in the arboreal environment where they have to respond to the coevolving lichens, their main food source (Maraun et al., 2009). Asexuality can be also more advantageous in soil because of the difficulties with seeking out sexual partners, less effective pheromone dispersal etc. (Karasawa & Hijii, 2008). Nevertheless, numerous contested AAs are soil inhabitants too: Glomales (Croll & Sanders, 2009), tardigrades (Jorgensen, Mobjerg, & Kristensen, 2007; Pilato, 1979), and *Meloidogyne* (Castagnonesereno et al., 1993).

It is also interesting in this regard that the selective pressures of biotic and abiotic environments in soil were proposed to be so weak they can ultimately (in a similar way to the presence of durable resting stages) lead to an evolutionary stasis (Pilato, 1979). This applies especially to Bdelloidea (Poinar & Ricci, 1992; Ricci, 1987) and Darwinulidae (Martens, Horne, & Griffiths, 1998; Schön, Butlin, Griffiths, & Martens, 1998; Schön et al., 2009) but, to some degree also to Oribatidae (Heethoff et al., 2007; Krivolutsky & Druk, 1986; Norton, 1994) and other AA mites (Norton, Kethley, Johnston, & O'Connor, 1993; Walter, 2009; Walter, Lindquist, Smith, Cook, & Krantz, 2009). Some evidence of evolutionary stasis can be seen in five of eight studied AA groups. Taking into account the contested AA groups, it can be found in Glomales (Redecker, Kodner, & Graham, 2000; Remy, Taylor, Hass, & Kerp, 1994) and tardigrades (Jorgensen et al., 2007; Pilato, 1979).

4.1.5 | Absence of life strategies with intensive biotic interactions

It is noticeable that there are practically no typical predators and parasites among the AAs we studied—this property is characteristic for all eight studied groups. Remarkably often they feed on dead organic matter or are autotrophic; parasites are almost absent, and in the case of a predatory lifestyle, they are phytophagous or filtering (see Table 3). One possible explanation is that they are unable to keep up in the coevolutionary race with their sexual hosts or prey. Thus, they may be successful in the long term, especially in the case of a predatory lifestyle, only if they adopt (or are preadapted to) such nonspecific ecological strategies. This, however, also applies to some of their sexual relatives and generally remains a hypothesis to be tested.

4.1.6 | Succumbing to domestication and delegation of concern for its own benefit to another biological entity

The tendency for asexual reproduction is particularly interesting in the contested AA fungi domesticated by ants (Formicidae) and bark beetles (Scolytinae). The ant symbionts are from the basidiomycete groups Tricholomataceae and Lepiotaceae (Mueller, Rehner, & Schultz, 1998), whereas bark beetles domesticate the ambrosia fungi of the ascomycete group Ophiostomatales (Farrell et al., 2001). The association is particularly close in the ants. They care for the fungi intensively, remove fungal predators and parasites, and the founding queen always carries filamentous bacteria, which synthetize an antidote against the main fungal pathogen—ascomycete *Escovopsis* (Currie et al., 1999, 1999) —not to mention the stable temperature and humidity in the nest. By doing so, they provide a very favorable, biotically and abiotically stable environments. Moreover, there is some evidence that they prevent fungi from their already minimal attempts at sexual reproduction. On the other hand, the situation may be more complicated because some of these fungi create sexual structures predominantly in the presence of ants (Mueller, 2002).

This phenomenon provides an alternative view on some aspects of human agriculture. Many plants raised by humans are sustained in agriculture by asexual reproduction (vegetative reproduction, fragmentation, or grafting), or at least self-pollinating, which probably facilitates their breeding but increases their susceptibility to parasites and pathogens, the problem that must be continuously fought by their symbiont—humans (Flegr, 2002). Life in association with another organism that takes care of the symbiont can also be found in the contested AA group Glomales (Croll & Sanders, 2009) and various prokaryotic and eukaryotic endosymbionts, see, for example, Douglas (2010). However, it has not been found in any of the eight well-supported AA groups we studied, and its effect on the long-term maintenance of asexual reproduction thus remains only speculative.

5 | CONCLUSIONS

The analytical part of this study, that is, the comparative analysis of the environment of AAs and their sexual relatives, mostly supported the hypothesis that AA groups are associated with overall (biotically and abiotically) more homogeneous environments in comparison with their sister or closely related ecologically comparable clades. This result was significant in two of three statistical tests we conducted, and only the most conservative approach did not come to a statistically significant result. This outcome consequently supported the theoretical concepts that postulate the essential advantage of sexual species in heterogeneous environments and consider the (biotic and abiotic, temporal and spatial) heterogeneity of the environment affecting the organisms to be one factor that can exhibit itself in many ways (Flegr, 2010, 2013; Roughgarden, 1991; Scheu & Drossel, 2007; Song et al., 2011; Williams, 1975 pp. 145–146, 149–154, 169). Particular ecological adaptations, from which durable resting stages, life in the absence of intense biotic interactions, and the association with soil and benthic habitats are most notable, might represent special cases of the general AAs' association with overall homogeneous environments.

Therefore, the general notion that proposed theories of sexual reproduction (see Introduction) need not exclude each other, that the effects proposed by some or all of them might intertwine and affect individuals and evolutionary lineages simultaneously, or that they even may, ultimately, represent only different aspects of one more general explanation, seems to be supported by our results. Moreover, overall environmental heterogeneity, regardless of its complicated conceptualization and study, seems to be a suitable candidate for this hypothetical general explanation.

Most putative AA lineages are still critically understudied. One way of elaborating the foundations laid out by this study would be comparing the heterogeneity of environments in a broader spectrum of AA lineages as soon as more lineages are discovered or confirmed (e.g., the protist lineages proposed by Speijer et al., 2015). It would also be very desirable to investigate the ecology of *Lasaea*, *Timema*, and Darwinulidae in greater detail. Additionally, it would be appropriate to focus on the interaction of biotic and abiotic environmental heterogeneities and their effect on organisms. According to Flegr (2008, 2010, 2013), sexual groups should exhibit more pronounced evolutionary conservation of niches in comparison with asexuals—on the whole, they are expected to stick closely around the phenotype of their common ancestor. This hypothesis could be tested by comparing the variance of properties of individual species within an AA and its related sexual clade. It would be also possible to test whether particular sexual species are able to survive under a wider range of conditions of the heterogeneous environment due to their high genetic variability and hypothetical "elastic" reaction on selection, as was suggested by Flegr (2008, 2010, 2013).

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DATA AND MATERIALS

All data generated or analyzed during this study are included in this published article and its supporting information files.

CONFLICT OF INTERESTS

The authors have no conflict of interests to declare.

AUTHORS' CONTRIBUTIONS

JT gathered the data, prepared the figures and tables and was the greatest contributor in writing the manuscript. JF contributed the analysis tools. Both JT and JF conceived and designed the study, analyzed the data and reviewed the drafts of the manuscript. All authors read and approved the final manuscript.

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7.2 PŘÍLOHA 2

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ORIGINAL PAPER

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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Stability-based sorting: The forgotten process behind (not only) biological evolution

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ABSTRACT

Natural selection is considered to be the main process that drives biological evolution. It requires selected entities to originate dependent upon one another by the means of reproduction or copying, and for the progeny to inherit the qualities of their ancestors. However, natural selection is a manifestation of a more general *persistence principle*, whose temporal consequences we propose to name "stability-based sorting" (SBS). Sorting based on *static stability*, i.e., SBS in its strict sense and usual conception, favours characters that increase the persistence of their holders and act on all material and immaterial entities. Sorted entities could originate independently from each other, are not required to propagate and need not exhibit heredity. Natural selection is a specific form of SBS—sorting based on *dynamic stability*. It requires some form of heredity and is based on competition for the largest difference between the speed of generating its own copies and their expiration. SBS in its strict sense and selection thus have markedly different evolutionary consequences that are stressed in this paper. In contrast to selection, which is opportunistic, SBS is able to accumulate even momentarily detrimental characters that are advantageous for the long-term persistence of sorted entities. However, it lacks the amplification effect based on the preferential propagation of holders of advantageous characters. Thus, it works slower than selection and normally is unable to create complex adaptations. From a long-term perspective, SBS is a decisive force in evolution—especially macroevolution. SBS offers a new explanation for numerous evolutionary phenomena, including broad distribution and persistence of sexuality, altruistic behaviour, horizontal gene transfer, patterns of evolutionary stasis, planetary homeostasis, increasing ecosystem resistance to disturbances, and the universal decline of disparity in the evolution of metazoan lineages. SBS acts on all levels in all biotic and abiotic systems. It could be the only truly universal evolutionary process, and an explanatory framework based on SBS could provide new insight into the evolution of complex abiotic and biotic systems.

1. Introduction

1.1. Theories on the origin of adaptations

The most important evolutionary discovery of Charles Darwin was probably the identification of natural selection (Darwin, 1859). This process offers the explanation of the origin and accumulation of adaptive, often functionally and structurally complex, characters in organisms. These characters enable organisms to effectively and often sophisticatedly react to the selective pressures of their environment, use its resources, and avoid its detrimental forces. Despite all of this, these adaptations that enable survival and successful reproduction of organisms in complex and changing environments originated through the "primitive" method of trial and error, i.e., without the intervention of any sentient being or existence of a preliminary plan.

Explanations and solutions based on the principle of natural selection were applied in a plethora of other systems in the fields of natural science, technology and even humanities. Over the years, evolutionary biologists discovered that selection has several components and many forms, and that biological evolution is also driven and markedly affected by many other mechanisms, e.g. genetic drift, genetic draft, evolutionary drives, gene flow, and species selection (see e.g. Mayr, 2003). It was also demonstrated that numerous adaptive traits did not originate as biological adaptations but, exaptations, or even spandrels (see e.g. Gould, 2002). Moreover, the complex nature of genetic inheritance, various forms of non-genetic inheritance, and the evolution of multi-level meta-adaptations (such as the ontogeny of metazoans) that affect the evolvability of lineages and canalize their ontogeny and anagenesis

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returned to the focus of evolutionary and developmental biologists in the last years (see e.g. Laland et al., 2015).

However, natural selection is probably a manifestation of a more general law that affects all material and immaterial entities in the universe, does not require replication and inheritance, and is usually called *survival of the stable,* according to the remark in the first chapter of Dawkins' book Selfish Gene (Dawkins, 1976, p. 13[1]). At first, it sounds like a tautology: Changeable entities change, whereas stable or rapidly emerging entities accumulate and predominate in the system. Indeed, the claim that the most stable (or persistent) entity lasts the longest time is undoubtedly an axiom (Grand, 2001, p. 34–38; Pross, 2012; Shcherbakov, 2012; Pascal and Pross, 2014,2015) and this "law" thus seems utterly trivial, at least in a simple model. However, in the real world, coexisting entities interact in a complex manner and the consequent evolution of systems of interacting entities with variable and context–dependent persistence is all but simple (while still characteristic of the perpetual search for states of higher stability) (see e.g. Bardeen, 2009, or Pross, 2003,2004,2012; Wagner and Pross, 2011; Pascal and Pross, 2014,2015,2016, and references therein). As Shcherbakov (2013) concludes: "This principle – "survival of those who survive" – sounds as a tautology, but it is *the great tautology*: Everything genuinely new emerges through this principle."

Remarks analogical to Dawkins' *survival of the stable* were made also by several other researchers (e.g. Lotka, 1922a,b; Simon, 1962; Wimsatt, 1980; Van Valen, 1989; Michod, 2000; Grand, 2001; Maynard Smith and Szathmáry, 2010) whereas possible relations between natural selection and various forms of self-organization were analysed by Weber and Depew (1996). However, to our knowledge, Addy Pross and his colleagues elaborated the idea most profoundly (see e.g. Pross, 2003, 2004, 2012; Wagner and Pross, 2011; Pascal and Pross, 2014, 2015, 2016). The phenomenon itself is very general and probably applies to all fields that concern any form of biological or non-biological evolution. Researchers that touched it from various angles during their investigations called it e.g. *natural selection in the non-living world* (Van Valen, 1989), *survival in the existential game* (Rappaport, 1999; Slobodkin and Rapoport, 1974), *contraction* (Slotine and Lohmiller, 2001), *Persistence Through Time of a lineage* (Bouchard, 2008; Bouchard, 2011), *thermodynamic stability* (Pross, 2003,2004,2012; Wagner and Pross, 2011), *the selection of long-lasting structures* (Shcherbakov, 2012), *sorting on the basis of stability* or *sorting for stability* (Flegr, 2010, 2013), *natural selection through survival alone* (Doolittle, 2014), *viability selection* or *selection on persistence* (Bourrat, 2014), *persistence principle* (Pascal and Pross, 2014,2015,2016),*ultrastability* (Bardeen and Cerpa, 2015), eventually *differential persistence* or *persistence selection* (Doolittle, 2017). This loose conceptual embedding is probably related to the fact that only a few theoretical researchers (at least in the field of evolutionary biology) attribute great importance to this phenomenon. For example, Okasha (2006, p. 214), who comments on the topic more thoroughly, calls this phenomenon *weak evolution by natural selection*. According to him, this process cannot generate interesting adaptations and thus he considers it to be (in contrast with *paradigmatic evolution by natural selection*) uninteresting from the evolutionary viewpoint. Godfrey-Smith (2009, pp. 40 and 104), presents a similar opinion. He considers such an extension of the term "natural selection" (i.e., *low-powered Darwinian process*) essentially possible but artificial and basically useless. The opposite opinion has been much rarer. It was explicitly presented, e.g., by Bouchard (2011), Doolittle (2014,2017) or Bourrat (2014). Bourrat (2014) even demonstrated that this process can lead to some class of adaptations in numerical models of evolution. He stated that it could actually stand on the very beginning of biological evolution—original non-replicating entities differing only in their persistence could transform into genuine replicators by the means of this process.

In this paper, we argue that this evolutionary mechanism, which is currently underappreciated and mostly is not taken into account in efforts to explain the origin of characters of living organisms at all, acts upon all biotic and abiotic systems that undergo evolution. In fact, this process may be responsible for a wide range of adaptive traits. In the reaction to its weak conceptual embedding, we propose to call this *survival of the stable* (Dawkins, 1976, p. 13) or, more exactly, temporal manifestation of *persistence principle* (Pascal and Pross, 2014,2015,2016), i.e., the general tendency for more stable, persistent and unchangeable entities and characters in the system, unambiguously stability-based sorting (SBS) according to the conception proposed by Vrba and Gould (1986) and Gould (2002, p. 659). This term avoids any connotations that attribute the phenomenon only to material, immaterial, living or non-living entities, its confusion with natural selection, which we consider a specific manifestation of this universal principle (see Section 2.1), and its confusion with sorting based on any other kinds of criteria. We will clarify the relationship of SBS and selection more thoroughly in the next section. More particularly, we will show that selection is just one special manifestation of the general process of SBS (a relationship that was implied by numerous evolutionary-biological scholars of the role of persistence in nature mentioned above, e.g. Dawkins, 1976, Okasha, 2006, Godfrey-Smith, 2009, Bouchard, 2011, Doolittle, 2014, or Bourrat, 2014). However, despite being related in their essence, selection, as a special case of SBS, has markedly different evolutionary consequences. Therefore, because the aim of this article is predominantly to demonstrate and stress the different evolutionary consequences of the two processes (deeply understudied SBS in the strict sense and usual conception, and its special case, selection), we will consider SBS and selection as separate phenomena from now on.

2. Results and discussion

2.1. The relationship between selection and SBS

All forms of selection, including species selection, require selected entities to originate in reproduction or copying (and thus have an ancestor–descendant relationship) and exhibit at least some degree of inheritance of ancestor qualities (Gould, 2002; Okasha, 2006; Godfrey-Smith, 2009). SBS, on the other hand, does not require any of this. It takes place in all systems with history, i.e., evolution in the broad sense. SBS acts upon all material and immaterial entities regardless of their origin, even entities that originate independently of each other such as snowflakes, cosmic objects during the history of universe, memes, or mutually isolated civilizations. According to the fact that—by definition—unstable and changeable entities expire or change into something else whereas the stable and invariable entities persist, more and more increasingly stable variants of sorted entities accumulate in the system over time, whereas less stable variants gradually vanish. This is true even in the case that less stable entities originate more often in a studied system than their stable variants.

SBS and selection act both in open and growing systems, and in closed systems with a stagnating number of entities. For example, in the course of a snowstorm, the number of competing entities (snowflakes) is not limited and will constantly grow in the snow cover (an open system into which new snowflakes constantly arrive from the system's surroundings). In such a system, the number of less stable entities will constantly decline, but never reach zero

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[1] „Darwin's 'survival of the fittest' is really a special case of a more general law of survival of the stable (...) The earliest form of natural selection was simply a selection of stable forms and a rejection of unstable ones. There is no mystery about this. It had to happen by definition."

because of the constant share of unstable variants among newly arriving snowflakes.[2] In a closed system, e.g. during the evolution of our universe after the Big Bang with a limited amount of matter available to form space objects, or during memetic evolution of some exclusive religious beliefs that is limited by the number of members of society, more stable entities will gradually replace less stable entities (space objects or memes). The same applies to selection. In an open system, e.g. an exponentially growing unlimited population, the number of individuals better adapted to their environment will gradually grow, but worse adapted individuals will remain in the system too. In a closed system, e.g. in a chemostat or a turbidostat (Flegr, 1997), worse adapted individuals with lower speed or effectiveness of reproduction are quickly displaced by their better adapted counterparts. Thus, in both cases, evolution will proceed faster in closed systems.

In most systems, SBS acquires solely the form of competition among entities for the highest *static stability*, i.e., lowest probability of expiration or transformation of individual entities or their traits into something else. In a particular class of systems—those in which new entities originate from parental entities and inherit their traits—SBS becomes predominantly the competition for the highest *dynamic stability* (Pross, 2003,2004,2012; Wagner and Pross, 2011; Pascal and Pross, 2014,2015,2016). The competition of stable coexisting entities for the longest static persistence becomes competition for the ability to produce the highest number of their own copies (i.e. the copies of the information how to copy itself), or more precisely, competition for the largest difference between the speed of generation and expiration of these copies. This difference is based both on the longevity of entities (e.g. length of the reproductively active life in organisms), as in the case of static stability, and on the speed of their generation, e.g. reproduction or speciation (*Malthusian kinetics* of Pascal and Pross, 2014,2015,2016; see also Pross, 2003,2004,2012, and Bourrat's, 2014, models). Darwin's natural selection (as well as Dawkins' interallelic competition, Dawkins, 1982, and Vrba's and Gould's species selection, Vrba and Gould, 1986; Gould, 2002) are thus special cases of general SBS. Sorting based on dynamic stability (i.e. selection) and sorting based on static stability differ in the nature of what is sorted—entity itself versus the *information* how to create its copies. From a certain perspective, information emancipates from matter in the case of selection (Shcherbakov, 2012). This makes us to expect both kinds of sorting to take place in evolution of systems of replicating entities with heredity, directly affecting its course and perpetually interacting in their effects.

This is in full agreement with Bourrat's (2014) arguments that were supported by numerical models of the continuous transformation of populations of entities sorted purely on the basis of static stability to populations of genuine replicators. Similar views were presented even earlier, (see e.g. Slobodkin and Rapoport, 1974; Rappaport, 1999; Bouchard, 2008,2011 or Bardeen, 2009). Doolittle (2017) also implied the interdependence of sorting based on persistence and natural selection but he aimed to accommodate his *differential persistence* or *persistence selection* into an expanded understanding of natural selection. (Pross, 2003,2004,2012; Wagner and Pross, 2011 and Pascal and Pross, 2014,2015,2016 and references therein) studied the role of stability in nature from another angle, differentiating physical forces standing behind stability kinds. Their concept and terminology, however, differ in some important details from the presented one (see Fig. 1 and Appendix).

In the case that selection, not only SBS in its strict sense, affects the evolution of a certain population; entities that do not invest in their maintenance (and thus have low longevity) but channel the majority of their resources to reproduction may easily prevail. Selection thus represents sorting based on dynamic stability, i.e., a specific form of SBS in the broad sense, whereas SBS in the strict sense and its usual conception represents sorting on the basis of static stability. Therefore, we will respect a traditional terminology, use the term SBS exclusively to refer to sorting on the basis of static stability, and call sorting on the basis of dynamic stability by its standard term—selection (for a more radical approach regarding the classification of selection, see e.g. Pross, 2004,2012). [Fig. 1 HERE]

It would be erroneous to consider SBS a process from whose direct influence the entities undergoing natural selection completely escaped. As Dawkins (1976, p. 13) stressed, this process is in each sense more general. It acts constantly and simultaneously on all levels. Moreover, the stable accumulates and unstable vanishes regardless of the origin of sorted entities or the nature of the sorting process. Shcherbakov (2012,2013) goes even further and argues on this basis that the inevitable consequence of every evolution is stasis. Invariance, not variability, is the attractor of evolution. According to this author, any evolutionary changes are only by-products of evolution, e.g. the inability of organisms to completely avoid mutations, or transient consequences of opportunism of selection-based evolution manifested by transient predominance of entities that are less stable in the long-term but have higher dynamic stability—higher fitness—in the short-term. This conclusion might seem quite extravagant taking into account all the variability of life forms on Earth. However, it is the logical consequence of the appreciation of the role of SBS in evolution. It is also worthy to note that Wagner and Pross (2011) and Pross (2012) take the opposite stand, reducing the role of static thermodynamic stability (see Appendix) in the systems of replicating entities only to a general constraint and postulating their general tendency to complexify.

Contrary to both of these approaches, we believe that the role of SBS in the systems of replicating entities with heredity is direct but subtle and selection is rather its tool than by-product, which was suggested only implicitly by Shcherbakov (2012) .[3] In a simple case (stable and homogenous environment), entities in the system would compete only for the highest number and accuracy of copies, i.e., the speed of reproduction associated with its precision, achieved, for example, by reduction of genomic size (which is also the outcome of numerous computer simulations of biological evolution, see e.g. Ray 1993,1997; Thearling and Ray, 1994,1996, or Ray and Hart, 1998, as well as experiments, see e.g. Mills et al., 1967). In the real world, the entities are affected by much more heterogeneous conditions of the environment, including other coevolving entities that undergo selection and mutually interact in a very complex manner. The outcome is constant tension between the pressure to conserve information (i.e., to increase the speed and precision of reproduction) and its evolution (i.e., adaptation to new conditions). Entities that reproduce most rapidly and precisely are not necessarily most successful under these conditions. The increased persistence of individual entities remains the ultimate attractor, yet not by trivial means (static persistence or speed of reproduction), but through more sophisticated adaptations. From our point of view, evolvability is not a mere by-product of evolution. It is an important meta-adaptation that enables an actual increase in the persistence of entities in the process of sorting on the basis of dynamic stability—selection.

Moreover, in the case of terrestrial life, the selected information, which was originally coded directly in the replicating sequence of nucleotides, emancipated to some degree from its material basis. Replicators evolved interactors—bodies—that interpret the information embedded in the sequence of nucleotides in various context-

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[2] Dynamics of such a system were modelled, e.g., by Doolittle (2014).

[3] "Evolution is resistance to entropy, the adaptation to environment being only one of the means of this resistance."

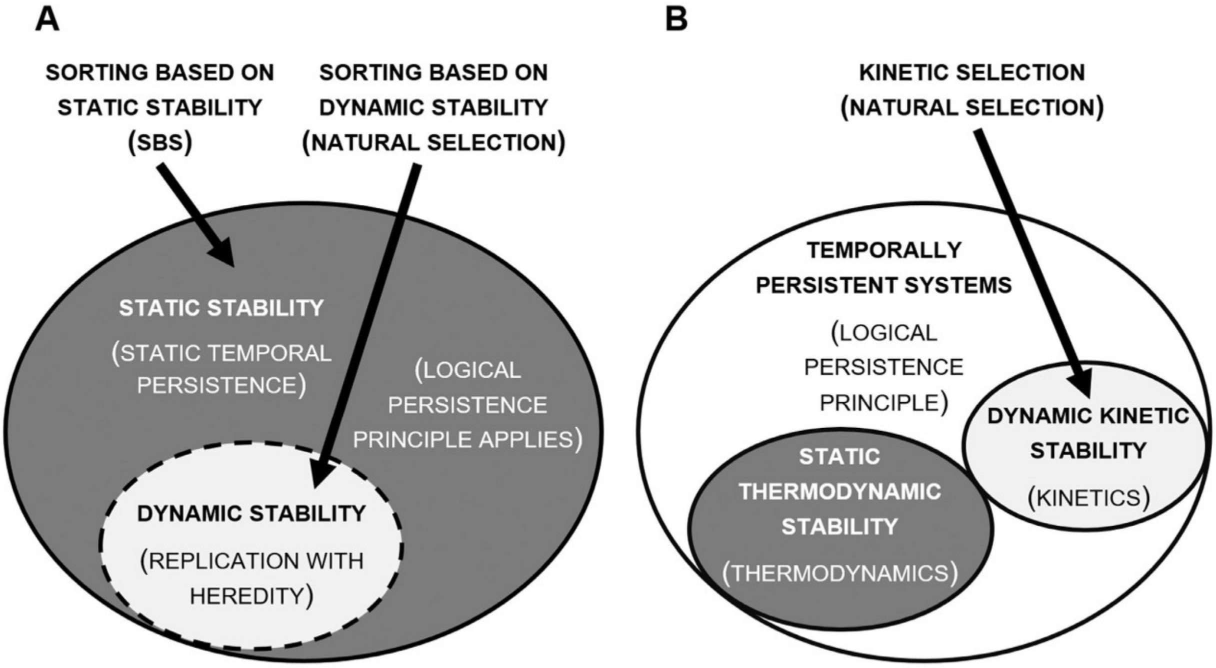

Fig. 1. The difference between presented stability concept (A) and the stability concept of Pross et al. (B). We differentiate two kinds of stability (A). Static stability equates to the entity's static stability in time, i.e. its persistence until its expiration or change into something else, regardless of the physical basis of this process. Statically more stable entities and their properties are sorted in time in the process of SBS. Entities replicating with heredity are sorted, or selected, on the basis of dynamic stability, i.e. largest difference between the speed of generation and expiration of their copies. Putting aside its physical basis and viewed from the evolutionary perspective, however, dynamic stability is only a special case of static stability in systems of entities replicating with heredity in which the statically sorted "thing" became the *information* how to copy itself. Pross (2003, 2004, A. 2012), Wagner and Pross (2011) and Pascal and Pross (2014, R. 2015, 2016), on the other hand (B), differentiate static thermodynamic stability and dynamic kinetic stability. Both of these stability kinds, i.e. the state of high entropy and the exponential multiplication of entities, are governed by the general logical "persistence principle": systems' tendency to change from less stable (persistent) to more stable (persistent). Note that other kinds of stable systems may eventually exist and be subject to the *persistence principle*. Dynamic kinetic stability equates dynamic stability in the first concept; kinetic selection indeed was proposed to be equal to natural selection (Pross, 2004; A. 2012). It is its relationship to static stability that differs among the two concepts. Note, (1) that our approach is more general, addresses all material and immaterial entities, and does not address the physical basis of stability, and therefore (2) the difference is mainly conceptual—both approaches need not exclude each other.

dependent ways. These interactors started new rounds of competition on higher levels, so that the meaning or interpretation of genetic information and the DNA–body complex became the subject of selection rather than the nucleotide sequence itself (Markoš, 2002; Ostdiek, 2011; Shcherbakov, 2012). The consequence is that interacting entities themselves (replicators), as well as the replicated information, change in the course of evolution but still maintain their historical individuality. The outcome of any such competition can be estimated with the help of game theory, particularly the theory of evolutionarily stable strategies (Maynard Smith and Price, 1973; Kolokoltsov and Malafeyev, 2010, p. 65), and if the whole system is complex enough (as e.g. the terrestrial biosphere), it need not immediately follow the path to evolutionary stasis. This, however, does not contradict the SBS-mediated accumulation of stable entities that resist selective pressures and have decreased evolvability; it continuously proceeds on all levels regardless of the effects of selection. The course of evolution on the largest scale can thus be seen as a constant struggle between stability or conservation on one side, and adaptation on the other, which, as will be shown in Section 3, can have interesting evolutionary consequences.

2.2. Differences between selection and SBS

SBS is much more widespread than natural selection and probably takes place in all evolving systems (i.e., systems with memory/history) with the exception of closed systems with a fixed maximum number of entities in which it proceeded completely, i.e., where only absolutely stable non-expiring entities that are incapable of any change accumulated and remained. In selection, the most successful entities are those that produce the most offspring until their expiration, i.e., death. In SBS, the most successful entities are the most stable ones—those that persist for the longest time without expiring or changing into something else. Selection is much more efficient. Ensuring that offspring inherit the traits of their parents and that the speed of offspring production is based on the number of beneficial traits of the individual, selection gradually accumulates and amplifies beneficial traits, which give individuals a higher dynamic stability—higher fitness. Thus, more (on average) better-adapted individuals and fewer worse-adapted individuals are produced in time. This pattern may be partially masked by the Red Queen effect (Van Valen, 1973). Competitors, predators and parasites evolve counter-adaptations so that, for example, the final speed or effectiveness of reproduction of members of a certain population or species seemingly stagnates until we artificially prevent the counter-evolving species to respond to evolutionary moves of the studied species (see e.g. Becerra et al., 1999). On the other hand, the same share of stable and unstable entities (e.g. snowflakes) originate in the course of SBS regardless of the previous evolution of the system, and especially regardless of the average stability of entities currently constituting the system. This does not fully apply to some memes. For example, new ideas are created with regard to past ones and authors of new ideas preferentially generate such that they have a higher chance of success in long-term competition with existing ones (a process analogical to "copy-the-product", see Blackmore, 1999, pp. 59–62). However, this is probably specific to entities created by conscious beings that are able to (at least partially) anticipate future development of the system (see e.g. Blackmore, 1999).

In the course of the evolution of a certain genealogical lineage, incomparably more complex adaptations originate by means of the gradual accumulation of mostly small changes (beneficial mutations) in natural selection than by means of much more widespread SBS. It is clear that random changes that increase the stability (persistence) of entities may also accumulate in systems without selection, but this process would be incomparably less effective and slower (see Bourrat, 2014). However, it is possible in principle, as was modelled by Doolittle (2014). In the course of selection in closed systems (which are, in the long term, all systems undergoing biological evolution), every beneficial change spreads to most or even all members of the population. Newly originated beneficial change thus would almost always affect the individuals that already bear the previous one. In SBS, the probability of a simultaneous occurrence of several changes that increase the stability of one newly originated individual is negligible, and the time necessary for the accumulation of a larger number of changes that are beneficial in terms of stability in one individual might be incomparably longer than its estimated lifespan (see Bourrat, 2014). For example, the chamber eye evolved multiple times independently by means of natural selection (Fernald, 2000). It is, however, very unlikely that such a complex organ would evolve solely by means of SBS.

In spite of lower efficiency of SBS, a certain category of adaptations that we see in modern organisms probably originated by means of SBS rather than selection. However, these can only be characters that originated by one or two changes, not a long chain of consequential changes that would continuously elaborate a certain function. An important source of adaptations that increase the stability of sorted entities (e.g. individuals in natural, i.e. intraspecific, selection or evolutionary lineages in species selection) are preadaptations. Such characters evolved by means of selection as adaptations to a certain function, but later turned out to be advantageous in terms of stability and thus spread and prevailed by the means of SBS. SBS works as a sieve that selects characters contributing to the long-term stability of entities that constitute the system and also the system itself (Doolittle, 2014,2017). An example of such a character may be obligate sexuality (Davison, 1998; Flegr, 2008,2010, 2013; Shcherbakov, 2010,2012,2013; Gorelick and Heng, 2011), which originated by natural selection, likely as one of the mechanisms of reparation of mutations, especially structural damage to DNA (Bernstein and Bernstein, 2013; Hörandl, 2013) .[4] Only *ex post* did it turn out that sexuality significantly contributes to the stability of its holders—sexual species—in heterogeneous, changeable and often unpredictable conditions ruling on most of the Earth's surface. Asexual species are constantly at risk of adapting to temporarily changed conditions, losing their genetic polymorphism and not being capable of re-adaptation to original (or any other) conditions fast enough. This could even lead to their extinction. Sexual species, on the other hand, adapt to transient environmental changes only imperfectly, and constantly maintain high genetic polymorphism (including currently disadvantageous alleles) because of the effects of genetic epistasis and pleiotropy in conjunction with frequency dependent selection. Therefore, they are always able to quickly re-adapt by the changes of allelic frequency (Williams, 1975, pp. 145–146, 149–154, 169; Flegr, 2008,2010,2013). From the perspective of individual selection, sexuality is, accompanied by the two-fold cost of meiosis, two-fold cost of sex and other handicaps of its holders (Lehtonen et al., 2012), disadvantageous. From the perspective of species selection—in this case the lower probability of extinction of species in heterogeneous environment—it is highly advantageous. However, species selection is weaker and cannot act against individual one. From the perspective of SBS, it is highly advantageous as well; species and lineages that reverse to asexual reproduction are sorted out, i.e., perish, those that cannot reverse to asexual reproduction for any reason accumulate, and by this mechanism sexuality might spread and prevail.

SBS cannot gradually generate such spectacular adaptations as, e.g., chamber eye, yet it always has the final word in evolution and is even able to completely reverse the course of evolution driven mostly by selection. For example, the human brain and consciousness are undeniably one of the most remarkable characters among terrestrial organisms. However, it is possible that this brain that enabled humans to dominate the Earth and establish a multi-billion population may also be the reason of our early extinction, either by the means of catastrophic warfare, failed physical or biological experiment or "prosaic" severe viral infection that could spread only in a sufficiently dense and interconnected population. From the macroevolutionary point of view, humans may be easily outlived by species in which some ontogenetic constraints in the role of preadaptation prevented the evolution of a sufficiently efficient brain.

Selection is opportunistic. It would beat seemingly "forward planning" SBS in a stable environment (see e.g. Ray, 1993,1997; Thearling and Ray, 1994,1996; Ray and Hart, 1998). However, in a changing environment, i.e., under the realistic conditions of Earth's surface, it is otherwise. Selection does not "plan in advance" and thus is only able to improve the adaptation of organisms on the current conditions regardless of the risk of impairing their future chances of survival, including the risk of extinction of the whole species. Considering the "adaptive landscape" (Wright, 1932), species and populations are able to move only in the upward direction under normal conditions and thus are able to occupy only local, not global, optima. Descending a little and then ascending on another slope for the occupation of a higher peak in the adaptive landscape would not be possible under the normal regime of selection. Mutants that descend have lower fitness and they or their offspring are removed from the population before accumulating other mutations, reaching the "bottom of the valley" and starting to ascend on another slope. On the other hand, SBS does not have such a limitation and is subject to much less opportunism.[5] In the case that a certain adaptation (e.g. a certain pattern of altruistic behaviour) decreases the chance of survival of an individual or slows down its reproduction, yet simultaneously enhances the chances of survival of the population of the individual's species, those (probably rare) populations and species in which the adaptation prevailed would prosper and survive in the long term.

In most species and within them in most populations, individual selection would act against these tendencies and prefer mutants that lose the individually disadvantageous character. However, populations and species that are preadapted with safeguards

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[4] The so called "reparation theories" are only one of many concepts proposed for the origin of sexual reproduction. See e.g. Birdsell and Wills (2003) for other proposed theories of the origin of sexual reproduction. However, the vast majority of them assumes that original purpose of sexual reproduction and the reasons of its subsequent spread and long-term maintenance differ.

[5] A certain degree of opportunism can manifest only in SBS ongoing in a closed system. Stable entities that are resistant to current effects of environment, or effects that do not actually affect the system but happen relatively often, could prevail there. In closed systems, this precludes the occurrence of entities that would be more resistant to another, possibly much stronger, effect of environment that happens much less often. On the other hand, SBS ongoing in open systems is not opportunistic at all. Ultimately stable entities always prevail there in the long term.

against such reverse changes would prevail in the end. Returning to the previous example, such safeguard against the reversal of asexual reproduction may be for example mammalian genomic imprinting that significantly reduces the chance of successful transition to asexual reproduction (Bartolomei and Tilghman, 1997). This and all similar safeguards originated as preadaptations, i.e., adaptations for another purpose, or as spandrels, i.e., characters without any function formed purely as the consequence of topological, physical, biochemical or ontogenetic constraints (see e.g. Gould, 2002). Many species presumably did not have any such safeguards, but we do not see them today because they lost to their counterparts in the process of SBS. Rare extremes are usually more important than average values both in intraspecific and interspecific evolution (see e.g. Dobzhansky, 1964; or Williams, 1975). Winner usually "takes all". The fact that the vast majority of populations do not have safeguards and are dominated by selfish individuals means nothing if a safeguard is present in at least some populations. It would be the populations that bear the safeguard that would determine the evolution of a studied species. Similarly, if there happens to be a safeguard against the loss of sexuality or altruistic behaviour in certain species that is absent in the vast majority of others, we will meet only the species with such a safeguard and their descendants in the long term.

3. General discussion

3.1. Phenomena in which SBS plays an important role

3.1.1. Microevolutionary phenomena

SBS is much more widespread than selection. However, in the reign of biological evolution, and especially in the processes operating on the human (ecological to microevolutionary) timescale, its significance is obscured by spectacularly manifesting natural selection. SBS is thus encountered especially in phenomena whose origin, establishment or maintenance wasn't convincingly explained by natural selection yet. Such products of SBS may be, for example, sexuality mentioned in Section 2.2 or some types of altruistic behaviour, including restrictions on individual reproduction under the risk of overpopulation that were widely discussed in the past (Dawkins, 1976; Wilson, 1983; Wynne-Edwards, 1986; Leigh, 2010). The usual assumption is that individuals that "voluntarily" reduce the speed of their reproduction would be displaced by selfish mutants (i.e., eliminated by selection). The whole phenomenon is interpreted not as an evolutionary adaptation that increases the long-term success of populations, but as an individual adaptation that enables the individual to save its resources in the situation of high offspring mortality. The proximate reasons for this phenomenon are also being emphasized, e.g. territoriality, social hierarchy, or that individuals in too dense a population disturb each other, reducing the success of each other's reproduction (Wynne-Edwards, 1986). However, these proximate reasons may act as the safeguards described in Section 2.2 that enables certain populations not to be dominated by selfish individuals, which are able to reproduce regardless of the risk of overpopulation. The existence of a safeguard, e.g. the population density-dependent ability "to be disturbed" by nearby individuals, might give the species a chance to overcome the risks of fatal overpopulation and thus give it the decisive advantage in SBS. Species without this or some similar safeguard were more susceptible to extinction and thus we do not meet them today.

Doolittle (2014) suggested that another product of the process that we call SBS may be widespread and often intensive horizontal gene transfer (HGT). According to this author, it may significantly accelerate the adaptations of (especially prokaryotic) organisms to environmental stressors. Such acceleration is probably advantageous in two ways: in terms of individual selection in the short to medium-term and, as will be shown in Section 3.1.3, in the long-term because of the gradual stabilisation of environmental conditions (Markoš, 1995; Doolittle, 2014). In a similar way to sexual reproduction mentioned in Section 2.2, the original purpose of HGT was probably completely different (it probably served for horizontal spread of selfish genetic elements, see e.g. Redfield, 2001). However, species and lineages that evolved safeguards against the loss of ability to undergo HGTs preserved the ability of relatively fast reactions to the changes of conditions. The most profound safeguard against the loss of HGT ability may be the extraordinary conservation of genetic code (Markoš, 1995; Syvanen, 2002; McInerney et al., 2011)—evolutionary lineages that deviated too much and compromised their ability to undergo HGTs were sorted out by lineages that could still enjoy its benefits.

Similarly, SBS can explain the wide distribution of certain strikingly restrictive traits of modern organisms, i.e., safeguards against the loss of a trait that is beneficial in the long-term. Some examples might be e.g. genomic imprinting of mammals mentioned in Section 2.2 or a similar phenomenon in gymnosperms, whose embryos require organelles from the paternal gamete for successful development (Neale et al., 1989); or the extraordinary conservation of genetic code that may enable mutual compatibility of organisms in horizontal gene transfers (Markoš, 1995; Syvanen, 2002; McInerney et al., 2011).

3.1.2. Macroevolutionary phenomena

SBS may also explain certain macroevolutionary phenomena. It is probably tightly connected to the phenomenon of evolutionary stasis, or the punctuated pattern of evolution of (especially) sexual organisms (see e.g. Eldredge and Gould, 1972; or Gould, 2002, pp. 745–1024, with particular examples on pp. 822–874). As was already mentioned, sexual reproduction spread and is still maintained by means of SBS—it helps to maintain high genetic polymorphism, prevents opportunistic one-way adaptation accompanied by loss of genetic polymorphism and enables fast and reversible evolutionary reactions to fluctuations of conditions in changeable and heterogeneous environments by means of epistasis and pleiotropy interconnected with frequency-dependent selection (Flegr, 2008,2010,2013). Another consequence of SBS in sexual species is the accumulation of functionally interconnected alleles on the level of an individual and a population. Alleles that are tightly and non-trivially interconnected in their effects on a phenotype, especially alleles that are maintained in a polymorphic state by frequency-dependent selection, are extremely hard to fixate or eliminate through any type of selection and thus are more persistent and accumulate in populations (Flegr, 2008,2010,2013). Such "microevolutionary freezing" may be beneficial even to individual organisms—for example, it may enhance the robustness of development to internal and external changes (Shcherbakov, 2012). Sexual species thus remain in evolutionary stasis for most of their existence and are able to irreversibly change only under certain conditions, as was suggested by Eldredge and Gould (1972).[6] This is in accordance with Sheldon's (1996) theory *Plus ça change* that highlights the difference between paleobiological evolutionary patterns of species of changeable environments (punctuated evolution) and species of stable environments (gradual evolution). The difference between these "generalists and specialists in geological timescale" may stem from the presence, or absence, of sexual reproduction.

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[6] Several alternative hypotheses for the conditions under which species in the state of evolutionary stasis may start to irreversibly respond on selective pressures were suggested already by Eldredge and Gould (1972). However, the transition between the "plastic" and "elastic" phase of the species' evolution is probably most thoroughly described by Frozen Plasticity Theory, see e.g. Flegr (1998, 2008, 2010). All types of punctuationalistic theories of evolution and proposed conditions for the above-mentioned transition were comprehensively summarized by Flegr (2013).

The very prominent and almost universal pattern of macroevolutionary processes is also a non-monotonous change in disparity, i.e., morphological and functional variability (e.g. in the number of body plans), in the course of the evolution of particular evolutionary lineages, or more precisely, particular taxa. Every clade of an evolutionary tree originates in a speciation event and initially contains a single species. Thus, it has minimal diversity (number of species) and minimal disparity at the beginning. The number of species and morphological and functional diversity then grow in the course of the evolution of a lineage, as do the number of different phenotypically distinct clades and number of higher taxa described by paleotaxonomists within the original evolutionary lineage. However, individual sub-clades die off in time and only clades whose species differ in continuously decreasing number of still less essential traits originate within the remaining clades. The number of species of the original taxon, diversity, need not necessarily decrease and may even grow for a considerable time. Its disparity, on the other hand, decreases (Rasnicyn, 2005; Erwin, 2007; Hughes et al., 2013). According to the class of developmental explanations of this phenomenon, the taxon exhibits high evolvability, i.e., "evolutionary plasticity", at the beginning. Its members can initially change in almost every trait under appropriate selective pressures. In time, more and more traits "macroevolutionarily freeze", so that modern members of the taxon are not able to evolve such profoundly new adaptations and lifeforms that were evolved by the species in earlier stages of the evolution of the clade (Foote, 1997; Eble, 1998; Erwin, 2007). The taxon thus gradually abandons different parts of morphospace and perhaps only one, often very specialized and phenotypically very uniform, clade survives at the end. For example, only the species-rich but morphologically rather uniform clade of birds (Aves) survived from original highly disparate clade of dinosaurs to the present (Chiappe, 2009). An even more extreme example of gradual loss of disparity, which is in the long-term probably accompanied by the loss of diversity because of decreasing evolvability, may be the so-called "living fossils" (see e.g. Lloyd et al., 2012). The phenomenon of dead clade walking (Jablonski, 2002), i.e., higher susceptibility to extinction in many isolated lineages of higher taxa that survived mass extinction, may also be a manifestation of the same process. It is probable that these lineages are macroevolutionarily frozen and their possible responses to selective pressures of the post-extinction environment are thus very limited.

A spectacular example of macroevolutionary freezing is the evolution of multicellular animals. The common ancestor of all bilaterians lived approximately 700 million years ago, whereas the common ancestor of all metazoans probably did not precede them by more than 100–200 million years (Douzery et al., 2004; Peterson et al., 2008; Erwin et al., 2011). However, metazoans did not exhibit any significant diagnostic characters until Cambrian or at least Ediacaran, and they probably consisted of mm-sized creatures without hard parts that would enable their identification and classification in fossil material. However, something happened in the early Cambrian approximately 540 million years ago, and metazoans started evolving rapidly and differentiating into many morphologically and ecologically distinct forms, future metazoan phyla (Shu, 2008). This initial period was short and lasted tens of millions of years maximally (Erwin et al., 2011). All current animal phyla, and several tens of other phyla that gradually died out in the next millions of years, originated during this time (Gould, 1989). No other animal phylum and, with the exception of certain groups of radically simplified parasitic organisms (Canning et al., 2004; Glenner and Hebsgaard, 2006; Murchison, 2008), no radically new body plans have originated since the end of the Cambrian. The trend of a gradual decrease of disparity in the course of the evolution of a lineage was also documented in many particular taxa of multicellular animals and plants (Erwin et al., 1987; DiMichele and Bateman, 1996; Eble, 1999). Other examples were summarized by Gould (1989) or Erwin (2007), and, according to Hughes et al. (2013), this trend is characteristic for Phanerozoic clades of metazoans in general. Particular macroevolutionary frozen traits are, for example, the patterns of head segmentation characteristic of main groups of arthropods, five-fingered legs of tetrapods, or (with a few exceptions) seven cervical vertebrae of mammals. All these currently frozen traits were, in some cases even considerably, changeable in the early stages of the evolution of respective taxa (Hughes et al., 2013).

The gradual macroevolutionary freezing of individual traits is almost certainly not just 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*). Freezing of individual traits in the course of macroevolution is a real phenomenon that is observed even on the intraspecific level. On this level, it was first described by Italian zoologist Daniele Rosa, and is known as Rosa's rule today (Rosa, 1899). For example, intraspecific variability of particular morphological characters and the number of characters in which this variability is exhibited are much greater in the early branched-off species than in later branched-off species of certain taxon. Particular evidence for this pattern is the gradual decrease of intraspecific variability in trilobites (Trilobita). Webster (2007) documented that the relative proportion of species with at least one intraspecifically polymorphic morphological character decreased from 75% in middle Cambrian to 8% in late Cambrian. After the subsequent rise to 40% in early Ordovician, it just more or less monotonically decreased until middle Devonian. At that time, the intraspecific polymorphism vanished completely, not to show again until the extinction of taxon at the end of Permian. The temporal pattern in proportion of characters coded as intraspecifically polymorphic is even more striking, declining from a median of 2,8% and 3,6% in middle and late Cambrian to a median of 0% in post-Cambrian. The primary reason for the freezing of individual characters in the course of macroevolution is therefore most likely the freezing of these characters within particular species. If species cease to vary in certain trait, there are no diverse variants of this trait among which selection might differentiate. Such species are thus unable to adapt to conditions to which species cleaved early in the evolution of respective taxon were able to adapt easily (Webster, 2007).

Frozen Evolution Theory (do not confuse with Frozen Plasticity Theory which describes the causes of alternation of short "evolutionarily plastic" and long "evolutionarily elastic" phases in species' lifetimes) assumes that the reason for the macroevolutionary freezing of individual traits and, consequently, taxa (monophyletic sections of the evolutionary tree delimited by a taxonomist on the basis of a unique combination of several diagnostic characters) of sexual organisms is SBS (Flegr, 2008,2010,2013). Various characters exhibit various degrees of evolvability, i.e., the ability to change under appropriate selective pressures, given by the way of their genotype–phenotype mapping and frequency-dependent effect on fitness (Flegr, 2008,2010,2013). In the initial phase of the evolution of a certain taxon, a large part of the characters of its members are easily changeable, a smaller part harder and only a small fraction, probably those that the members of the taxon inherited from their evolutionary ancestors, not at all or to a very limited extent. Individual characters change in the course of the taxon's evolution, even in terms of their variability and evolvability. Traits that are able to change easily and distinctly under proper selective pressures appear and disappear, whereas stable traits persist and accumulate in the taxon. More and more traits irreversibly freeze by means of this sorting, both on the intraspecific and interspecific level. Intraspecific variability is decreasing in a growing fraction of traits. The disparity of the whole taxon is decreasing because old evolutionary lineages of the taxon slowly die out and newly originating species can be distinguished from the original species only to a limited degree in a small and constantly decreasing number of traits.

Organisms, or their evolutionary lineages, may theoretically avoid irreversible macroevolutionary freezing through species selection (Stanley, 1979). Competition for the highest rate of speciation and lowest rate of extinction should theoretically ensure that the lineages with the highest (remaining) evolvability prevail in the long-term. However, SBS, whose manifestation is also macroevolutionary freezing, probably cannot be reversed by species selection, i.e., sorting on the basis of dynamic stability at the species level. Irreversible macroevolutionary freezing is a ratchet-like process that continuously accumulates stable characters and traits in all lineages simultaneously. It cannot be ruled out that certain new species may rarely acquire a unique combination of characters that was not sorted on the basis of stability yet, which would probably mostly accompany its transition to a completely different environment or the adoption of a new ecological strategy. A certain seemingly irreversibly frozen character, or combination of characters, may also exceptionally "thaw" in the course of the evolution of a lineage and start to respond to selection again. Both these events might stand on the beginning of the evolution of birds whose common ancestor conjoined several unique adaptations (Brusatte et al., 2014) and uncoupled the development of front and rear legs to a considerable degree (Dececchi and Larsson, 2013). However, a more fundamental thaw, e.g. thawing of whole body plan, is probably extremely rare, and if it happens, it has the character of a radical simplification of current individual development. This can be demonstrated, e.g., on the example of endoparasitic crustaceans from the clade Rhizocephalia (Glenner and Hebsgaard, 2006), seemingly unicellular endoparasitic cnidarians from the clade Myxozoa (Canning et al., 2004) or sexually- or biting-transmitted mammalian cancers (Murchison, 2008). These radically simplified species may become founders of entirely new, initially macroevolutionary very plastic, but gradually irreversibly freezing high-ranking taxon.

3.1.3. Ecological and geophysiological phenomena

SBS acts even on the ecosystem level, and, in the largest spatial and temporal scale, on the level of the whole planet. Communities in a newly establishing ecosystem (e.g. after severe fire, deglaciation, or emersion of a new island) undergo ecological succession. With a certain degree of simplification, ecosystems are heading towards an equilibrium state—climax—in which they can stay, or around which they can oscillate, for a considerable time in the absence of significant changes to environmental conditions (see e.g. Walker and del Moral, 2003) .[7] The development of communities towards the stage of climax is of various lengths and complications and the final climax communities may vary according to the character of disturbances, amount of available resources and energy etc. (in other words, a climax community may be a polar growth of lichens, as well as a tropical rainforest). Ecological succession is a multidimensional process and takes place on many levels. It may even lead to significant changes in abiotic conditions of the environment. However, it always follows the rules of SBS. Individual species are sorted based on their persistence in the context of a dynamically changing community. An important component of this persistence is their current ecological success. In the long-term, however, their contribution to the stability of the ecosystem is much more important (Bardeen, 2009). This contribution need not be active and need not be paid at the expense of individual fitness (such a system could be extremely easily invaded by selfish entities). It is, rather, based on the species' ecosystem function, its by-products and side effects—safeguards on the ecosystem level. Species that unidirectionally change the environment towards the conditions suboptimal for them disappear, whereas species that are incorporated in various negative feedback loops that maintain conditions favourable for them persist. Thus, an ecosystem at an advanced stage of development is usually able to compensate (at least to some degree) for the effects of biotic and abiotic environments that lead it off current balance. However, if the intensity of these effects exceeds a certain threshold, the ecosystem may, sometimes profoundly, change (e.g. after distortion of the ecosystem by an invasive species, or change in the soil pH caused by certain tree species). Such change leads to further change in the course of ecological succession (Walker and del Moral, 2003). Certain changes may be destructive—exceptional cases even on the global scale—e.g. the origin of oxygenic photosynthesis that completely altered global conditions on Earth. Such events are described by the Medea hypothesis, see Ward (2009). However, Medea-class events are probably very rare and organisms are thus able to adapt to the resulting changes with the help of selection on the evolutionary timescale. On the other hand, if the changes exceed a critical threshold, or if they are too fast (this applies more to the catastrophic events of abiotic character, e.g. the impact of large cosmic bodies), they can lead to the extinction of all (at least surface) life on the planet.

The strong version of the Gaia hypothesis (Lovelock, 1979) was rejected by most evolutionary biologists because of its assumption that planet Earth (with the help of terrestrial organisms) actively maintains conditions suitable for life. According to the hypothesis, this "planetary homeostasis" is ensured by a broad array of negative-feedback cycles of chemical elements and energy and Earth thus shows signs of a superorganism. The main argument against it is that the only known possible natural origin of such a purposeful system involves natural selection (Doolittle, 1981; Dawkins, 1982; Gould, 1988). However, the group selection on behalf of a whole biosphere postulated by Lovelock would collapse under the pressure of individual selection favouring selfish individuals. The same is true for species selection. The only other alternative, selection on even higher level—the level of whole planets or biospheres—is impossible for one non-reproducing and non-competing individual (the Earth).

Nevertheless, such a long-term stable system integrated by negative feedback loops might develop through sorting of individual geological, atmospheric and biological entities and processes on the basis of stability, i.e., their contribution to the long-term stability of the terrestrial environment. This contribution is possible to estimate with the help of game theory, or more specifically, the theory of evolutionarily stable strategies (Maynard Smith and Price, 1973; Bardeen, 2009; Kolokoltsov and Malafeyev, 2010, p. 65). Entities and processes that did not contribute to the stability of the system or directly led it out of balance acted only temporarily, whereas the ones that supported the long-term maintenance of stability in the context of other forces accumulated. The main difference from ecological succession mentioned earlier in this section, besides the role of biogeochemical cycles that manifest themselves only on higher spatial and temporal scales, is that it operates on evolutionary, not ecological, timescales and new biological entities enter the system through speciations, not colonizations. In a similar way to ecological succession, entities and processes acting against the establishment of homeostasis might (even substantially) change conditions in the system. Nevertheless, the general

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[7] Taking into account the plethora of factors of biotic and abiotic environments that affect terrestrial organisms, it is better to consider the concept of climax as depicted here a simplification; a mobile attractor at best, towards which all ecosystems are usually heading but almost never reach. This, however, does not contradict the general tendency of ecosystems to evolve towards a stable climax stage, i.e., the accumulation of species that maintain stable conditions for their survival in the context of other biotic and abiotic factors.

SBS-mediated tendency of the system to develop towards higher stability via the accumulation of contextually stable elements affects it all the time, on all levels. The later the system is observed, the more long-term stability supporting entities and processes it accumulates and thus remains in stable states for longer periods (Doolittle, 2014). This agrees with the observed decrease in extinction and speciation rates (Raup and Sepkoski, 1982; Gilinsky and Bambach, 1987; Gilinsky, 1994; Benton, 1995; Alroy, 2008) and accumulation of long-lived genera in the terrestrial biosphere during the Phanerozoic (Rohde and Muller, 2005). Decreasing sensitivity of the ecosystem to the effects of newly arriving species was also observed in certain computer simulations, see e.g. Post and Pimm (1983). Another consequence of SBS is that it is more probable that any such system (Earth, certain exoplanet etc.) will be met in a long-term stable state than in an ephemeral unstable one.

SBS acts on any space body, even lifeless ones, and always leads to the most stable states under current circumstances. The equilibrium among geological, geochemical and atmospheric processes need not be static even on lifeless bodies; it could be dynamic, as was observed, e.g., on Venus or Titan, and continuously evolve in relation to changes of outer and inner conditions. However, only in the case when biological entities with a significant effect on the conditions of the environment take part in this sorting, the whole system is heading towards the long-term stable and negative-feedback-regulated conditions favourable for this specific class of entities. The establishment of biogeochemical cycles (planetary homeostasis) is probably further facilitated by the multilevel character of the sorting of biological entities based on their contribution to long-term stability—they are sorted on all levels simultaneously including the global level. SBS is thus able to explain the accumulation of biological entities and processes that maintain conditions suitable for their own survival with the help of negative-feedback processes without greater difficulties. As in the preceding examples, we should not be surprised that, *ex post*, the whole system looks strikingly non-evolutionary, almost like it was planned. This is the common feature of systems evolved by SBS.

Doolittle (2014, 2017) and Bardeen (2009) reached similar conclusions regarding the possibilities of establishing Gaian planetary homeostasis; they also postulated the evolution of a system (Earth) towards more stable states through the accumulation of contextually stable elements. Both these researchers supported their arguments by computer simulations: selection of non-replicating non-competing entities in the first case and Gaian “daisyworlds” in the second. Doolittle (2014) got especially close to our conception of SBS. According to this author, classical adaptations do not originate in this process. It can, however, sort adaptations that originated by means of natural selection. These adaptations thus serve as mutations of a higher level. Note, however, that Doolittle (2017) recently stressed differential reproduction of co-adapted parts of the persistent entity (e.g. Gaia) as a more “credible way” for the emergence of certain complex traits of non-reproducing entities in an attempt to reconcile Gaia with Neo-Darwinism. Bardeen (2009) elaborated the basic idea even further and proved that persistence, i.e., long-term stability, is *de facto* the true fitness. Similar reasoning also lies behind proposals to define fitness as the rate of actual or potential persistence of biological entities (in Bouchard’s words “differential survival through a time of a lineage”) in the context of a system (Bouchard, 2008,2011). However, this is (at least to a high degree) a direct implication of an even older theory of evolutionarily stable strategies. According to this theory, organisms compete for the highest persistence, or the continuing in an “existential game” (Slobodkin and Rapoport, 1974).

3.1.4. Cultural and other phenomena

SBS-based explanations may be naturally applied even in many non-biological fields that deal with evolving systems. The principle of SBS was described and used as an explanation for numerous phenomena e.g. in the fields of artificial intelligence (Slotine, 1994; Runarsson and Jonsson, 1999), cybernetics (Slotine and Lohmiller, 2001; Slotine, 2003), and even cosmology (Safuta, 2011). Its role is probably even more significant in cultural evolution. SBS is able, e.g., to explain the continuous freezing of social institutions and slowing down of social development: It is possible to change almost everything immediately after the establishment of a society, or a revolution that broke down current organization. However, self-maintaining institutions and forces, whose changes gradually slow down and eventually stop, accumulate in time by means of SBS. Numerous authors have highlighted this aspect of cultural evolution. For example, Kováč (2015, p. 26), stressed the evolution of laws, morals, culture and political arrangements towards greater stability. Charles Sanders Pierce named this aspect of cultural evolution “the origin of habit” and “sedimentation” (see e.g. Eco, 2000). Rappaport interprets evolution as constant struggle to maintain stability that is manifested in cultural evolution by the origin, formalisation and petrification of rituals under whose paradigm the society develops (Rappaport, 1999, pp. 416, 425–437). According to Rappaport, the “aim” of all entities is to persist in the existential game as long as possible. This existential game follows the rules of evolutionarily stable strategies, whereas entities that are most stable in the context of their environment and other interacting entities persist for the longest time (Slobodkin and Rapoport, 1974; Rappaport, 1999, pp. 6–7, 408–410, 420, 422–424). However, in a similar way to biological evolution, cultural evolution also need not unidirectionally lead to absolute stability.

Cultural evolution usually has a punctuated character: the alternation of short periods of dynamic changes with long periods of stasis. Systems theory calls this pattern an alternation of “ultrastability” and “breaks” that occur after the deviation of an ultrastable system beyond the limits of its adaptability, which leads to its rearrangement, whether the systems are biological, economical or technological (Bardeen and Cerpa, 2015). This aspect of cultural evolution was highlighted from another angle by Lotman (2009, pp. 7–18, 114–132), who distinguished the periods of cultural “stasis” and “explosion”. Bardeen and Cerpa (2015), presented many particular examples from cultural, or technological, evolution. Numerous particular examples of the punctuated character of cultural evolution were also presented by Gould (2002, pp. 952–972). Markoš (2014) explicitly pointed out the analogy of this pattern of cultural evolution and biological punctuationalism, particularly the processes described by the Frozen Plasticity Theory. In another article (Markoš, 2015), this author connects the ideas of Pierce, Lotman, Rappaport and Flegr and interprets them as various views of the general property of all semiotic systems (historical systems with evolution, ancestor–descendant relationships, memory and experiences): Original chaos “charged” with possibilities follows one specific trajectory, which is plastically changeable at the beginning, but gradually freezes and passes into the state of stasis characteristic of reversible “elastic” reactions to internal and external influences. According to Markoš (2015), the evolution of all semiotic systems ends either by their expiration, or return to the original state of chaos. The biosemiotician Ostdiek (2011) analogically connects the “solidification” of the meaning of a particular symbol and the transition of a system to a state of evolutionary stasis characteristic of elastic reactions. This author even explicitly emphasizes the Frozen Plasticity Theory and argues for the homology of processes causing microevolutionary freezing and solidification of a symbol (particularly its usage by a bigger population and in a higher number of connotations and interactions with other signs and symbols) or the restoration of its original plasticity (only if the symbol loses most of its original meaning). SBS thus takes place even in cultural evolution, although, because of its specifics, SBS sometimes proceeds there in a slightly different manner than in biological evolution.

3.2. Historical dimension

The relatively late discovery of the principle of natural selection is considered one of the greatest enigmas of science. This principle is simple and evident from the modern point of view, yet it was not discovered until the latter half of 19th century, i.e., later than the vast majority of comparably complex and many even more complex processes in other fields (Komárek, 2003, pp. 37–44). One reason for this lateness may be cognitive bias. The human brain is specialized in solving problems of interpersonal relations, and every problem that is not easily translated into such a relation or does not have evident analogies with these relations is disproportionately harder to solve (Cosmides, 1989; Gigerenzer and Hug, 1992). For example, it was demonstrated that only a small fraction of unaware respondents solves the *Wason selection task* (Wason, 1966,1968) easily and correctly: “You are shown 4 cards labelled A, D, 3 and 8 on the visible faces. You know that each card has a letter on one side, and a number on the other. Which card(s) must be turned over to test whether following statement applies to these 4 cards: *If* a card shows A letter, then there is an odd number on the other side?” On the other hand, if we translate the same task into the question on interpersonal relationships: “There are 4 persons in the bar: one elderly and one young, in which we can’t recognize the nature of their drinks, and two persons of uncertain age, one of which drinks an alcoholic beverage and the second soda. Which of these persons must be controlled by a policeman to test whether the bar serves alcohol to minors?”, it is solved easily and correctly by nearly everyone, including many policemen.

The concept of *sociomorphic modelling* (Komárek, 2009) shows that Darwin’s model of natural selection, which explains the evolution of organisms as the consequence of competition of individuals for the highest fitness, could not have been generally thought of and formulated until 19th century England, in which analogous competition among individual economical subjects led to striking and immensely fast development in industry and society. The process of industrial development based on the prosperity of successful and demise of unsuccessful companies was easily thought of, which greatly facilitated insight into an analogical process among living organisms. It is no coincidence that a more or less identical model of evolution was independently formulated by Matthew (1831), Darwin (1859), Darwin and Wallace (1858) and Wallace Darwin and Wallace (1858) within a few years. It is true that ideas preceding the exact formulation of the theory of natural selection could be traced several decades back (see e.g. Rádl, 2015). However, a similar insight would be much more difficult just 100–200 years earlier—back then, there was almost no substantial industrial development and companies; rather, craftsmen workshops were associated with guilds that guaranteed stable prices and quality of their products, and offered practically the same spectrum of products as they did for centuries (Ogilvie, 2004).

On the other hand, the very same rapid development of the material world that has surrounded us until now might have precluded the identification of another universal process that drives biological evolution—SBS—until recently. It is telling that this process was known already in ancient Greece and some historical models of biological evolution were based exclusively on it. For example, Empedocles formulated a model of the origin of living organisms through random combinations of individual limbs (i.e., organs) (Campbell, 2000). Most organisms that arose this way were not successful or even viable because their randomly combined limbs did not fit together very well. However, some of these organisms proved to be well organized, were successful and persistent, and prevailed. Thus, we cannot exclude the possibility that we will not be able to fully recognize and appreciate the true value of the most universal process that drives the evolution of practically all living and non-living systems until the rapid development of our material world slows down or ceases completely.

3.3. Conclusion

Natural selection is neither the only, nor the most general process that drives biological evolution. It is a manifestation of a more general but underestimated *persistence principle* (Pascal and Pross, 2014, 2015, 2016), for whose temporal—and hence evolutionary—consequences we have proposed the name “stability-based sorting”. We believe that this neutral term may enable the unification of different approaches to the study of SBS-related phenomena and facilitate the interconnection of different narrowly focused field-specific studies on this topic with related general theoretical-biological concepts.

Our broad concept of stability that consists of (1) static stability and SBS in its strict sense and usual conception, i.e. the accumulation of temporally persistent unchanging entities and characters, and (2) sorting based on dynamic stability, i.e. selection, being a special case of this phenomenon in systems of entities replicating with heredity (see Fig. 1) has broader scope than any other attempt to study these phenomena in the field of evolutionary biology or related disciplines. Therefore, despite our primary goal was to show the paramount importance of the effects of SBS on various levels of diverse evolutionary systems—a fact that has been practically neglected among evolutionary biologists—our conception may also serve as a new standpoint and universal platform for students of various kinds of evolving systems.

All complex novelties in biological evolution originate from the joint influence of two kinds of SBS in the broad sense, the force that drive the system towards dynamic stability and the force that drive the system towards static stability. The same applies to all natural and artificial systems whose entities multiply by reproduction or copying and exhibit at least some degree of inheritance—e.g., cultural evolution or even simulated systems with those properties. Indeed, there are clear analogies between the SBS-related phenomena observed in various kinds of evolving systems, for example, the punctuated character of their evolution or increasing resistance to change (see e.g. Post and Pimm, 1983; Ostdiek, 2011; Markoš, 2014,2015). Explanatory framework based on SBS thus could provide new insight into the evolution of any complex system.

In future, simulations that recognize the difference between *static* and *dynamic* nature of the sorting the evolving systems undergo and discriminate the role of these two kinds of sorting under various parameters may significantly contribute to the understanding of the general rules of evolution of any systems, and, consequentially, our theoretical understanding of some of the most profound phenomena of existence—e.g., the nature of life.

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Appendix

The relationship between the presented concept and the conception of Pross et al

Pross (2003,2004,2012), Wagner and Pross (2011) and Pascal and Pross (2014,2015,2016 and references therein) studied the role of stability in nature thoroughly, differentiating static thermodynamic stability that affects non-living entities and dynamic kinetic stability that is based on replicative chemistry and characteristic of living entities. The identification of the exact physical basis of the stability kinds is out of scope of this article. However, the equation of static stability to thermodynamic stability, i.e. the state of highest entropy (Pross, 2003,2004,2012; Wagner and Pross, 2011; Pascal and Pross, 2014,2015,2016), is an evident one. Pross and his colleagues stress that this kind of stability is fundamentally different to dynamic kinetic stability based on replicative chemistry and Malthusian kinetics, whereas the two stability kinds are unified under the umbrella of purely logical *persistence principle*: The general tendency of systems to change from less stable (persistent) to more stable (persistent) forms (Pascal and Pross, 2014,2015,2016).

Our conception that integrates all evolutionary systems regardless their physical basis is slightly different (see Fig. 1). In our concept, thermodynamic stability is just one option how to ensure static stability, although it could be speculated whether all other options (regarding e.g. immaterial entities such as memes, or even dynamically stable entities) could be ultimately converted or do naturally converge onto this one. Dynamic stability in our conception is not defined by the physical properties of particular system (i.e. replicative chemistry) either. Although the degree of dynamic stability must depend on the Malthusian kinetics of the dynamically stable entities (it would probably be better to say context dependent evolutionary stability in the sense of evolutionary stable strategies of Maynard Smith and Price (1973)) as in the Pross' concept, we stress especially the second, somehow "static", aspect of this sorting—heredity. Dynamic stability in our concept can be explicated as a special case of static stability in which the stable sorted "thing" changed from the entity itself to the heritable information necessary for its copying or reproduction. Therefore, static stability in our conception is more general and *de facto* corresponds to Pross' general persistence in time or *persistence principle* (see Fig. 1).

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SYNTHESIS PAPER

A Virtue Made of Necessity: Is the Increasing Hierarchical Complexity of Sexual Clades an Inevitable Outcome of Their Declining (Macro)evolutionary Potential?

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Abstract

The increasing maximal hierarchical complexity of organisms is one of the best-supported macroevolutionary trends. The nature and causes of this trend, as well as several accompanying macroevolutionary phenomena are, however, still unclear. In this theoretical article, we propose that the cause of this trend could be the increasing pressure of species selection, which results from the gradual decrease of (macro)evolutionary potential (i.e. the probability of producing major evolutionary innovations). As follows from the Theory of Frozen Evolution, this process is an inevitable consequence of the sorting of genes, traits, and their integrated groups (modules) based on their contextually dependent stability. In turn, this causes effectively unchangeable elements of genetic architecture to accumulate during the existence of evolutionary lineages. Although (macro)evolutionary potential can be partially restored by several processes, a profound restoration of (macro)evolutionary potential is probably possible only by means of a transition to a higher level of hierarchical complexity. However, the accumulation of contextually more stable elements continues even on this higher level. This leads to the integration of the modular character of composite organisms and a repeated pressure to increase the level of hierarchical complexity. Our model explains all components of McShea's "Evolutionary Syndrome," i.e. the trend of increasing the hierarchical complexity of organisms, the growth of variability among elements on the immediately lower level, and their gradual machinification. This pattern should be characteristic of sexual eukaryotes and especially their complex representatives. Our model also sheds new light on several related macroevolutionary phenomena, such as the gradual acceleration of the trend or the striking difference between pre-Neoproterozoic and Phanerozoic evolution.

Keywords Evolvability · (Macro)evolutionary potential · Evolutionary trends · Hierarchical complexity · Frozen evolution theory · Frozen plasticity theory · Stability-based sorting

Introduction: The Trend of Increasing Hierarchical Complexity

An evolutionary trend is usually understood as a "persistent, directional change in a character state, or set of character states, resulting in a significant change through time" (McNamara 1990, 2006). More broadly, they constitute "identifiable patterns in which the overall evolution of a trait occurs in a given direction within a group for a prolonged period of time" (Gregory 2008). The most interesting global evolutionary trend—at least from the macroevolutionary point of view—is probably the increasing organismal complexity in the history of life on Earth. Dozens of theoretical concepts aim to explain this pattern, either as a driven or a passive trend (these concepts are extensively summarised, e.g. in Novák 1982; McShea 1991, 1994, 2001a, b; Petersson 1996; Michod 2000; Jablonka and Lamb 2006; Buss 2014; or; Corning and Szathmary 2015). Despite all this effort, there is no agreement on the nature, or even existence of this trend. The major source of confusion is the difficult conceptualisation of this trend that results from an unclear definition of the term complexity. Indeed, complexity could be understood in several different ways (see, e.g. McShea

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1991, 1996; Carroll 2001; Mitchell 2009). For example, it can mean morphological complexity on the level of organisms or their parts (see, e.g. Bonner 1988, 1998; McShea 1993, 1996; Valentine et al. 1994; Carroll 2001). In another way, it can be defined as the complexity of genetic information (i.e. the number and complexity of genes or proteins, eventually interactions of these entities or some of their classes, such as developmental genes) (Adami et al. 2000; Carroll 2001; Rasskin-Gutman and Esteve-Altava 2008), but also, for example, the complexity of behaviour (McShea 1991).

The trend of increasing morphological complexity has been tested most often. At least in some evolutionary lineages, its maximum was proven to have been growing for a considerable time (see, e.g. McShea 1996, 2001a, b; Marcot and McShea 2007). Therefore, there is probably a relatively frequent trend in the growth of the maximal level of this factor. However, it is not clear whether this trend is driven or passive. Moreover, it is not present in all groups, and certain evolutionary lineages may even exhibit a directly opposite trend (McShea 1996, 2001a, b; Marcot and McShea 2007). Testing the general nature of this trend is even more difficult (McShea 1996). In spite of that, it was well supported that a certain type of morphological complexity—hierarchical complexity—increases even globally (McShea 1996, 2001a, b, 2015; McShea and Changizi 2003; Marcot and McShea 2007). This trend can be described as the increase in the hierarchical level of organisms by the means of their modular builds, i.e. nesting of lower-level entities within higher-level individuals (McShea 1996, 2001a, b; McShea and Changizi 2003; Marcot and McShea 2007). The whole process is also called the growth of vertical complexity (Sterelny 1999).

Hierarchical increasing of organismal complexity was widely commented upon by a number of authors, as was summarised, e.g. by Novák (1982), McShea (1991, 1994, 2001a, b), Pettersson (1996), Michod (2000), Jablonka and Lamb (2006), Marcot and McShea (2007), Buss (2014), or Corning and Szathmary (2015). One characteristic evolutionary motive that is common in all transitions to a higher level of organismal complexity is the combination of lower-level entities into a higher-level individual followed by differentiation and specialisation of formerly independent parts and their integration. This is usually followed by a transition to an even higher hierarchical level of organisation after some time (McShea 2001a). Moreover, the trend of increasing hierarchical complexity is seemingly associated with several other macroevolutionary phenomena. The frequency of transitions to a higher level probably accelerates in time and with the increasing hierarchical level of complexity (McShea 2001a, b, 2015; McShea and Changizi 2003). This acceleration is remarkable, and it is not probable that it would be an artifact. Another major question is why hierarchical complexity started to increase more markedly as late as in the Neoproterozoic (about 1.2 billion years ago) and especially at the beginning of Phanerozoic (about 540 million years ago), even though life on Earth has existed for about 4 billion years (Carroll 2001; McShea and Changizi 2003; McShea 2015). It also remains an open question as to why the trend is more pronounced in sexual, and especially complex multicellular, organisms (Flegr 2015; Toman and Flegr 2017b, 2018). On top of that, as a consequence of the transition to a higher level, we see an increase in the number of parts and differentiation among them on the immediately lower hierarchical level. However, this pattern is inseparably associated with strong a decrease in complexity, streamlining and simplification on this and lower levels (machinification) (Schank and Wimsatt 1986; McShea 2002, 2015; McShea and Anderson 2005). These two phenomena are associated with increasing hierarchical complexity so tightly that McShea (2015) termed the whole trinity “Evolutionary Syndrome,” a prominent macroevolutionary pattern that asks for a common explanation. At the same time, this explanation need not be trivial (see McShea 2005).

In this theoretical paper, we propose that that the trend of increasing hierarchical complexity may be caused by a growing pressure of effectively irreversible decreasing of (macro)evolutionary potential (i.e. the probability of producing major evolutionary innovations) that is probably characteristic of sexual organisms (Toman and Flegr 2018). This is a direct consequence of the accumulation of effectively unchangeable genes, traits and their integrated groups (modules) in the evolution of sexual lineages that is postulated by Frozen Evolution Theory (FET) (Flegr 2008, 2010, 2013, 2015), or, more generally, how follows from the principle of stability-based sorting (SBS) (Toman and Flegr 2017b). In other words, we propose that the trend of increasing hierarchical complexity in the history of life, as well as other points of McShea’s (2015) “Evolutionary Syndrome” and associated macroevolutionary phenomena, might be by-products of species selection on the restoration of (macro) evolutionary potential.

Results and Discussion: Macroevolutionary Freezing and Restoring of the (Macro) evolutionary Potential

Macroevolutionary Freezing

Stability-based sorting (SBS) is a universally recognised but rarely studied process that affects all entities on all levels of historic (evolving *s.l.*) systems (Toman and Flegr 2017b). Whether these are systems consisting of material or immaterial, living or non-living entities, as long as they undergo historical development, they accumulate contextually more stable (persistent) entities and their groups. These entities, over time, predominate in the system. On the other hand, entities that are less stable sooner or later change or perish and disappear from the system. Abstract on the first sight, this is a rather trivial (although fundamentally important) phenomenon. Stable space objects such as planets, stars and galaxies in the history of our Universe, heat more resistant snowflakes in a melting snowdrift, or even more stable memes and their complexes, such as stories, religions, and useful technological processes in human cultural history, all accumulate by SBS (whereas their less stable counterparts disappear). SBS in its strict and usual conception therefore represents sorting based on static stability (the slowest disappearance of entities that constitute the system). It is true that Toman and Flegr (2017b) documented that even natural selection (sorting based on dynamic stability), or the largest difference among the speeds of originating and disappearance of new entities, is in fact a special case of SBS in the systems of entities that reproduce with heredity. However, SBS, in its strict sense, still operates (in parallel with selection) on all levels of systems whose evolution is driven mostly by natural selection.[1]

SBS is a decisive force in evolution and it is capable of completely changing the course of evolution driven by opportunistic natural selection (2017b). One of the examples of this phenomenon, and also one of the most spectacular manifestations of SBS in biological evolution, might be its effect on evolvability, or the (macro)evolutionary potential of evolutionary lineages. As was emphasized by Toman and Flegr (2018), SBS likely plays an important role in the evolution of evolvability. Evolvability is usually defined as "the genome's ability to produce adaptive variants when acted upon by the genetic system" (Wagner and Altenberg 1996). In simpler words, the ability to evolve in an adaptive way. It can be, however, understood in several interrelated but distinct ways associated with the extent or mode of evolutionary change—from the ability of a population to adaptively and "plastically" respond to selection (Flegr and Ponížil 2018), to the ability of an evolutionary linage to evolve major evolutionary innovations, i.e. (macro)evolutionary potential (see, e.g. Pigliucci 2008; Toman and Flegr 2018). On longer timescales, SBS decreases (macro)evolutionary potential in evolutionary lineages, which leads to a decreasing intraspecific and interspecific disparity during their existence. Later in this paper, we will argue that this trend may apply more strongly to sexual lineages.

We have already demonstrated elsewhere (Flegr 2008, 2010, 2013, 2015; Toman and Flegr 2017b, 2018) that the gradual reduction of (macro)evolutionary potential, intraspecific and interspecific disparity are real trends, which have been documented in various eukaryotic clades by a long series of paleontological and paleobiological observations (see also "General Discussion"). The cause of this "macroevolutionary freezing" is probably two complementary manifestations of SBS (Toman and Flegr 2017b, 2018) described by previously postulated FET (Flegr 2008, 2010, 2013, 2015).

The first of these two processes follows from the fact that various organismal traits exhibit varying degree of evolvability, which is based on the specificity of their genotype-phenotype mapping. This genetic architecture, i.e. a sort of transducer between genotype and phenotype, and, consequently, the evolvability of traits may change during evolution. It follows from the principle of SBS that more stable traits with limited evolvability and their groups will accumulate during the existence of evolutionary lineages. The character and common features of macroevolutionary freezing traits were described elsewhere in considerable detail (Toman and Flegr 2018). In this place, we can summarise that macroevolutionary freezing traits are generally coded by a high number of strongly integrated genes. Such genes are usually also essential for multiple processes, deployed in the early stages of individual development and phylogenetically older. These are, for example, the genes that govern basic metabolic pathways in the cell, mitosis, meiosis, or early stages of the development of multicellular body (e.g. polarization of body axis, regionalization etc.) (Riedl 1977, 1978; Schank and Wimsatt 1986; Galis and Metz 2001; Wimsatt and Schank 2004; Wimsatt 2013, 2015). As a result, evolvability should be (at least theoretically) irreversibly decreasing in all evolutionary lineages (Flegr 2008, 2010, 2013, 2015; Shcherbakov 2012; Toman and Flegr 2017b, 2018).[2]

The idea that the ultimate outcome of biological evolution is stasis, or, more plainly, that evolution is going to end, sounds quite radical (although it was proposed, e.g. by Shcherbakov 2012). Nevertheless, it is clear that the whole process is not so simple (see, e.g. Toman and Flegr 2018). In the first place, there are some traits coded by one gene or a small number of genes (e.g. hair colour) that are highly evolvable (not very burdened in the Riedl's 1977, 1978, sense) and considerably resistant to evolutionary freezing.

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[1] Similar or comparable claims were made also by several other theoretical biologists (see, e.g. Bouchard 2011; Pross 2012; Shcherbakov 2012; Bourrat 2014; Doolittle 2014). For details on SBS, the aforementioned concepts, and their mutual relationships, see Toman and Flegr (2017b).

[2] Note that major innovations, including meta-adaptations that increase variability (e.g. sexual reproduction), may still originate, albeit with a very low probability. Moreover, smaller adaptations that may later become important exaptations (preadaptations) still originate with considerable probability (at least initially, see the section "Transition to a Higher Level of Complexity" and Toman and Flegr 2018).

More importantly, evolvability in general probably does not simply decrease, but also gets to some extent optimised during its evolution. To a considerable degree, genetic architecture evolves to most effectively reflect the structure of a phenotype and the environment with all its selective pressures (Riedl 1977, 1978; Wagner and Altenberg 1996; Kirschner and Gerhart 1998; Turney 1999; Pigliucci 2008). On the one hand, this reduces the risk of lethality or deleteriousness of mutations, or even increases the probability that a mutation will be adaptive. This reduces the number of mutations necessary to produce an adaptive phenotype. On the other hand, the same process strongly constrains the origin of major evolutionary innovations. By accumulating constraints that channel the depth and character of further possible evolutionary reactions, the evolution of evolvability optimises microevolution at the expense of macroevolution. In other words, evolvability on the lower level (in the sense of the ability to respond to selective pressures of natural environment) increases at the cost of decreasing evolvability on the higher level (in the sense of the (macro)evolutionary potential, or the ability to produce major evolutionary innovations) (Wagner and Altenberg 1996; Pigliucci 2008; Toman and Flegr 2018).

This sounds rather abstract, but it is similar to the way that we adapt in our lives. For example, after moving to a new city (evolution of evolvability and learning are, in fact, intriguingly similar phenomena, see, e.g. Watson and Szathmary 2016). At first, we are totally unaware about the layout of the city. We explore new routes every day with a high probability of experiencing something new—discovering a new shop, making a new friend, finding whole new neighbourhood, driving through a dangerous road crossing, or even getting stabbed in a back alley. In time, we learn our routines. Sometimes we do something “new”, but this is usually only iteration of something we are already used to doing (i.e. visiting a new shopping centre). This makes us more effective in daily life, more easily able to adapt to “new” but familiar things, and much less likely to experience any inconvenient “adventures”. However, it also reduces the probability of finding or experiencing something genuinely unexpected.

It seems that the most common way that organisms optimise their evolvability is by structuring further unchangeable (or only narrowly changeable) natural groups of genes with a closely related influence on phenotype into internally largely unchangeable quasi-independent modules. Such modules are characterised by strong pleiotropic links within the module and weaker linking in relation to its surroundings. Therefore, these (developmental, morphological or functional) modules can be duplicated in evolution. The duplicates can be individually regulated and deployed (to a considerable degree) independently in different settings, i.e. on different locations of the body or at different developmental phases (Simon 1962; Lewontin 1978; Schank and Wimsatt 1986; Bonner 1988; Wagner and Altenberg 1996; McShea 2000; Schlosser 2002, 2004; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005; Melo et al. 2016). This is corroborated by the fact that a large number of developmental genes, their modules, and signalling pathways are shared in nearly identical state—even among phylogenetically very distant lineages. Schlosser (2004), for example, stresses this evolutionary-developmental pattern and lists a broad array of gene regulatory (transcriptional regulation), signalling (e.g. hedgehog, TGFβ, Wnt, receptor tyrosine kinase, or Notch pathways), or positional (e.g. *Hox* or *Pax* genes) modules that are shared among large groups of metazoans. Evolution based on the combination and regulation of semi-independent modules is sometimes compared to playing with a Lego building kit. Using relatively few types of essentially unchangeable modules, it enables construction of extremely variable outcomes.

However, even organismal modularity cannot stop macroevolutionary freezing in the long term. SBS acts on all levels. Therefore, it causes macroevolutionary frozen elements (in this case higher order integrated modules consisting of the genes and modules of the lower level) to accumulate even on the higher level of the modular organism. On this level, the process of macroevolutionary freezing is expected to manifest as a gradual specialization and integration of the initially modular organismal build. An excellent macroevolutionary example of this process is the evolution of arthropod appendages. A series of identical modules (that probably originated by multiple copying of the same module) differentially specialized in various arthropod groups (see, e.g. Shubin et al. 1997). Some of them gained locomotory function, others serve for reproduction, etc. Different groups of these modules integrated (e.g. because they serve for a common function) and formed evolutionary modules of a higher level (see, e.g. Schlosser 2004). These modules of a higher order are bound internally by numerous pleiotropic interactions, they share morphogens that specify their development (e.g. *Hox* genes), etc. This renders them less evolvable internally. For example, it is not easy to change the right leg without changing the left one and compromising the locomotory function. An extreme example of this is when several initially (semi)independent appendages in the anterior part of the body became highly integrated and formed mouthparts (see, e.g. Hughes and Kaufman 2002, or; Auman and Chipman 2017 on genetics of arthropod development). Note that similar integration may proceed indefinitely. It may proceed because it is adaptive, but also for purely random reasons—for example, when a new selectively neutral interconnection among modules arise. As a general consequence of this process, modularly structured organisms are expected to decrease their (macro)evolutionary potential in the long term as well (Toman and Flegr 2018).

It can be argued that lineages maintaining relatively high (macro)evolutionary potential are initially advantageous in species selection. This makes them less prone to extinction when the conditions change and more likely to split off into significantly distinct daughter species that would be able to colonize new areas of ecophenotypic space, or even undergo adaptive radiations under such conditions. It would make them displace more "frozen" lineages and ultimately stop macroevolutionary freezing on a global level. However, species selection based on the highest remaining (macro)evolutionary potential probably cannot stop macroevolutionary freezing. The reason is that SBS proceeds in all lineages simultaneously and most changes that reduce (macro)evolutionary potential probably remain under the resolution of species selection.

As we outlined above, different genes, modules and traits are differentially evolvable. Some of them may change easily in evolution. From time to time, however, integrated units that cannot be easily changed emerge. The first problem (from the viewpoint of adaptive evolution) is that such evolutionary frozen units may be advantageous in the individual selection. This can be because they are adaptive, and because they are not easily evolvable. (It was proven that the evolvability of a trait correlates with its developmental robustness and that developmental robustness might be highly advantageous in the individual selection, see, e.g. Pavlicev and Wagner 2012). In case the frozen elements gravely reduced the evolvability of a species, they would probably be easily eliminated by species selection. This might be the case of some uniform taxa with low phenotypic disparity and species diversity, such as modern lungfish (Dipnoi) (Lloyd et al. 2012). However, most of the macroevolutionary frozen units probably reduce only one aspect of evolvability—the (macro)evolutionary potential of evolutionary lineages. They likely do it very moderately (for example, binding together the development of eyes and pigment patches on *Heliconius* butterfly wings by co-option of the eye selector gene *optix*, see Monteiro 2012). Any individual advantage stemming from their presence would therefore trump any long-term disadvantage stemming from the reduction of (macro)evolutionary potential (because individual selection is stronger than species selection, see Williams 1966). The second (and more important) problem, is that most of the macroevolutionary frozen units probably appear selectively neutral in the short term under most circumstances (birds, for example, seem morphologically rather constrained but reached immense diversity, see, e.g., Dececchi and Larsson 2013). Therefore, they accumulate in the history of evolutionary lineages purely based on their stability. Whereas other possible configurations change constantly, macroevolutionary frozen units persist. In other words, minor decreases of (macro)evolutionary potential probably remain (especially in sexual eukaryotic organisms, as will be shown later) under the resolution of species selection, and gradually accumulate (Toman and Flegr 2018).

The decreasing of the (macro)evolutionary potential may, in fact, be a process similar to the accumulation of slightly deleterious mutations by the principle of Muller's ratchet in realistically sized populations of asexual species (Toman and Flegr 2018). Muller's ratchet cannot be easily stopped in finite populations because most of the mildly deleterious mutations remain under the resolution of individual selection and new mutations appear in all individuals (Muller 1964). Analogically, our "macroevolutionary ratchet" cannot be stopped because most of the macroevolutionary frozen elements remain under the resolution of species selection and various macroevolutionary frozen elements originate in all lineages simultaneously.[3] It has been proven that the accumulation of deleterious mutations may lead to a considerable decrease of fitness, or even a complete non-viability of the affected population (Chao 1990). It is, therefore, conceivable that the accumulation of macroevolutionary frozen elements may lead to a comparably severe decrease in (macro)evolutionary potential.

To sum up the previous section, the process of macroevolutionary freezing seems to be effectively irreversible under normal conditions (later in the paper, we will note several specific ways that evolutionary lineages can avoid decreasing their (macro)evolutionary potential or even restore it) and continue even on the higher level of whole genetic modules.

The second SBS-driven process that may cause an irreversible decrease of (macro)evolutionary potential brings us from the field of macroevolution and evolutionary developmental biology to the realm of microevolution and population genetics. This process is based on the SBS-driven accumulation of alleles and their groups, which are kept in stable frequency in the gene pool of a species by some form of the frequency-dependent selection. When the negative dependence of fitness of a particular allele on the frequency of another allele (of the same or another gene) is steep enough, the allele cannot be fixed or eliminated by positive selection. Alleles with these properties probably originate by mutagenesis in relatively low frequency. However, they continuously accumulate in the populations via the process of SBS. Due to the complex genetic architecture of modern organisms (namely due to pleiotropy, i.e. the effect of one gene on many traits, and epistasis, i.e. the effects of many genes on the same trait), even a small number of alleles with a frequency dependent effect on fitness may stabilise

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[3] The problem of Muller's ratchet has been heavily studied, pointing especially to the importance of the form and strength of epistasis among slightly deleterious mutations. Mutual interactions among freezing genes, modules and traits, as well as their consequences for evolvability in general therefore may also be of great importance for the study of the "macroevolutionary ratchet".

the composition of a whole gene pool, and by this make the population resistant to natural selection of usual strength (Flegr 1998, 2010).

We are limited by the maximal length and scope of this paper, but we can illustrate the nature of these alleles with several brief examples. A recessive *HBB* allele for sickle cell disease is relatively benign in heterozygous condition. On the other hand, it significantly impairs human health in homozygous condition. However, both homozygotes and heterozygotes have a significantly elevated resistance to malaria. Providing protection from one of the most dangerous parasitoses, the frequency of the allele for sickle cell disease elevates in areas with abound *Plasmodium falciparum*. However, when the frequency of this allele rises too much, a disproportionate fraction of nonviable homozygotes is born. Therefore, it is kept in the polymorphic condition with the frequency of both alleles closely following the risk of the exposure to the parasite. The heterozygous advantage is only one special type of frequency-dependent selection. Other examples are, for example: the presence of colour polymorphisms in prey under predation pressure, the frequency-dependent fitness of various MHC variants under the pressure of parasites and pathogens (see, e.g. Ridley 1994), or the frequency-dependent sexual success of three male morphs of the lizard *Uta stansburiana* (Sinervo and Lively 1996).

As is predicted by the Frozen Plasticity Theory (FPT) (Flegr 1998, 2008, 2010, 2013; Toman and Flegr 2017b, 2018), the evolutionary theory describing the microevolution of sexual species and specific aspects of their adaptive evolution, the effectively irreversible accumulation of polymorphic alleles should be predominantly related to the diploidy of sexual species. In asexual species, the diploidy is not stable, as one of the gene copies in a locus is always inactivated by mutations. On the other hand, many genes can be sustained in the polymorphic state in diploid organisms due to their context-dependent fitness value, heterozygote advantage, and other forms of frequency-dependent selection. According to punctuationalist evolutionary theories formulated by Wright, Mayr, Carson, Templeton, Eldredge, and Flegr (see Flegr 2013), some of these polymorphic alleles may get fixed or eliminated during specific periods of a species' evolution. Under FPT, this is expected to be possible after a major non-selective reduction in population counts followed by a long period of survival in small population dominated by genetic drift and ended by a rapid inflation of the population. (Complicated at first sight, this is in fact a typical situation accompanying successful colonization of a new island and subsequent speciation). In such a situation, a population can start to transiently respond to selection until new alleles with frequency-dependent effects on fitness accumulate in its gene pool. From the viewpoint of (macro)evolutionary potential, it is important that some of the polymorphic alleles would require such a radical reduction in population counts and/or such long survival at such a low number of individuals that they cannot be fixed or eliminated under any realistic conditions. Therefore, they would only accumulate in the gene pool of the evolutionary lineage and reduce its ability to respond to directional selection.

It should be also noted that Toman and Flegr (2018) have proposed that it is possible that such alleles may act as persistent "crystallization cores" around which modules of functionally interconnected genes can form. Moreover, polymorphism in a large and still growing number of genes that increase the diversity of genetic background may increase the pressure on robusticity of development (Von Dassow and Meir 2004; Wimsatt 2013) and thus further accelerate the accumulation of any (macro)evolutionary frozen elements (Toman and Flegr 2017b, 2018).

Both aforementioned processes proposed to reduce (macro)evolutionary potential were documented in particular studies (summarised, e.g. in Flegr 1998, 2008, 2010, 2013, 2015; Toman and Flegr 2017b, 2018). Whereas irreversibly polymorphic alleles (second process) accumulate almost exclusively in sexual species (see Flegr 2015), more stable elements of genetic architecture (first process) could theoretically accumulate even in the evolution of asexual species. This raises the question as to whether we should expect (macro)evolutionary potential to decrease in all evolutionary lineages, or whether is this trend restricted to sexual clades. Equally important queries can be made as to its possible consequences such as increasing hierarchical complexity. In our opinion, the restriction of the trend to sexual clades is more probable. The reason is that asexual (overwhelmingly prokaryotic) species usually have large populations that are characterised by strong individual selection. Moreover, individual selection is *de facto* analogous to species selection in asexual organisms because each of their members establish his own asexual evolutionary lineage. Consequently, species selection is strong enough in these groups to effectively select lineages with the highest remaining (macro)evolutionary potential and to stop (or at least considerably slow down) macroevolutionary freezing.

If we return to the example with Muller's ratchet, asexual organisms might be in the same position as prokaryotes in the Muller's concept. Prokaryotic populations are large enough for individual selection to detect and eliminate even very slightly deleterious mutations and effectively stop Muller's ratchet. Species selection in (most) asexual organisms might be strong enough to detect and eliminate frozen elements that reduce their (macro)evolutionary potential only very slightly and effectively stop "macroevolutionary ratchet" (Toman and Flegr 2018). Macroevolutionary freezing and the accompanying phenomena thus should be characteristic of eukaryotic sexual organisms and, as we suggested above, it is possible that they are more prominent in those of their representatives that are endowed with complex multilevel genetic architecture, i.e. especially complex multicellular animals.

Transition to a Higher Level of Complexity

SBS thus causes further effectively unchangeable components of genetic architecture to accumulate effectively irreversibly (especially) in sexual eukaryotes. Are there any ways out of this "dead end"? One possibility is to organise genetic architecture differently. It has been repeatedly suggested that organisms may be organised on a different (macroevolutionary possibly more perspective) basis than the macroevolutionary freezing modular arrangement. However, empirical studies show that modular organisation completely dominates among complex organisms with elaborate adaptations. This is probably due to the fact that it brings substantial short to medium term natural advantages over other ways of forming and operating organisms (see Carroll 2001; Toman and Flegr 2018).

It follows that, statistically speaking, the (macro)evolutionary potential should only be decreasing in the long term. Let us start with a simple, possibly unrealistic, example that takes this into extreme consequences (Toman and Flegr 2017b, 2018). Every clade (including clades of high taxonomic rank such as eukaryotes or metazoans) has minimal diversity and disparity at the beginning. The number of species and phenotypic disparity, as well as the number of different phenotypically distinct clades, later described as higher taxa by paleotaxonomists, then grow. However, as particular (sub)lineages go extinct over time, newly originated species (the potential founders of new evolutionary lineages) in the remaining (sub)lineages differ in a low and still decreasing percentage of increasingly derived and less essential traits. Species diversity of the whole clade does not necessarily decrease. In fact, it may even grow for a considerable time, producing variations on the gradually freezing phenotypic motive. This may be the reason we observe increasing species diversity in Phanerozoic (see, e.g. Smith 2007). Disparity of the clade, however, decreases. Strange at first sight, similar trends were in fact documented in numerous clades (see "General Discussion").

Setting aside other factors, eukaryotic clades should be gradually abandoning large areas of morphospace. In some cases, their places can be occupied by other, perhaps even completely unrelated, clades, in which the (macro)evolutionary freezing has not yet gone so far, or which have maintained sufficient developmental plasticity or evolvability in traits relevant for adaptation to the current environment. In the long run, however, the(macro)evolutionary potential of all sexual lineages approaches zero (see the previous section "Macroevolutionary Freezing"). The decreasing probability of producing major evolutionary novelties associated with the sorting out of more persistent species should also manifest by changing the dynamics of their evolution. A large and still growing percentage of traits should become more or less unchangeable and evolution should gradually limit itself to small peripheral changes. In the end, Earth should be inhabited only by several universal and broadly distributed or obscure and distinctly stable environment inhabiting sexual eukaryotic clades. However, even these clades would ultimately succumb to a sufficiently large fluctuation of environmental condition, leaving the Earth to prokaryotes and possibly several lineages of ancient asexual eukaryotic organisms (Toman and Flegr 2017a). These organisms would probably be prone to macroevolutionary freezing and maintain their (macro)evolutionary potential.

In such a situation, lineages capable of restoring their (macro)evolutionary potential would have a great advantage over macroevolutionary more frozen lineages. We commented on the processes that may stop evolutionary freezing or even restore (macro)evolutionary potential thoroughly in Toman and Flegr (2018). Since particular traits and modules differ in the depth of their freezing, some of them may probably rarely loosen their inner links and "thaw" (see, e.g. Melo et al. 2016). This may be facilitated by a small population size, a relaxation of selection, a redundancy, and other factors that were summarised, e.g. in Toman and Flegr (2018). Such an event could happen, for example, at the beginning of angiosperm (Magnoliophyta) evolution. It is likely that the enormous success of this plant group was enabled by their ability to quickly and operatively change the size of their genome. Although the original purpose of this ability is unknown, a subsequent "miniaturization" of genomes, nuclei and cells of some angiosperm lineages lead to a more elaborate leaf morphology and an improved effectiveness of photosynthesis. This has resulted in their expansion to almost all conceivable habitats beginning in the Cretaceous period (Simonin and Roddy 2018). One possible alternative may be a heterochronic change in development (e.g. neoteny) that has the potential to release some modules from their functional links for other purposes. These events were documented in the evolution of several taxa (e.g. the famous *Axolotl* but also many other, see Raff and Wray 1989). Moreover, as was pinpointed by one of our reviewers, many cases of simplified interstitial meiofauna indicate that it might be a relatively frequent mode of evolution (Westheide 1987). More radical cases of such events (i.e. developmental changes that would lead to "thawing" of even very deeply macroevolutionary frozen modules or traits) are usually associated with fundamental simplification of individual development (i.e. *sacculinization*). Radical simplifications of development might play an important role in the evolution of Rhizocephala (Glenner and Hebsgaard 2006), Myxozoa (Canning et al. 2004), or biting- or sexually-transmitted mammalian cancers (Murchison 2008).

Although we know of several occasions in which the above-mentioned processes took part in evolution, it seems that none of them can completely stop macroevolutionary freezing in the long term. Evidence supporting this conclusion is mainly empirical. Although current major successful taxa are probably descendants of lineages that managed to produce a major evolutionary innovation or simplify their development, disparity in many of them, as well as higher eukaryotic taxa such as metazoans, was shown to be generally decreasing (see "General Discussion"). The reason is that the probability of evolutionary "thawing" is inversely proportional to the degree of macroevolutionary freezing of the module. (This is imperative; if it does not apply, macroevolutionary frozen entities would not be stable, persistent, and would not accumulate via SBS in the first place). Weakly frozen traits and modules may "thaw" relatively easily. Deeply frozen ones, however, remain basically unchangeable and accumulate. Considering *sacculinizations*, these events are probably very rare. We do not know any large, diverse and successful eukaryotic lineage that would have originated this way. These macroevolutionary events thus probably have only a limited role in evolution. If we return to the comparison with Muller's ratchet one more time, the processes mentioned above can be analogized with rare reverse mutations in Muller's case. Mutations that restore the original function of a defective allele are possible. The same counts for changes that restore the (macro) evolutionary potential of the evolutionary lineage. However, both of these events are probably so rare that they do not play major role in evolution.

In our opinion, the only way to completely and at least temporarily restore (macro)evolutionary potential is through a transition to a hierarchically higher level, which makes the entity of the original level a limitedly changeable module within a new (macro)evolutionary potent whole.[4] The organism of the higher level is thus naturally modular (Carroll 2001). Macroevolutionary frozen units, i.e. quasi-independent modules, then can be to a large degree independently regulated, multiplicated, combined, or deployed in different places, in different times, or different contexts by a higher-level individual (Simon 1962; Lewontin 1978; Schank and Wimsatt 1986; Bonner 1988; Wagner and Altenberg 1996; McShea 2000; Schlosser 2002, 2004; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005; Melo et al. 2016).

Various transitions to a higher level of organisation significantly differ. Some of them are natively less burdened by constraints, and thus evolutionary more perspective than others (Nedelcu and Michod 2004; Calcott 2008). However, under normal circumstances, a transition to a hierarchically higher level is usually a relatively risky endeavour that is under the threat of breakdown from many directions. The initial, usually not very significant, benefits may not outweigh the risks associated with a transition to a higher level (Michod 2000, 2007; Queller 2000; McShea 2001a; Michod and Nedelcu 2003; Michod and Herron 2006; Calcott 2008; Godfrey-Smith 2009; Queller and Strassmann 2009; Corning and Szathmary 2015). The risk of selfish behaviour of individual parts at the expense of the whole is especially noteworthy. Therefore, long-term stable and successful transitions to a higher level are relatively rare (see, e.g. Novák 1982; Szathmáry and Maynard Smith 1995; McShea 1996, 2001a, b, 2015; Pettersson 1996; Knoll and Bambach 2000; Michod 2000; Calcott and Sterelny 2001; McShea and Simpson 2001; McShea and Changizi 2003; Jablonka and Lamb 2006; Okasha 2006; Marcot and McShea 2007; Maynard Smith and Szathmáry 2010, 2015; Bouchard and Huneman 2013; Buss 2014; Corning and Szathmary 2015). However, the perpetually decreasing (macro)evolutionary potential on one level causes a constantly growing pressure favouring entities with (if only very slightly) restored (macro)evolutionary potential. In a situation when this factor decreases to a critical point at one level, even a momentarily very suboptimal but evolutionary viable solution associated with restoration of (macro)evolutionary potential—transition to a higher level of hierarchical complexity—may become competitive.

However, SBS that leads to macroevolutionary freezing acts even on the new, hierarchically higher, level of organisation. Although one of the sources of irreversible (macro) evolutionary freezing—the accumulation of irreversibly polymorphic alleles and their groups—acts only on the level of populations of sexual species (see the section "Macroevolutionary Freezing"), the second source of macroevolutionary freezing—the accumulation of stable elements of genetic architecture—applies to all levels. This should not be surprising. It is the nature of SBS to accumulate further unchangeable parts on all levels of all systems regardless of their nature. Consequences of this process can be more interesting.

In time, a modular organism of a higher level may delegate many functions of initially identical subunits only to some of them. For example, a newly originated multicellular organism (i.e. volvocine algae) initially consists of many identical cells. However, a lot of essential organismal processes can be maintained only by one or few cells. Some cells may thus specialise for these purposes (i.e. reproduction, digestion, movement etc.), whereas the same function is lost in other cells who are free to specialise differently (Nedelcu and Michod 2004). As a result, the mutual diversity

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[4] We are aware that this might be a bold claim. It could be—and should be—debated. Especially in the light of the evolutionary processes that can theoretically restore (macro)evolutionary potential or at least slow down the macroevolutionary freezing mentioned above.

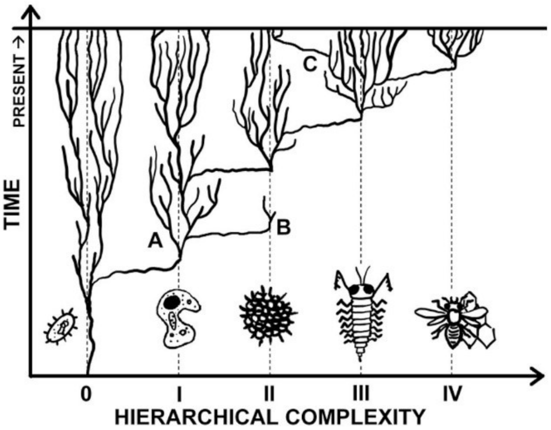

Fig. 1 Schematic representation of the trend of increasing maximal hierarchical complexity according to FET. Reaching a higher hierarchical level of organization is advantageous because of the temporary restoration of (macro)evolutionary potential that otherwise gradually decreases on every level. For the same reason, the overall disparity of numerous groups on the lower level could have been higher in the past compared to the present (**a** see also "General Discussion"). Not every evolutionary attempt to establish an organism of higher hierarchical level is equally successful; many such attempts could end up being evolutionary nonviable or marginal in the long term (**b**) because organisms on the original level still retained enough (macro) evolutionary potential or because the organisms of the higher level were loaded with a number of constraints that severely limited their further evolution. Reversals to a lower level of hierarchical organization (**c**) are possible but, based on the available evidence (see "Results and Discussion" or Toman and Flegr 2018), seem to be very rare in the history of life on Earth. The transition from hierarchical level 0 to level I (i.e. the origin of eukaryotic cells) corresponds to the egalitarian transition in individuality. The transition from level I to level II (i.e. the origin of simple multicellular organisms) corresponds to the fraternal transition in individuality. The third transition (i.e. the origin of complex multicellular organisms with modular genetic architecture and development) corresponds to the internal modularization. The last depicted transition (i.e. the origin of colonial or eusocial complex multicellular organisms) corresponds to the fraternal transition in individuality. Note that this is only a schematic representation, i.e. it does not follow the evolution of any particular lineage and does not make any claims about the proportions of the three ways to increase hierarchical complexity or the overall number of the levels of hierarchical complexity (those that are depicted, 0 to IV, surely need not be comprehensive)

of subunits (or, from the viewpoint of the whole organism, the variability among its subunits) grows at the next lower level of a modular organism (Lewontin 1978; Bonner 1988, 1998; Wagner and Altenberg 1996; McShea 2000, 2002, 2015; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005; McShea and Anderson 2005). Note that this does not count only for multicellular organisms or organisms of this hierarchical level. It applies to organisms of all subsequent levels of organismal complexity, from simple unicellular eukaryotes to colonies of eusocial insects. Even neutral mechanisms such as Zero Force Evolutionary Law (McShea and Brandon 2010) contribute to this process of increasing variability among subunits—they may also diversify as a result of pure chance.

However, as modules at the next lower level specialise, they establish new functional interconnections. Those interconnections that are further unchangeable accumulate by SBS. Modules gradually form a complex web of functional links, whereas those integrated wholes that reach higher persistence (i.e. become integrated by effectively unbreakable interconnections), will preferentially accumulate. Modules become less and less (semi)independent and the originally modular organism integrates. Just as on the lower hierarchical level before, this process is probably effectively irreversible. (Macro)evolutionary potential on this level decreases again, and when it reaches a critical level, even suboptimal organisms of the new, even higher, level of hierarchical complexity get the advantage (see Fig. 1). Moreover, it cannot be ruled out that the resulting increasingly complex multilevel genetic architecture that is characteristic of many functional interconnections on the current level (and among different levels) further accelerates macroevolutionary freezing on every subsequent level (see, e.g. the model of Thomas 2005).

We can only speculate as to whether this complication of organismal structure and function will continue indefinitely, or whether organisms may eventually reach their limits, become indifferent to selectional pressures, and stop restoring their (macro)evolutionary potential (Bonner 1988; Carroll 2001; Wimsatt 2013). As was mentioned by one of our reviewers, it seems that there could be an upper limit, because we don't see any super–super organisms, e.g. colonies of colonies, integrated enough to qualify (at least theoretically) as individuals. Moreover, such entities are hardly even imaginable. On the other hand, this scepticism may result only from our lack of creativity. It was documented that in some organisms, e.g. in the ant *Linepithema humile*, loosely arranged supercolonies are slowly emerging (Human and Gordon 1996). In a similar manner, human societies become integrated on a growing number of levels (states, federations of states etc.). These higher-level entities surely do not qualify as individuals, but it somehow urges us to be cautious. It is not set in stone that super-superorganisms or organisms of even higher hierarchical levels are impossible, or that they would resemble any organism already present on Earth. Could we imagine eusocial insects with their specialized castes, complex life strategies and complicated mounds if we did not know them? In any case, transitions to a new level repeated many times, especially in the evolution of sexual eukaryotic organisms (as was described, e.g. by McShea 2001b).

Various Types of Transitions

The first way through which an organism can achieve a higher level of hierarchical complexity was de facto described in the section "Macroevolutionary Freezing". It is the internal modularisation of an organism that is based on the establishment of genetic, strongly interconnected modules that are to a considerable degree unchangeable, but independently regulable, repeatable, combinable, and deployable. This results in the modular character of an organism on physiological, morphological and other levels. The proximal reasons of modularisation (which is intimately connected to the evolution of evolvability), the direct mechanism of the origin of modules and, eventually, the involvement of various ways of modularisation are beyond the scope of this article (see, e.g. Lewontin 1978; Wagner and Altenberg 1996; McShea 2000, 2002; Schlosser 2002; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005); it was also summarised in Toman and Flegr (2018). It is, however, important to note that both selection on multiple levels and SBS may play important roles in this process.

In most cases, internal modularisation probably happens through multiple duplications of the original modules. This occurs at lower levels of hierarchical complexity represented by genes (as was summarised, e.g. by Wagner and Altenberg 1996), and at higher levels of hierarchical complexity represented by whole (genetic, physiological, morphological, developmental etc.) modules. It broadly corresponds to the origin of modularity by the process of parcellation (loosening of interconnections in a tightly integrated whole). This process should manifest externally by the origin of organismal genetic modularity, and, in multicellular animals, also by the origin of developmental modules such as body segments or appendages that reflect the modular organisation of the genotype-phenotype map (Wagner 1989a, b). At every level, however, we should expect a subsequent integration (creating new interconnections among elements at a given level) of the modular character (see the section "Transition to a Higher Level of Complexity") and the formation of higher-level modules of organisation (see McShea 2002, 2015; McShea and Anderson 2005). This mode of transition to a higher level of complexity may repeat several times in the evolution of the lineage, which leads to the complication of its genetic architecture. It has already been suggested by some authors that the processes of parcellation and integration may regularly alternate at neighbouring hierarchical levels (Wagner and Altenberg 1996; Kirschner and Gerhart 1998; Eble 2005). This is a nontrivial pattern that was, at least to our knowledge, never satisfactorily explained. It is, however, predicted by our theory as a natural consequence of macroevolutionary freezing and the restoration of (macro)evolutionary potential. An extreme example of the rebuilding of genetic architecture is the duplication of the whole genome. Such events are relatively frequent in certain evolutionary lineages and could play a key role, e.g. in potentiating early evolution of vertebrates (Vertebrata) of actinopterygian fish (Actinopterygii) (Meyer and Van de Peer 2005).

Evolutionary entities may also reach a new hierarchical level of organisation and restore their (macro)evolutionary potential on the higher level by combining several originally separate entities of the lower level. The remaining two ways thus correspond with two types of transitions in individuality—fraternal and egalitarian (Queller 1997, 2000).

Fraternal transition in individuality is based on either the multiplication of identical or nearly identical entities of the lower level, e.g. closely related individuals, the progeny of one individual, or clones (Queller 2000). This transition in individuality might play a role in the formation of cells, specifically the formation of compartments consisting of the same molecules. Beyond that, it is the process through which the colonies of prokaryotic and eukaryotic unicellular organisms originate, as well as various forms of multicellular organisms, their colonies, and eusocial organisms (see, e.g. Novák 1982; McShea 1991, 1994, 2001b; Szathmáry and Maynard Smith 1995; Pettersson 1996; Knoll and Bambach 2000; Michod 2000; Calcott and Sterelny 2001; Jablonka and Lamb 2006; Okasha 2006; Calcott 2008; Maynard Smith and Szathmáry 2010, 2015; Bouchard and Huneman 2013; Corning and Szathmary 2015). The close relation of entities that constitute the higher-level individual brings specific advantages but also specific disadvantages. The immediate advantage is a lower risk of intraindividual conflict that follows from the close relation of constituting entities (see, e.g. Michod 2000, 2007; Queller 2000; Michod and Nedelcu 2003; Michod and Herron 2006; Calcott 2008; Godfrey-Smith 2009; Queller and Strassmann 2009; Corning and Szathmary 2015). The major problem of such higher-level entities is their weak initial advantage over lower-level individuals (see, e.g. Calcott 2008). This advantage, if any, apparently results mainly from body enlargement and the economics of scale (see, e.g. Bonner 1988, 1998; Queller 1997). Secondarily, the selective specialisation (i.e. separation of germinal lineage, or general division of labour and its synergistic effects) of the elements composing the composite entity may occur (see, e.g. Bonner 1988, 1998, 2003; Szathmáry and Maynard Smith 1995; Queller 1997; Calcott 2008; Maynard Smith and Szathmáry 2010, 2015; Simpson 2012; Corning and Szathmary 2015). Regardless of this, another major advantage that would manifest, especially in species selection, over the longer term may result from the restoration of (macro)evolutionary potential.

An egalitarian transition in individuality is based on the combination of two or more different entities of the lower level, not exclusively organisms from very remote evolutionary lineages (Queller 2000). Generally, it is the case of all symbioses and symbiogenetic events. From the macroevolutionary point of view, the origin of endosymbiotic organelles (and probably also the nucleus) seems to be the most important of these events (see, e.g. Szathmáry and Maynard Smith 1995; Pettersson 1996; Knoll and Bambach 2000; Michod 2000; Calcott and Sterelny 2001; McShea 2001b; Sterelny 2004; Jablonka and Lamb 2006; Okasha 2006; Queller and Strassmann 2009; Maynard Smith and Szathmáry 2010, 2015; Bouchard and Huneman 2013; Corning and Szathmary 2015). This transition could also play an important role in the early evolution, specifically during the formation of compartments consisting of different molecules, or chromosome consisting of linked genes. In contrast to the previous case, the advantages and drawbacks of egalitarian transitions in individuality stem from the unrelatedness of the constituting entities. The major initial advantage lies in the combination of different functions and properties, i.e. the division of labour and further synergistic interactions. A further advantage may stem from the restoration of (macro)evolutionary potential. The major problem is probably the control over conflicting interests of unrelated individuals that can be ensured by a fair distribution of reproduction allocations and enforced by their mutual dependence (see, e.g. Szathmáry and Maynard Smith 1995; Michod 2000, 2007; Queller 2000; Michod and Nedelcu 2003; Michod and Herron 2006; Calcott 2008; Godfrey-Smith 2009; Queller and Strassmann 2009; Maynard Smith and Szathmáry 2010, 2015; Corning and Szathmary 2015). Therefore, it can take some time for egalitarian entities to evolutionary merge, integrate and start producing common propagules.

General Discussion: The Context of Frozen Evolution Theory

"Evolutionary Syndrome" and Related Phenomena

As was mentioned in Introduction, several accompanying phenomena are clearly associated with the global trend of increasing maximal hierarchical complexity. These phenomena correlate with the aforementioned trend on a macroevolutionary scale, but their mutual relationship is unclear. These are especially: (1) an increasing number and differentiation of parts at the next lower hierarchical level that follows transition to a higher level, and (2) a radical decrease of complexity on this level and all lower levels (i.e. their machinification) (Schank and Wimsatt 1986; McShea 2002, 2015; McShea and Anderson 2005). The coincidence of these three phenomena is so noticeable that McShea (2015) labelled it an "Evolutionary Syndrome"—a striking, yet unexplained, macroevolutionary pattern.

In the event that the trend of increasing hierarchical complexity is really caused by decreasing (macro) evolutionary potential accompanied by growing pressure on its restoration by transitions to new hierarchically higher modularly organised levels, as we suggest in this paper, then the above-mentioned accompanying phenomena are natural side-effects of these processes. After reaching a new hierarchical level, macroevolutionary freezing starts anew. The modules, initially separate organisms or units that originated by internal modularisation, are regulated largely independently of each other at first. As we described in Results and Discussion, various neutral mechanisms and forms of selection make them multiplicate, differentiate, and deploy in various contexts, which leads to the documented increase in horizontal variability (Lewontin 1978; Bonner 1988, 1998; Wagner and Altenberg 1996; McShea 2000, 2002, 2015; Schlosser and Wagner 2004; Callebaut and Rasskin-Gutman 2005; McShea and Anderson 2005). The second accompanying phenomenon of "Evolutionary Syndrome," streamlining or even machinification of modules, is related to the same processes. According to FET, the streamlining of modules is the consequence of their gradual specialization and integration caused by stability-based sorting on the highest level of composite entities. Variability among modules and their specialisation over time inevitably leads to differentiation, the emergence of new interconnections, the sorting of further unchangeable interconnections and elements by SBS, integration, and finally the diminishing of the originally modular character of the organism (Toman and Flegr 2018). One symptom of this is the simplification of lower levels that usually lose many of their functions and get streamlined in order to achieve an increased effectiveness (McShea 2002, 2015; McShea and Anderson 2005). Modules themselves are variable only in a very limited way. They are largely macroevolutionary frozen units of lower levels, which makes them much more prone to lose functions than to gain them. Considering the developmental viewpoint, adding new hierarchical levels increases the macroevolutionary freezing (see also the concepts of burden and generative entrenchment in the next section) of the lower levels of development. We can therefore expect complexity on the lowest levels to minimize up to a macroevolutionary completely frozen state that is characteristic of minimal evolvability and a high resistance to changes—the most machine-like state. It is noteworthy that this tendency to mechanize deep mechanisms in complex organisms was already predicted by Schank and Wimsatt (1986). Beyond that, machinification may be facilitated by other factors. Selection probably leads to a preferential preservation of interconnections that ensure a higher robusticity, which is favourable in the development and function of composite organisms (Kirschner and Gerhart 1998; Schoch 2010; Brigandt 2015). A greater interconnection of subunits may be also advantageous as a prevention against their eventual selfish actions at the expense of the whole individual (Szathmáry and Maynard Smith 1995; Michod 2000; McShea 2001a, b; Michod and Herron 2006).

It is noteworthy that the whole pattern—the reduction in the number of initially identical modular and serially repeated parts, their gradual specialisation and integration—is known as Williston's law (Gregory et al. 1935). FET therefore also offers an explanation for this macroevolutionary rule. To summarise, FET can explain "Evolutionary Syndrome" without major difficulties as a series of interrelated and causally following events resulting from the evolutionary dynamics of macroevolutionary freezing organisms. The common cause of all phenomena that compose the McShea's (2015) evolutionary syndrome thus may be the process of macroevolutionary freezing. On top of that, our concept can shed new light on several related mysterious evolutionary patterns.

As we argued in "Results and Discussion", macroevolutionary freezing and the associated trend of increasing hierarchical complexity should, according to FET, apply dominantly to sexual, i.e. eukaryotic, organisms. The effectively irreversible accumulation of further unchangeable elements is facilitated by sexual reproduction itself, the associated ability to form species that has changed the intensive struggle among asexual lineages to a much slower classical species selection, and the generally smaller size of eukaryotic populations (Flegr 2008, 2010, 2013, 2015; Toman and Flegr 2017b, 2018). Therefore, we should not be surprised that the trend of increasing hierarchical complexity has not proceeded evenly since the origin of life. After the initial increase that had accompanied the origin of cellular life approximately 4 billion years ago, there followed a long period when the maximal hierarchical level more or less stagnated. This period lasted about 2.2–2.8 billion years until the next impetus for further advancement of the trend took place—the invention of sexual reproduction by first eukaryotes (Carroll 2001; McShea and Changizi 2003; McShea 2015).

The more puzzling question is: why has the trend of increasing hierarchical complexity, as appears from available paleontological indices, gradually accelerated since that time (McShea 2001a, b, 2015; McShea and Changizi 2003)? It has been proposed, for example, that this acceleration might be caused by increasing biodiversity, or that it was potentiated by the rise of oxygen content in the atmosphere. However, the ratio of internal and external influences on this phenomenon remains unclear (McShea 2001a, b). The explanation based on FET, i.e. the hypothesis that macroevolutionary freezing proceeds faster on every subsequent level due to the evolution of evolvability, thus seems at least a realistic alternative worthy of further testing. As we mentioned in "Results and Discussion", polymorphism in an ever-increasing number of genes that increases the diversity of genetic background can put pressure on the robustness of development (Von Dassow and Meir 2004; Wimsatt 2013) and can further accelerate the accumulation of (macro)evolutionary frozen elements (Toman and Flegr 2017b, 2018). Also, it cannot be excluded from consideration that macroevolutionary freezing on every subsequent level is further accelerated by an ever-complicating multilevel genetic architecture that is characterised by many functional interconnections at a given level and between levels (see, e.g. the model of Thomas 2005). This should be clearly observable, especially on the evolution of organisms with the most complex individual development. It is consistent with observations that the most pronounced acceleration of the increasing of hierarchical complexity can be seen in complex multicellular organisms and that its beginning can be dated to the time shortly preceding Cambrian and Cambrian explosion, i.e. the time when multicellular animals (Metazoa) evolved and reached their modern forms (McShea 2001a, b; Davidson and Erwin 2006).

For the same reasons, we should not be surprised by the fundamentally different character and dynamics of pre-Neoproterozoic (and especially pre-Cambrian) and Phanerozoic evolution (see, e.g. Knoll and Bambach 2000; Carroll 2001; Butterfield 2007). While the time preceding the Neoproterozoic was dominated exclusively by prokaryotes characterised by their "two dimensional" evolution (i.e. in the absence of significant selective pressures usually slow and stabilizing evolution devoid of a continuous increase of hierarchical complexity), the Neoproterozoic gave birth to eukaryotes with their "three dimensional" evolution characterised by the trends of increasing diversity and hierarchical complexity. It is true that more complex cells (see, e.g. McInerney et al. 2011) or hierarchically more complex colonies (see, e.g. Claessen et al. 2014) emerged several times in the prokaryotic evolution. However, if we exclude one of their very specialised derived lineage—eukaryotes—prokaryotes do not exhibit any continuous trend of increase in any form of complexity (McShea 2001a, b, 2015; McShea and Changizi 2003; Marcot and McShea 2007). In contrast to that, the maximal level of hierarchical complexity has increased several times in eukaryotes, which has led directly (through the development of new ecological strategies, the occupation of new areas of ecophenotypic space, etc.) and indirectly (through the (co-)creation of new habitats, the influence on environmental conditions etc.) to the complete rebuilding of the whole ecological space of our planet and a fundamental change in the dynamics of evolution (Knoll and Bambach 2000; Carroll 2001; Butterfield 2007; Toman and Flegr 2017a).

Analogical Older Concepts

The study of the trend of decreasing evolvability (including its special cases such as (macro)evolutionary potential), or the reduction of intraspecific and interspecific disparity during the existence of clades, has a long history. A number of theoretical studies (see, e.g. Riedl 1977, 1978; Wagner and Laubichler 2004; Budd 2006; Schoch 2010; Wimsatt 2013) and observations (see, e.g. Rosa 1899; Erwin et al. 1987; Gould 1989; DiMichele and Bateman 1996; McShea 1996; Foote 1997; Eble 1998, 1999; Kirschner and Gerhart 1998; Rasnicyn 2005; Budd 2006; Erwin 2007; Webster 2007; Hughes et al. 2013; Lee et al. 2013) have supported its existence. Especially in the macroevolution of eukaryotic organisms (metazoans were most thoroughly studied in this context), the above-mentioned trend applies almost universally (it was summarised, e.g. by Toman and Flegr 2017b, 2018).

If we leave out some more eccentric explanations (e.g. that the trend is caused by meiosis, which is understood as a derived process hampering any adaptive change; Davison 1998), or that the evolution of any system leads to stasis (Shcherbakov 2012), we can divide the proposed explanations of this trend into two groups (Erwin 2007)—ecospace and developmental (or genetic) hypotheses. According to the ecospace concept, the success of newly originating and significantly differing evolutionary lineages is inversely proportional to the saturation of the ecospace in which representative groups reside. Their chances of significant success thus decrease in time. According to the developmental (genetic) explanations, the trend is based on the decreasing potential of lineages to generate major evolutionary innovations (Valentine 1995; Davidson and Erwin 2006; Erwin 2007; Webster 2007). Both of these groups of explanations were supported by evidence and it should be noted that they need not exclude each other (Erwin 2007). However, the global trend of gradually decreasing intraspecific variability during the evolution of taxa, which is known today as Rosa's rule (Rosa 1899), speaks in favour of the developmental explanations. Leaving aside older anecdotal evidence, Rosa's rule was demonstrated even quantitatively. As was proven by Webster (2007), the number of intraspecifically variable traits and the degree of their variability were much higher in older species of the taxon Trilobita in comparison to the younger ones. Moreover, certain data indicates that similar phenomena might also take place in the evolution of cockroaches (Blattodea) (Vrsansky 2000; Vrsansky et al. 2017). The above-mentioned trends therefore most likely result from the decreasing variability on the species level.

The possible long-term consequences of one-way constraining of the clades' evolution were studied, e.g. by Wimsatt (2013) or Riedl (1977, 1978; see also Wagner and Laubichler 2004; Budd 2006; and; Schoch 2010). However, an analogous view was also offered by Arthur (1982) and similar topics were touched upon even by other, often much older, researchers that have been summarised, e.g. by Riedl (1977, 1978), Schank and Wimsatt (1986), Gould (2002), Schoch (2010), or Wimsatt (2013, 2015). According to these authors, evolutionary lineages may ultimately reach the extreme state when the origin of major evolutionary novelties becomes limitally improbable (Budd 2006). According to Riedl (1977, 1978; Wagner and Laubichler 2004; Budd 2006; Schoch 2010), processes or elements that are associated with a greater number of more important features and functions, i.e. processes or elements that are more substantial and probably also phylogenetically older, exhibit a decreasing changeability (increasing "burden") due to a high risk of rendering organism unviable when changed. This leads to a gradual "cementation" of traits and consequent "evolutionary sclerosis" of evolutionary lineages. This manifests in strong restrictions to their evolvability, constraining of possible adaptations, and changeability limited only to minor peripheral traits or one direction. The resulting evolution of clades has a cyclistic (i.e. assuming a gradual transition of taxa from adaptive and experimenting "youth" to strongly constrained "old age") and typostrophic (i.e. assuming changeable nature of new traits and their increasing conservativeness as they are burdened by characters build upon them) character (Schoch 2010). In such a case, evolvability can be restored only through radical rebuilding of the organism's development, i.e. major heterochronic change (Budd 2006).

In a similar vein, Wimsatt (2013; Schank and Wimsatt 1986; Wimsatt and Schank 2004) writes about "generative entrenchment," which is a property of traits analogical to burden, but derived from timing in the individual development and (consequently) integration into the system. In any case, sets of genes and genetic modules that take place early in development (so that they influence a high number of various characters and processes), those that code characters and processes more fundamental for the functioning of the organism, and those that code characters and processes phylogenetically older, should, to a large extent, correspond (see Riedl 1978; Arthur 1982; Schank and Wimsatt 1986).[5] Strongly entrenched traits are under constant risk that their change through internal (e.g., mutation) or external (e.g., change of environment) factors would negatively influence some of the later developmental processes or elements. They also have a lower probability that their change would be adaptive. The modification or extension of individual development is therefore possible only on the least entrenched components of development. Moreover, every extension of

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[5] This does, in fact, follow already from von Baer's laws of development, see Schoch (2010).

development increases the entrenchment of all the developmental components that it is built upon. Wimsatt (2013) went even further and considered an extreme situation in which the system reaches a state when any further increase of effectivity or size of an organism that would be selected upon would be redeemed by a disproportionately large increase of its inner complexity and the risk of catastrophe of complexity. At the same time, Wimsatt was also probably the first author to propose that the only possible way out of this dead end is to transition to a higher level of organisation. Such a radical and restrictive conception of evolutionary constraints became one of the sources of criticism on Riedl's account (Schoch 2010) and accounts of older understandings of evolution of evolvability in general (Brigandt 2015). However, in the light of FET and SBS (Toman and Flegr 2017b), which inevitably proceeds on all levels, these ideas seem greatly justified (Toman and Flegr 2018). Moreover, the conserved nature of early embryonic development (the phylotypic stage), especially due to intensive pleiotropic interactions among genes, is becoming increasingly supported (Galis and Metz 2001; Hu et al. 2017).

Concerning the increasing hierarchical complexity in the history of life, the trend itself, as well as the existence of "transitions in individuality," have been known to biologists for a long time and are the subject of intensive research in several directions (for some recent discussions, see, e.g. Novák 1982; McShea 1991, 1994, 1996, 2001a, b; Szathmáry and Maynard Smith 1995; Pettersson 1996; Knoll and Bambach 2000; Michod 2000; Calcott and Sterelny 2001; Jablonka and Lamb 2006; Okasha 2006; Marcot and McShea 2007; Maynard Smith and Szathmáry 2010, 2015; Bouchard and Huneman 2013; Buss 2014; Corning and Szathmary 2015). The best-known concept in this area is probably "Major transitions in evolution," which emphasizes the merging of originally separate entities into higher-level units, their specialisation and the fact that these transitions were accompanied by the emergence of new ways of storing, transmitting, and interpreting information, i.e. the origin of new forms of inheritance (Szathmáry and Maynard Smith 1995; Calcott and Sterelny 2001; Maynard Smith and Szathmáry 2010, 2015; Corning and Szathmary 2015).

Similar alternative approaches ("levels of organisation," "integrative levels," "levels of selection," various kinds of major transitions, etc.) and their resulting hierarchies differ in their emphasis on partial aspects of the growth of biological complexity (horizontal, vertical, filial, ecological, integration on various levels etc.) and terminology (see, e.g. the concepts and reviews of this problem in Novák 1982; McShea 1991, 1994, 2001a, b; Pettersson 1996; Knoll and Bambach 2000; Michod 2000; McShea and Simpson 2001; Jablonka and Lamb 2006; Buss 2014; or; Corning and Szathmary 2015). Concerning lesser-known concepts, the theory of sociogenesis of Novák (1982) is worth mentioning. In his theory, Novák postulated that the growth of hierarchical complexity by the repeated merging of modular wholes into higher-level units and the integration of initially autonomous modules are processes common to the whole universe. The author largely neglected the role of egalitarian transitions (especially symbiogenesis). On the other hand, he considered both fraternal transitions and internal modularisation of organisms to be possible ways to a new level. According to Novák, sociogenesis occurs on all five postulated organismal levels including the psychological-social level in humans. In modern terminology, Novák considered the trend to be driven. Increasing hierarchical complexity was considered to reflect a universal tendency for cooperation and to be selectively advantageous both in the short and in the long term. However, the concept was based on *a priori* ideological, specifically Marxist, assumptions and has no realistic support in the paradigm of modern evolutionary biology. Among other problems, the theory (as well as Marxism in general) completely ignores natural threats to a higher-level entity resulting from the selfish interests of its partial elements.

Only some of the previously proposed concepts have addressed the issue of the causes of the trend of increasing hierarchical complexity. Even so, many potential explanations of specific transitions to higher levels, or entire trends leading to repeated transitions to higher levels, have been proposed over time. These concepts were summarised, for example, by McShea (1991), Corning and Szathmáry (2015), McShea and Simpson (2001), or Marcot and McShea (2007). Nevertheless, we should note that the whole problem historically overlaps with the problem of the general increase in organismal complexity (see Introduction). Darwinian and non-Darwinian (Corning and Szathmary 2015), or internalistic, externalistic, and undriven (McShea 1991) mechanisms can be distinguished. It is, however, clear that most proposed concepts cannot be considered disparate because of the high number of commonalities (McShea 1991).

According to Darwinian (or externalistic) explanations of this phenomenon, transitions to higher levels of organisation are generally selectively advantageous. This applies (albeit with some reservations, as transitions may also bring a number of problems, see the section "Various Types of Transitions") also to FET. However, the main cause of transitions is not a simple advantage of increasing biological fitness after reaching a new hierarchical level in our concept. The primary cause is the restoration of (macro)evolutionary potential and, consequently, the advantage in species selection. Moreover, FET exhibits at least some elements of internalist concepts that consider the source of the trend to be some non-Darwinian, most often developmental, mechanism. In our case, this mechanism is proposed to be SBS mediated macroevolutionary freezing. From the formal viewpoint, it is thus hard to decide whether FET is (in the sense of McShea 1991) rather internalist (and consider the trend to be a side-effect of decreasing (macro)evolutionary potential) or externalist (and consider the trend to be a side-effect of species selection on restoration of the (macro) evolutionary potential). In any case, the trend of increasing hierarchical complexity appears undriven most of the time. However, when the (macro)evolutionary potential of the evolutionary lineage reaches a critical point, the chances that an entity of a hierarchically higher level would be evolutionary viable, succeed, and establish a new major evolutionary lineage dramatically rise. From the global perspective, this trend thus constitutes a special case of a driven trend in the sense of McShea (1994, 1998; Marcot and McShea 2007) that is based on SBS and "driven" at the large scale. Therefore, we expect its course (see Fig. 1) to correspond to the pattern depicted section E of Fig. 7 in McShea (1996) or Fig. 2 in McShea (1998).

In some respects, our concept approaches the hypotheses of Cope and Gregory, who stressed the role of multiplication and diversification of modular wholes in evolution, or Sauders and Ho, who postulated asymmetry between the simple addition of components and their much harder deletion due to their integration into functional units (this was summarised, e.g. in McShea 1991). The possibility that the trend of increasing hierarchical complexity is a result of species selection has been proposed in the past (see, e.g. Wagner 1996; McShea and Changizi 2003; Marcot and McShea 2007). However, according to our knowledge, the trend has never been associated with decreasing evolvability or (macro) evolutionary potential. Theories that assume a similar drive as SBS at the base level (see, e.g. Zuckerkandl 1997) are generally quite exceptional. In any case, the permanence of this trend, its characteristic course with diversification and machinification of lower-level subunits, its occurrence predominantly in primary sexual eukaryotes and especially complex multicellular organisms, its gradual acceleration and significant boost since Neoproterozoic-Cambrian, cannot be coherently explained by any other theory presented so far.

Conclusions

Several global macroevolutionary trends, particularly the trends of decreasing (macro)evolutionary potential, disparity, and intraspecific variability in the evolution of (especially) sexual lineages, and the trend of increasing of the maximum of their hierarchical complexity may have one common explanation—stability-based sorting (SBS). Moreover, it may also coherently explain the accompanying phenomena of these processes: (1) the gradual acceleration of the growth of hierarchical complexity, (2) the boost in this acceleration since the Neoproterozoic-Cambrian, (3) the typicality of the aforementioned trends for sexual eukaryotes (and, especially, complex multicellular organisms), (4) the modular character of higher-level organisms, (5) the increasing mutual diversity (from the viewpoint of subunits), or variability (from the viewpoint of higher-level organism) on the next lower level of organisation, and (6) the decrease in complexity at this level and at lower levels.

We have previously demonstrated that all complex adaptations probably have their origin in the joint action of SBS and its special case, sorting based on dynamic stability, i.e. natural selection (Toman and Flegr 2017b). Moreover, SBS itself can explain many mysterious evolutionary phenomena. In this article, we proposed that one of these phenomena may be the trend of increasing hierarchical complexity of organisms that is based, according to Frozen Evolution Theory (FET), on the repeated nearly irreversible accumulation of effectively unchangeable genes, their interrelated groups, traits, and whole functional or morphological modules (i.e. the process of macroevolutionary freezing). According to FET, this phenomenon is characteristic of sexual eukaryotes and it can be more pronounced in organisms with complex development. Because of the ratchet-like character of the accumulation of macroevolutionary frozen elements, selection both on an individual and a species level seem rather ineffective at stopping it or slowing it down (see also Toman and Flegr 2018). It is widely accepted that the evolution of evolvability leads to the origin of the genotype-phenotype map that enables existence, development, and evolution of complex organisms. However, the same processes may significantly limit the (macro)evolutionary potential of these organisms in the long term (Toman and Flegr 2018). The accumulation of effectively unchangeable elements by SBS decreases the (macro)evolutionary potential of evolutionary lineages at a given hierarchical level and increases pressure to restore this property, which is essential in species selection. (Macro)evolutionary potential can be restored, at least theoretically, by the means of the rare "thawing" of seemingly irreversibly frozen elements, heterochrony, or radical simplification of individual development, i.e. *sacculinization* (Toman and Flegr 2018). However, it remains an open question whether these processes can restore (macro) evolutionary potential completely, at least significantly, or only partially (i.e. only in some, potentially less frozen traits or modules). We are convinced (and we presented some arguments to support this idea in "Results and Discussion") that the (macro)evolutionary potential can be significantly restored only through a transition to a higher hierarchical level by means of internal modularisation, fraternal, or egalitarian transition.[6] Continuously originating lineages

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[6] Nevertheless, note that transitions to higher levels of complexity might be important ways to overcome the decreasing of (macro)evolutionary potential even if other means to restore this property were open.

of modular organisms increase their advantage as (macro) evolutionary potential of the whole lineage decreases. At one point, they reach evolutionary viability. Initially, they have a great advantage. They can produce major evolutionary innovations and occupy (or even co-create) new niches or whole so-far unoccupied environments. Neutral processes and processes that increase the fitness of composite organisms on the new level (i.e. the differentiation of modules, their specialisation, integration of the whole organism, or even the origin of further unchangeable elements of body organisation), however, irreversibly lead to SBS induced macroevolutionary freezing at the new level. Therefore, the whole process repeats itself.

FET can explain McShea's (2015) "Evolutionary Syndrome" and associated aforementioned macroevolutionary patterns that have defied simple explanation so far. Consequently, it can shed new light on other problems met by researchers in fields of evolutionary and theoretical biology. One of the largest problems of traditional hypotheses that predict the trend of increasing complexity in evolution is the fact that this trend has never been replicated in computer models or laboratory experiments aimed at simulating the conditions of open-ended evolution (see, e.g. Oehlenschläger and Eigen 1997; Bedau et al. 2000; Channon and Damper 2000; McMullin 2000; Watson 2006; Bedau 2009). Neither computer simulations of open-ended evolution (see Langton 1984; Ray 1993, 1997; Thearling and Ray 1994, 1996; Yaeger 1994; Bedau et al. 1997; Ray and Hart 1998; Sayama 1999; Adami et al. 2000; Channon 2001; Suzuki et al. 2003; de Vladar et al. 2017), nor observations of the evolution of simple pre-cellular or prokaryotic systems in the laboratory (see Spiegelman et al. 1965; Mills et al. 1967; Oehlenschläger and Eigen 1997; Lenski 2004; Blount et al. 2008) led, under natural conditions (i.e. without introducing a strong artificial selection to the advantage of more complex entities), to open-ended evolution with continuously emerging novelties or even increasing hierarchical complexity. On the contrary, after the facultative short phase of the origination of new phenotypes, streamlining, simplification, and reduction of replicating entities, which did not change much after that, took place (Adami et al. 2000). Reasons for these failures may vary. It is possible that a sufficiently complex environment with practically unlimited variability, unlimited genetic system, dispersion of entities, and possibly other factors are necessary aside from basic prerequisites for the action of natural selection (the inheritance of properties and the overproduction of variable offspring) (de Vladar et al. 2017). However, even if these conditions are met, it may be necessary to simulate the evolution of evolvability and effectively irreversible freezing of (macro)evolutionary potential on the given level to reproduce the trend of increasing (hierarchical) complexity.

Given that the 'complexification' of life on Earth has directly and indirectly affected (and still affects) all lower levels of the organismal organisation, the trend of increasing hierarchical complexity may represent one of the most important macroevolutionary phenomena. From a conceptual point of view, FET enables microevolution to be connected with macroevolution, classical modern synthesis with "extended synthesis", and an ecologically-population genetic approach to study evolution with a developmentally-paleontological one (Budd 2006). Although other hypotheses and theories have been proposed to explain all the trends and patterns mentioned above, only FET can explain these phenomena as an integral set of interconnected macroevolutional processes.

Regardless of how conceivable the theory might sound, testing it will be essential. It is obvious that FET is a wide theoretical concept whose direct testing will not be an easy task. In our view, there are basically two ways to easily falsify this theory. It is clear it would not hold in the case that the trends of decreasing evolvability or (macro)evolutionary potential, intraspecific disparity (i.e. Rosa's rule), or interspecific disparity do not apply to most clades. These patterns are still disputed, especially in the field of paleobiology, and it would be fruitful to verify their existence (and possibly explore details of their form) in more fossil taxa. Taking the opposite approach, particular developmental processes that lead to a solidification of development are being studied in the field of evolutionary developmental biology (see, e.g. Galis and Metz 2001; Hu et al. 2017). Finding that development is comparably evolvable for the whole time of clades' existence, or that evolution of evolvability follows no clear trends in its evolution would greatly challenge our theory as well.

These are, however, quite negative and non-specific tests. Concerning more specific ways to test our concept, it may be best to verify whether the process of SBS (in this case the accumulation of further unevolvable components of organisms) may lead to transitions to new hierarchical levels in the first place. This could be done, for example, in a virtual simulation of open-ended evolution. There were several comparable attempts (see above). Alternatively, it is possible to model the evolution of evolvability in particular (see, e.g. Crombach and Hogeweg 2008). However, it might not be easy to construct a model that enables SBS. Even those models which are capable of simulating the evolution of evolvability might not be able to incorporate decreasing evolvability or an indefinitely increasing hierarchical level of simulated entities. Note that FET is not only about pleiotropic interactions, origin of modules, and evolvability on the given level, but rather ever increasing and complicating genetic architecture. Concerning numerical models, it may be also useful to calculate the range of conditions under which the "macroevolutionary ratchet" that accumulates further unchangeable components of organismal structure, function, and development may operate. Related equations might be similar or even identical to those used in calculations concerning the operation of Muller's ratchet. It is also clear that factors important for the progression of Muller's ratchet (i.e. epistasis among harmful mutations) may be of great importance also in the macroevolutionary case (Muller 1964). All of this, however, remains open to further research. It would be also extremely interesting to compare the dynamics of evolution in sexual and asexual lineages. According to FET, trends mentioned above should be characteristic exclusively for sexual clades or be more prominent in the evolution of sexual organisms. It is, however, unclear whether we could detect macroevolutionary changes in a laboratory experiment without extreme simplification of tested hypotheses (e.g. replacing sexual organisms by recombining viruses as in some earlier studies on the evolution of sexuality). Quantitative study of macroevolutionary patterns may present another way to test our concept. In the case that FET holds, we should expect some evolutionary lineages to be much more changeable and express a disproportionately larger disparity than other lineages in every time slice. This should follow a transition to a higher hierarchical level or any other restoration of (macro)evolutionary potential. The same lineages should, however, gradually loose this potential, whereas other lineages may randomly gain it. This tendency would probably lead to specific macroevolutionary patterns that could be detectable, for example, in paleobiological or phylogenetical data and possibly distinguished from other possible causes (see, e.g. Morlon et al. 2010; Hughes et al. 2013). Last but not least, nontrivial insights into these problems can also be achieved by the study of analogical processes in other evolving systems, e.g. cultural evolution (Toman and Flegr 2017a, 2018).

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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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