Journal of Phylogenetics & Evolutionary Biology

Crother and Murray, J Phylogenetics Evol Biol
2018, 6:1
DOI: 10.4172/2329-9002.1000192

Review Article Open Access

Linking a Biological Mechanism to Evolvability

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Received date: Feb 03, 2018; **Accepted date:** Feb 12, 2018; **Published date:** Feb 15, 2018

Abstract

Evolvability has become a concept used to explain the common observation of clade asymmetry. However, the concept of evolvability means different things to different workers. Recent work has formalized the concept and we apply the formalized concept to a developmental system (primordial germ cell determination mechanism) that has been proposed to explain clade size disparity. In a simplified view, there are two general primordial germ cell (pgc) determination mechanisms: determinative and induced. The determinative mechanism is associated with species rich clades and the induced mechanism with species poor clades. The formal equations of evolvability provide a theoretical framework under which we can assess the relative influence of pgc determination mechanisms on clade evolvability. We propose that the determinative mechanism has enhanced evolvability in most clades that possess the trait.

Keywords: Primordial germ cell determination; Species richness; Disparity

Introduction

Disparity and asymmetry of species richness across monophyletic groups of organisms is an observation that has invited much explanation [1-6]. One approach to explaining this pattern has been the transformation of the concept of evolvability, from simply referring to variation available to natural selection [7] to the notion that some lineages inherently possess greater potential (because the evolution of some trait with relatively higher evolvability is not guaranteed) for speciation than other lineages [8-11]. Most of the cited works on evolvability differ in details, yet they indicate speciation as a product. Kirschner went beyond increased rates of speciation and suggested evolvability could contribute to acquisition and refinement of traits to enhance fitness [12]. Evolvability has become a central theme in evolution-development research, replacing developmental constraint as more important in understanding origins of diversity [13].

The relationship between selection, evolvability, and the origins of diversity are complex. Selection may act upon evolvability [14-16], i.e. determines which lineages are constrained and which have a high potential to evolve [17]. Dawkins viewed evolvability as the ability to generate diversity and that although it was under selection, it was not the selection of survival and reproduction, but "a kind of higher-level selection… for evolvability" [18]. Evolvability and selection have been considered processes ontologically separated in evolution, where evolvability occurs at the initial level and selection functions on the products of evolvability [13]. In Brigandt's view, which we share, evolvability enhances/increases the production of variation/novel traits and selection determines the success of those traits. These novel traits represent the Exaptive Pool of Gould, which he argued represented the "structural basis of evolvability" [19].

Something missing in these discussions of evolvability is the identification, or a proposed hypothesis, of a biological trait/process/mechanism that could be argued to fit the concept of evolvability, where evolvability explains asymmetrical diversification rates of species or potential to yield some modification via descent. For example, anurans and caudates are sister clades with anurans having an order of magnitude greater number of species. What might explain this disparity? Clade age can be ruled out because they are sisters. Ecology? Extinction rates? Differences in evolvability? Perhaps there is an intrinsic biological difference between anurans and caudates that enhances evolvability in anurans but is absent in caudates, for example. The goal of this paper is to propose a specific biological mechanism that fits the concept of evolvability. Moreover, we aim to explain differences in clade size between sister clades via a developmental mechanism that directly influences the relative evolvability of clades. Such an application provides a novel link between theoretical evolvability and empirical evolutionary biology considering metazoans in general.

Evolvability

In Brown's review and further development of the concept of evolvability, she explained that evolvability really is both the explanation (=explanans) and the thing to be explained (=explanandum) and presented formal language for identifying it in biological systems. However, Brown specifically regarded evolvability as an explanandum in evolutionary-developmental biology, thus not an explanation for asymmetrical patterns of clade size (or speciation rates), but instead an observation that requires explanation [20]. Formally E: Pr x, b(f_t)

where E (evolvability of a particular lineage) is the probability of F_t (the probability of some trait appearing at time T) being true, given the truth of X and B. In general, X describes the inherent characteristics of the lineage of interest (e.g. PGC mechanism), while B describes environmental characteristics (e.g. temperature, geography, weather stochasticity) relevant to modification of the population over time. Brown presented a formal way to state the hypothesis to discover evolvability (E): Pr a,b(l_t) > Pr m,b(l_t),

says (for a putative mechanism) that the probability that clade A [with mechanism, X_1] would have increased evolvability (L) over time T, in environment B, is > the probability that clade M [with the mechanism, X_2] would have increased evolvability (L) over time T in environment B [20].

A Biological example of evolvability: Primordial germ cell determination

One empirical system in which evolvability has been invoked to explain species richness asymmetry in sister clades and differential rates of speciation, has been primordial germ cell (PGC) determination mechanisms [21-24]. Primordial germ cells are the precursor cells that eventually form eggs and sperm in the developing embryo. In a broad sense, there are two developmental mechanisms for determining which cells become PGCs in the embryo. One mechanism is termed "determinative" and here the PGCs are predetermined by cytoplasmic elements in the oocyte. Essentially, the cells that form in the presence of these elements become PGCs. In the determinative (=predetermined in some literature) mechanism the PGCs are determined very early in development and subsequently set aside and thus are not influenced by later inducing factors during development.

The other mechanism is termed "induced" and here the PGCs are determined later in development in response to a cascade of inducing signals and gene expression [25]. Previous work by Johnson et al. [26]; Crother et al. [6 , 21] has shown that groups that exhibit the determinative mode are significantly more species rich in general and are always more species rich than their sister clade with the induced mode. For example, urodeles are induced and anurans are determinative and anurans have an order of magnitude more species. Other examples include teleost fish (determinative), which has three orders of magnitude more species than its sister clade (induced; probably bowfins and their extinct relatives), and the crown clade of mollusks (determinative; gastropods, cephalopods, scaphopods, bivalves) has an order of magnitude more species than its sister clade (induced; polyplacophorans and relatives). In fact, in every sister clade case where one clade has the predetermined mechanism and the sister clade is induced the sister clade is always greatly more species rich [6,21].

It has also been shown that vertebrate groups with the determinative mode have significantly faster rates of evolution than groups with the induced mode, as would be predicted by the asymmetry in species richness of the sister clades. In comparisons of protein coding sequences of vertebrate species that use the determinative mechanism with their sister clades that use the induced mechanism, genes were found to evolve significantly more rapidly in the determinative clades. An observation of equal importance by Evans et al. is "No other biological property correlates as well with the observed changes in rate." The biological property they refer to is the determinative mechanism (through the proxy of the presence of germ plasm) [24]. Crother et al. statistically demonstrated that phyla with the determinative mechanism have significantly more species than phyla with the induced mode [6]. The body of empirical work already performed on the relationship between PGC mechanism and clade richness abolishes any speculation for autocorrelation as a correlative explanation, as the observations are not artifacts.

The explanation for the association of the PGC determinative mechanism with increased species richness and increased rates of evolution has been attributed to the hypothesis that the induced mode is a developmental constraint and the determinative mode is a constraint release [21]. The explicit molecular developmental pathways that are thought to function as constraint or release have been characterized and reviewed by Chatfield et al. [25] and Johnson and Alberio [16]. As a constraint release, it has been argued that this increases the opportunities for the development of evolutionary novelties, some of which become key innovations that enhance speciation rates. Thus, lineages characterized by the determinative mode have high evolvability and this mode explains the increased rates of evolution of clades with that mode [6,21,23,27]. However, the use of evolvability in this sense, while seeming to fit the meaning of the concept, appears to be simply an un-quantified, abstract, buzzword.

However, observed species richness and the disposition of a clade to be species rich (high probability of rapid evolution, i.e. evolvability) are two different things, and the latter does not always play out to the former. Thus, the question, under the reformulation of evolvability [20], is whether the determinative PGC mechanism can be shown to enhance evolvability in a way that is more than just pinning the concept onto a system, but an increase in disposition.

Materials and Methods

A formal application of PGC mechanisms and relative constraints on evolvability

Brown's formal language provides a logical probability framework for looking at any putative mechanism that may be associated with evolvability, as both explanation for clade asymmetry and thing to be explained for the increased rates of speciation associated with the determinative mode. For the PGC system, a general view would say the evolvability of the determinative *versus* induced clades is both the explanans (they are more species-rich because those lineages have relatively higher evolvability) and the explanandum (why is evolvability higher in one *versus* the other). If we can assign explanans/explanandum to specific systems, then species rich clades and increased rates of evolution based on PGC mechanism (relative to depauperate sister clades) are hypothesized to be the explanandum (i.e. those clades exhibit evolvability) and the explanans (i.e. depresses/allows increased rates of speciation, thus evolvability).

For the PGC mechanisms problem, X is the developmental mechanism and B represents relevant features of the environment in which F_t is achieved. F_t is the relatively higher probability for increased rates of speciation as determined by relative species richness to the sister clade, and T is time, which is unproblematic in the context of sister lineage/clade comparisons. Thus, if the determinative mechanism increases evolvability (in this case the propensity to be speciose), then clade A with the determinative mechanism [(X_{DT}) in environment B] may have observable increased rates of speciation. The contra should also hold with the constraint, that clades X_I with the induced mechanism should have depressed relative rates of speciation (Figure 1).

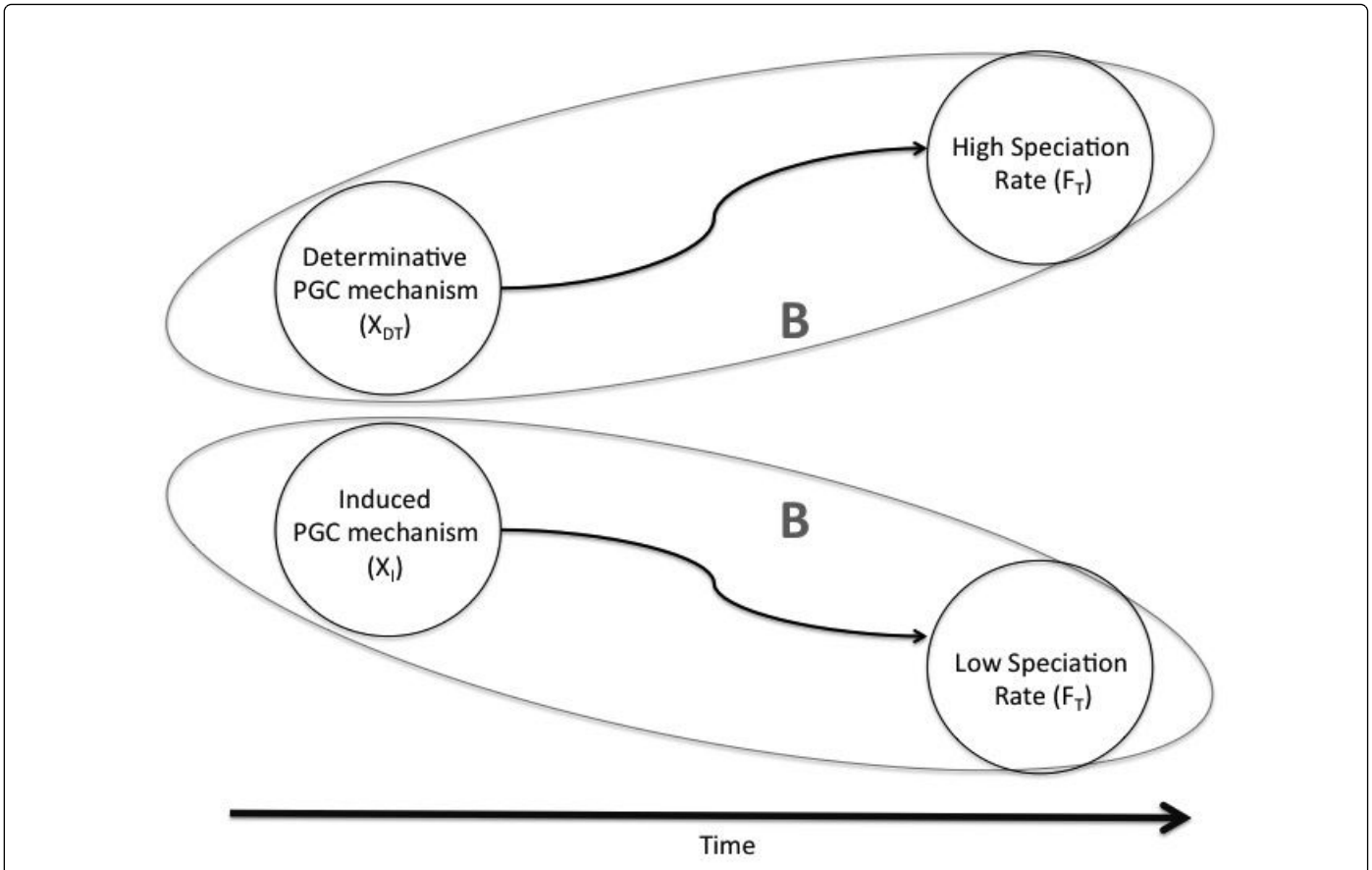

Figure 1: An illustration of the differential role of evolvability variables X, B and F_t. The theoretical outcome under Brown's formulation would be the expectation that (X_{DT}) and (X_I) with different evolvabilities yield different outcomes in speciation rates under the environmental influence of B. See text for explanation of the variables.

Results and Discussion

In reference to Brown's formal way to hypothesize evolvability (E):

Pr a,b(l_t) > Pr m,b(l_t),

says (for the PGC mechanism problem) that the probability that clade A [with the determinative mechanism, X_{DT}] would have increased rates of speciation (L) over time T, in environment B, is > the probability that clade M [with the induced mechanism, X_I] would have increased rates of speciation (L) over time T in environment B. In all sister clade comparisons we are aware of [6,21]. E is true and the inequality is also true for the determinative mode *versus* the induced mode.

Young et al. [28], as noted by Brown [20], attributes differences in limb diversity between apes and quadrupedal monkeys to the release of an ambiguous developmental constraint. Brown grouped such developmental processes as a causal subset of X, noting the existence of other parameters, inherent to the relevant population, capable of causally influencing the probability of change to a future state. Unique to Brown [20] and Young et al. [28], however, the mechanism of PGC determination directly influences the modification of lineages in the context of descent. In other words, the mechanism of PGC determination is an 'X,' a variable of utmost relevance that characterizes a piece of the inherent traits of a population and drastically influences its evolvability. Evolutionary biology paints with broad strokes when unknowingly applying 'X' to specific systems [20], i.e. capacity to generate genetic, phenotypic and adaptive variation. Here, Crother et al. [21] atypically and directly elucidated a developmental character (X) that empirically dictated the evolvability of animal lineages. In fact, the influence of 'X' is seemingly quantifiable, in this developmental system, as the difference in speciation between the determinative and induced PGC mechanisms. Perhaps the quantification could simply be counting, for example comparing species number of Anura to Caudata would yield an approximate value of +4300 for Anura, which in turn could be evaluated statistically [29]. Or, the quantification may be associated with rate of speciation. For example, for sequences evolving at significantly different rates, 87% of the sequences show anurans evolving faster than caudates [24].

The variable 'b' also requires clarification here. As mentioned, 'b' represents the surrounding context in which 'F_t' is achieved. Such a vague variable captures all extrinsic and intrinsic properties relevant and/or influential to the passive and active manipulation of a trait to the observable state. Extrinsically, as described by Brown [20], 'b' reflects the environmental context that evolution happens within. We posit, using the PGC example, that the relevance of 'b' is situational and scale-dependent. For instance, in many cases, 'b' may be simply

the climate, plate tectonics, geography, and weather stochasticity that provide a loose extrinsic constraint or drive on evolvability. In other instances, 'b' may be the predator-prey interactions or competitive ecology that provides a more defined, selective constraint or pressure on F_t. In the PGC system, extrinsic 'b' is observable as the suite of environmental/ecological influences that participate in the constraint of speciation for the determinative PGC mode (the developmental constraint release), as opposed to the induced mode, because the induced mode is constrained by 'x' as well. Intrinsically, 'b' may represent the developmental environment that is relevant to 'x' captured broadly in the gene expression cascades of gene regulatory networks. The variable 'b' may even be more complicated in that it could also encompass interactions between extrinsic and intrinsic influences in the form of environment-development interactions causing epigenetic influences on the developmental system.

Further, and with respect to contributing to the abstract definition of evolvability by Brown, the probability of evolving, given present population and environmental influences, to some known outcome of character states, constrains evolvability to a robust-process orientation. Here, PGC determination mechanisms provide an example of a lineage disposition that inherently increases the probability of descent with modification irrespective of a specific character state outcome. Teleosts and anurans, for example, are not bound by a character state [e.g. unequal limb length from Young et al. [28] that separates them from respective sister lineages, but are rather constrained (or released) to a suite of phenotypes by other suites of constraints (or releases) less restrictive than the induced PGC determination mechanism. PGC determination mechanisms, as presented here, are evo-devo mechanisms inherent to the evolvability of Animalia, irrespective of an observable modification, but modification as a whole.

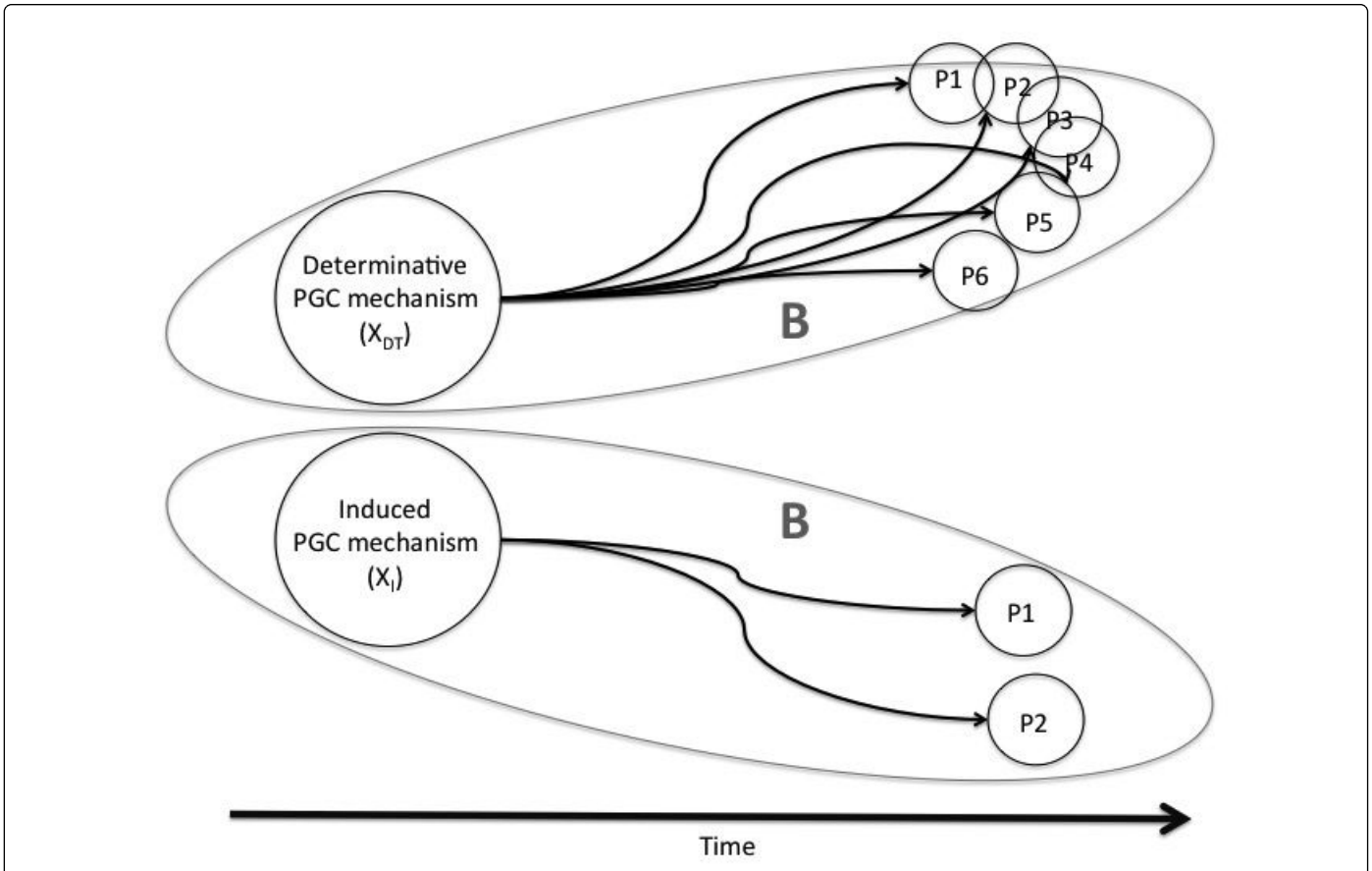

Figure 2: A schematic depicting the relative probability of observable change within each PGC mechanisms [the number of potential phenotypes (P1-6)], within a given quantification of 'B' in each scenario. Under the determinitive mechanism, the expectation is the production of phenotypic variation at all levels, from micro to macro. Under the induced mechanism, developmental constraints inhibit the production of variation.

Implications

Wiens [30] recently reviewed and expanded upon explanations for patterns of biodiversity, and interesting to us was that the concept of evolvability was absent. Wiens did note that the focus should not be on specific traits, but be on what affects differential rates of diversification, where the explanation resides in evolvability. Maybe some of the explanations in Wiens could be couched/tested in terms of evolvability. Regardless, as a general explanation evolvability should not be excluded and in specific, developmental mechanisms need to be included in hypotheses to explain asymmetrical patterns in biodiversity among major clades.

Evans et al. [24] wrote, "They (refers to the asymmetry in species richness and rates of evolution in predetermined clades) support the hypothesis that enhanced evolvability is responsible for the repeated

evolution of germ plasm." Is the evolvability of Evans et al. the same as characterized by Brown [20]? Is the PGC determination mechanism and corresponding speciation asymmetry an appropriate use of evolvability as explanandum and of explanans? In other words, can we make claims that the determinative mechanism is a robust explanation for increased rates of speciation, for enhanced evolvability? Brown [20] attributed the developmental program and associated genetic architecture as the governing body for phenotypic evolvability. In the absence of testable selection hypotheses [as is the case with Young et al. [28], and likely many others], developmental constraints and release are the default governance of observable phenotypic differences. Providing both causal and mechanistic substance to evolvability, 'X' serves as the internal population features that relate to the probability of some change in an evolvability-based explanation. Unique to the understanding of evolvability, and newly presented here, is the ability for 'X' to represent an exact developmental constraint pertinent to the probability of observable change (Figure 2), the relative quantification of 'b' in such a scenario, and for that observable change to be relative evolvability itself.

This scenario is exemplified by PGC mechanism evolution in the context of evolvability. We formally propose the hypothesis that the determinative mode of PGC determination has high evolvability and perhaps explains asymmetrical patterns of biodiversity across the Metazoa.

Acknowledgements

R. Brown and I. Brigandt kindly answered questions. C. Beachy critiqued an early version. The Edward G. Schlieder Foundation partially funded the project. The authors have no conflict of interest to declare.

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