Regime interiority and the structural conditions for natural selection

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Abstract

The organizational closure tradition in theoretical biology holds that self-maintaining organization must precede natural selection, while the Darwinian population framework characterizes how populations vary in their evolutionary character. If closure must precede natural selection, then selection-based explanation has structural prerequisites that can be present or absent. Existing frameworks do not provide a diagnostic for whether those prerequisites hold in a given system. This paper develops such a diagnostic. A null condition specifies system dynamics in the absence of the structural prerequisites for selection, and three criteria, reversibility of organizational roles (***R***), retention of constraint across transitions (***M***), and perturbability of organized response (***P***), diagnose when selection-based explanation applies and whether the conditions under which it operates are themselves sustained. The framework is illustrated using Wrangel Island mammoths and modern cheetahs, two populations with comparable genetic depletion but different structural outcomes. The *regime interiority* framework identifies a diagnostic distinction not specified by existing approaches.

Keywords: regime interiority, organizational closure, natural selection, Darwinian populations

Section 1. Introduction

Two traditions in biology address the most fundamental questions about living systems. The organizational closure tradition asks how physical and chemical processes become organized into self-maintaining wholes (Rosen 1991; Moreno and Mossio 2015). The Darwinian tradition asks how, once life exists, natural selection generates adaptation and novelty (Godfrey-Smith 2009). Between these traditions lies a persistent conceptual gap: neither provides a way to determine whether the structural conditions that license selection-based explanation currently hold in a given system. Closure alone cannot bridge the gap because under sufficiently generous description, even non-living systems can be made to satisfy the formal definition of closure (Cusimano and Sterner 2020). The Darwinian tradition does not address this question from the other side, because its tools assume the very structure whose presence is in question. What remains to be specified is a diagnostic for whether the structural conditions for selection are present.

Serious efforts have been made to close the gap from both sides. Moreno and Mossio (2015) argue that organizational closure is a prerequisite for natural selection rather than its product, but their framework specifies what closure is without providing criteria for determining whether it currently holds in a particular system, a limitation that they acknowledge (2015, p. 145, n. 4). The difficulty of identifying which actual biological structures correspond to the formal categories of closure remains unresolved, and closure attribution itself is sensitive to how a system's causal structure is described (Letelier, Marin, and Mpodozis 2003; Cárdenas *et al*. 2010; Cusimano and Sterner 2020). From the Darwinian side, Godfrey-Smith (2009) provides a framework for characterizing how populations vary in their evolutionary character, but his parameters are state descriptions. A population undergoing mutational meltdown can score adequately on every parameter while the structural substrate on which selection depends erodes beneath it (Lynch *et al.* 1993; Gabriel *et al*. 1993). Other approaches address evolutionary individuality or internal conflict (Bourke 2011; Queller and Strassmann 2009; Schenkel, Patten and Ågren 2025), but presuppose rather than diagnose the structural conditions under which such analyses apply.

This paper develops a null condition that specifies what system dynamics look like when the structural prerequisites for selection are absent. Under the *null condition*, a system's state-to-state transitions are determined by its current state and external inputs, with no system-generated constraints carried forward across transitions. Departure from this baseline is diagnosed through three conditions, reversibility of organizational roles (***R***), retention of constraint across transitions (***M***), and perturbability of the system's organized response (***P***), whose status determines whether and in what sense selection-based explanation applies to a given system. Where ***R***, ***M***, and ***P*** are each nonzero, the system has a transition structure on which selection can operate. This paper further distinguishes a stronger condition, *regime interiority*, in which the structural conditions under which selection operates are themselves sustained through the system's own activity. The distinction between these two conditions is the central diagnostic contribution of this paper. The framework does not redescribe natural selection, but diagnoses whether the structural conditions for selection to do adaptive work are present. The *null condition* makes attribution principled rather than *ad hoc*, providing the explicit diagnostic baseline that the closure tradition has not supplied (Moreno and Mossio 2015, p. 145, n. 4) and that the Darwinian population framework does not require of itself.

The framework is illustrated at both ends of the diagnostic range. Glycolysis and a candle flame are shown to satisfy the *null condition*, the former despite being biologically essential and thermodynamically sophisticated, the latter despite being redescribable as satisfying the formal definition of closure (Cusimano and Sterner 2020). Two population-level case studies then demonstrate the framework's capacity to distinguish structurally different outcomes from comparable population-genetic data: woolly mammoths isolated on Wrangel Island before extinction (Vartanyan *et al*. 1993; Rogers and Slatkin 2017; Dehasque *et al*. 2024), and modern cheetahs following severe demographic bottlenecks (O'Brien *et al*. 1983; Dobrynin *et al*. 2015). These case studies are selected for their empirical clarity rather than their representativeness, in order to make the structural distinction visible in well-characterized systems. Despite comparable genetic depletion, the diagnostic yields different structural classifications.

To develop this argument, the paper proceeds in five steps. Section 2 establishes the conceptual foundations by tracing the closure tradition and Darwinian population theory to the diagnostic gap between them, showing what each provides and why neither was designed to fill that gap. Section 3 develops the *regime interiority* framework, specifying the three diagnostic criteria, the *null condition*, and the framework's position relative to existing approaches. Section 3 also introduces a three-category distinction among biological systems. Under the *null condition*, no unified transition structure exists and selection is inapplicable. Under the *minimal Darwinian regime*, the diagnostic criteria are each nonzero but not mutually sustaining, and selection operates on an eroding substrate. Where *regime interiority* is present, the criteria form a reciprocal closure and the conditions under which selection operates are self-maintaining. The threshold between the *minimal Darwinian regime* and *regime interiority* is the point at which selection becomes structurally sustained rather than merely operative. Section 4 applies the diagnostic to the mammoth and cheetah cases. Section 5 addresses objections, including the concern that the diagnostic criteria merely redescribe natural selection in unfamiliar terminology, that the language of organized transitions imports teleology, and that the distinction between regime-preserving and regime-dissolving transitions introduces evaluative normativity. Section 6 identifies the empirical work that remains. A companion paper operationalizing the diagnostic criteria as quantitative empirical measures in an experimental system is in preparation.

Section 2. Foundations

Regime interiority rests on two bodies of prior work, the organizational closure tradition in theoretical biology (Rosen 1991; Moreno and Mossio 2015) and the analysis of Darwinian populations in philosophy of biology (Godfrey-Smith 2009). Understanding what each provides, and where each leaves a diagnostic gap, is necessary before the framework developed here can be introduced.

Section 2.1. The Closure Tradition

The organizational closure tradition distinguishes two levels of biological causation. Moreno and Mossio (2015, chapter 1) argue that biological systems realize an open regime of thermodynamic processes and a closed regime of dependence among the constraints that act on those processes. A constraint is a structure that channels or harnesses a thermodynamic process without being consumed by it, as an enzyme catalyzes a reaction while remaining intact at the timescale of that reaction (Montévil and Mossio 2015; Pattee 1972). In a system realizing closure of constraints, each constraint enables the persistence of at least one other constraint in a network while depending on at least one other for its own maintenance. This is what distinguishes the mutual dependency among constraints in a cell from the self-perpetuating transformations of a physical cycle such as the hydrologic cycle (evaporation, condensation, precipitation, collection), where every entity is consumed in producing the next and no entity persists through the process it governs (Mossio and Moreno 2010).

Rosen's (1991) work on metabolism-repair systems formalized this principle.[1] A material system is an organism, in Rosen's framework, if and only if it is "closed to efficient causation", meaning that all of the productive agents within the system are themselves produced by processes within that same system (Rosen 1991, p. 244). Montévil and Mossio (2015) developed this insight into a rigorous framework, defining biological organization as the closure of constraints. Earlier formulations, from Kant's (1790) analysis of organisms as "natural purposes" through Maturana and Varela's (1980) autopoiesis, had recognized that living systems exhibit a distinctive form of self-maintenance. But as Moreno

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[1] The letters M and R in Rosen's (M, R)-system formalism refer to metabolism and repair. They should not be confused with the diagnostic criteria introduced in section 3 of this paper, where ***R*** denotes reversibility and ***M*** denotes retention. The diagnostic criteria of this paper will always appear in bold, italics.

and Mossio (2015) have argued, autopoiesis locates closure at the level of processes rather than constraints, a formulation that can in principle encompass physical systems that lack biological organization.

A crucial further development, due to Ruiz-Mirazo and colleagues (2004), recognized that two conditions must be jointly satisfied for a system to count as a living organization. The first is organizational closure itself. The second is the capacity for open-ended evolution, meaning the capacity to reproduce while bringing about unlimited functional variety. Neither condition suffices alone. Organizational closure can exist without hereditary mechanisms for open-ended evolution, and the minimal conditions for Darwinian evolution may be satisfied by systems that lack organizational closure. Moreno and Mossio (2015, chapter 5) developed this dual requirement as a historical narrative, arguing that organizational closure is a prerequisite for natural selection rather than its product. Selection cannot drive systems toward increasing complexity unless those systems already possess a minimal degree of organized complexity (Moreno and Mossio 2015, p. 116).

One further point constrains everything that follows. Organizational closure is a property of ongoing process, not of any particular material structure. The enzymes, membranes, and regulatory molecules that constitute a cell's organization are all transient, continuously degraded and replaced. Throughout this paper, "transition" refers to any event in which components, configurations, or organizational states are replaced, degraded, or reorganized, including molecular turnover, generational replacement, and perturbation response. What persists is the pattern of mutual dependency. Thompson (2007, pp. 44-45) distinguishes organizational closure, the abstract network of relations defining which constraints depend on which, from operational closure, the recurrent dynamics of the system's metabolism and component turnover. A system can maintain operational closure, with its processes continuing to run, while its organizational closure degrades. The present framework diagnoses the persistence of organizational closure specifically, not the continuation of operations.

Section 2.2. Darwinian Populations

Godfrey-Smith (2009) developed a framework for characterizing Darwinian populations by locating them in a multidimensional parameter space. The dimensions include ***H*** (fidelity of heredity), ***S*** (dependence of reproductive differences on intrinsic character), ***C*** (continuity between phenotypic variation and fitness variation), and ***V*** (abundance of variation). Populations range along each dimension, and the framework distinguishes paradigm cases, in which selection can produce complex adapted structures, from marginal ones, in which Darwinian properties are present but weak or partial (Godfrey-Smith 2009, chapter 3).

A further distinction will matter for what follows. Godfrey-Smith separates distribution explanations, which assume existing variants and explain their frequencies, from origin explanations, which explain how variants came to exist. Paradigm Darwinian processes are those in which selection plays a role in origin, reshaping the population so that new variants become more likely to appear. This paper's question, when the structural conditions for selection-based explanation hold at all, is logically prior to where a population sits in Darwinian parameter space. A population can be located in that space and graded by its parameters while the structural conditions sustaining selection's effectiveness are eroding. The Darwinian population framework describes what selection is doing. The framework presented here asks whether the substrate on which selection operates remains intact.

Section 2.3. The Diagnostic Gap

Neither the closure tradition nor the Darwinian population framework provides the operational criteria for diagnosing whether the structural conditions for selection-based explanation currently hold in any particular system. Such a diagnostic would bear on questions across biology, from whether genetically depleted populations retain the capacity for adaptive responses (Frankham 2005; Lynch *et al*. 1993), to when new levels of biological organization achieve the structural conditions for selection to operate at that level, to what distinguishes living systems from complex non-living ones. The empirical tools that biologists currently use to assess evolutionary capacity, such as effective population size, heterozygosity, and mutational load, already assume that the structural conditions for selection are in place. They measure how selection is working, not whether the conditions for it to work are present.

The closure tradition's diagnostic gap is straightforward. The formal definition of closure specifies that constraints must be mutually dependent, each constraint both enables and is enabled by others in the network (Montévil and Mossio 2015, p. 21). It tells us what closure is. It does not tell us how to determine whether closure holds in any particular system. As noted in the introduction, Moreno and Mossio themselves acknowledge this gap. Rosen's formalism provides a mathematically precise characterization of what closure requires, but the difficulty of identifying which actual biological structures correspond to the formal categories remains largely unsolved (Letelier, Marin and Mpodozis 2003; Cárdenas *et al*. 2010). The most recent attempt proposes a systematic protocol for mapping the (M,R)-system categories onto concrete biological structures (Weckström 2026), but even this does not provide criteria for diagnosing whether that closure is currently sustained through the system's own activity or what it would mean for that closure to be degrading or absent.

The difficulty runs deeper than mere incompleteness. Cusimano and Sterner (2020) have shown that closure attribution itself is sensitive to how investigators describe a system's causal structure. What counts as a constraint depends on how the system is described. Under sufficiently generous redescription, even a candle flame can be made to satisfy the formal definition of closure. This means that biologists attributing organizational closure typically rely on tacit recognition of relevant properties rather than application of stated criteria. Such tacit recognition may be reliable in paradigm cases, but it provides no principled basis for adjudicating disputed ones, and no basis at all for detecting gradual erosion of the system. Attempts to resolve this from the information-theoretic side have met similar limits, capturing behavioral independence from the environment but not organizational self-maintenance (Bertschinger *et al.* 2008).

A parallel gap exists on the Darwinian population side. Godfrey-Smith's parameters are state descriptions. They measure what selection is currently doing. A population can score adequately on every parameter while the structural conditions for selection-based explanation are eroding, and it can score poorly on some parameters for purely contingent reasons while those conditions remain fully intact. They do not diagnose whether a regime that sustains selection's effectiveness will continue to hold. Godfrey-Smith approaches this threshold question in his treatment of cultural evolution, arguing that "quite specific conditions are required for a cultural process to be Darwinian" and that the structural basis for parent-offspring lineages "first attenuates and then disappears" as agents integrate information in more complex ways (2009, chapter 8). The question of when structural conditions for Darwinian explanation hold is thus present in his own framework, but he does not develop a diagnostic for the biological case.

The closure tradition provides the conceptual architecture but no diagnostic for whether it currently holds. The Darwinian population framework provides the grading but no threshold for when the structural conditions sustaining selection have eroded or collapsed. Work on evolutionary transitions in individuality illustrates the practical consequence. Black, Bourrat, and Rainey (2020) have shown that Darwinian properties, variation, differential reproduction, and heredity, can be externally imposed on collectives through ecological scaffolding before those collectives acquire the capacity to sustain such properties endogenously. A scaffolded collective participates in selection-like dynamics but does not yet own its transitions in the sense that the present framework will make precise.

The distinction between externally scaffolded and internally sustained Darwinian properties is precisely what a diagnostic for the structural conditions of selection-based explanation would need to draw, and neither framework currently draws it. Section 3 introduces the diagnostic that fills the space.

Section 3. ***Regime Interiority***

This section introduces the diagnostic framework. *Regime interiority* does not redefine organizational closure but provides criteria for diagnosing whether closure is being sustained through a system's own activity. Section 3.1 specifies three diagnostic criteria, reversibility (***R***), retention (***M***), and perturbability (***P***), whose joint satisfaction indicates that organizational closure is being sustained through the system's own organized transitions, the condition this paper calls *regime interiority*. Section 3.2 develops the *null condition* against which *regime interiority* can be diagnosed. Section 3.3 positions the framework relative to existing approaches.

Section 3.1 Diagnostic Criteria

When closure is sustained through the system's own organized transitions rather than maintained by external circumstances, this paper refers to the condition as *regime interiority*. Organizational closure and *regime interiority* are not synonyms. Closure is a constitutive property that specifies what a system must be. *Regime interiority* is a diagnostic property. It specifies how to determine whether closure is being sustained through the system's own activity. A system can satisfy the formal definition of closure while the conditions sustaining that closure are maintained by external scaffolding or are in the process of eroding. The framework developed below specifies three conditions whose joint satisfaction indicates that organizational closure is being sustained through the system's own organized transitions. The three criteria are selected because each captures a distinct and necessary aspect of sustained organizational closure across transitions: availability of alternative organizational roles (R), persistence of constraint through turnover (M), and regulated reorganization under perturbation (P). These conditions are not proposed as a new definition of closure but as operational criteria for determining whether closure persists through turnover, perturbation, and environmental change, rather than merely obtaining under present conditions. Because the criteria are assessed directly rather than derived from a prior attribution of closure, the diagnostic does not inherit the redescription-sensitivity that Cusimano and Sterner (2020) identified as a problem for closure attribution.

The first condition is reversibility of organizational roles (***R***). A system satisfies this condition when alternative functional configurations remain counterfactually available across component turnover. This does not require that the system can literally return to prior microstates, which is thermodynamically impossible, but that roles or patterns previously instantiated remain accessible as organizational possibilities. In population-genetic terms, a population that loses a genetic variant through drift but retains standing variation from which equivalent functional capacity could be reconstituted satisfies reversibility (Barrett and Schluter 2008). A population in which loss is irreversible because no such variation remains does not (Frankham 2005). Reversibility operationalizes the intuition that closed systems "own" their transitions rather than being pushed through state space by external forces. Throughout this paper, "ownership" refers to whether a system's own constraints distinguish trajectories compatible with continued unity from those that dissolve it, and carries no implication of agency, normativity, or experiential states.

The second condition is retention of constraint across transitions (***M***). A system satisfies this condition when its history durably restructures the space of future transitions in a way that goes beyond the cyclic regeneration of its current constraint network. This distinction requires care. Organizational closure already requires that constraints be regenerated through component turnover. An enzyme degrades and other constraints in the network produce a replacement. The organizational loop continues. What closure does not require is that the system *accumulate* organizational constraint from past encounters in a way that reshapes what transitions are subsequently available. Heredity does not merely regenerate the current organism. It carries forward specific constraint, shaped by selection in prior generations, that structures what the next generation can become (Jablonka and Lamb 2005). CRISPR arrays do not merely maintain the current immune capacity. They incorporate fragments of past viral encounters into the host genome, durably restructuring the cell lineage's future response repertoire (Barrangou *et al*. 2007). Adaptive immune memory does not merely regenerate lymphocytes. Clonal selection and long-lived memory cells reshape the repertoire based on what has been encountered, so that the system's future differs from its past (Lam *et al*. 2024). What these mechanisms share is that they are not simply maintaining a loop but accumulating constraint from past perturbations in a way that is not erased by molecular turnover.

The third condition is perturbability without collapse (***P***). A system satisfies this condition when perturbations elicit internal reorganization that preserves organizational unity rather than either being passively absorbed or causing dissolution. Moreno and Mossio (2015, section 1.8) characterize regulation as the capacity of the whole organization to respond to and compensate for variations that would otherwise disrupt closure, and Ruiz-Mirazo and colleagues (2004) describe the capacity of autonomous systems to "adaptively modify internal organization as a response to external changes." ***P*** draws on this work but serves a different purpose. Where Moreno and Mossio characterize what regulation *is*, ***P*** provides a testable criterion. Subject the system to perturbation and observe whether it reorganizes or dissolves. A system too rigid to be perturbed fails, as does one that dissolves. Only systems that reorganize while maintaining closure satisfy it. The difference is between defining a capacity and diagnosing its presence.

The diagnostic status of a system with respect to selection-based explanation depends on two conditions, each assessed through ***R***, ***M***, and ***P***. The first condition is departure from the null. Where ***R***, ***M***, and ***P*** are each nonzero, the system possesses a transition structure on which selection can act. Each condition is individually necessary for this departure. Without reversibility, a system with retention and perturbability would be locked into a single trajectory. Without retention, it would reset at each moment, carrying no organizational history forward. Without perturbability, a system with reversibility and retention would be a static archive. Where all three are nonzero, selection can operate. It can sort variants, remove deleterious mutations, and transmit what remains. But this does not establish that the conditions under which selection operates are themselves being maintained. The second condition is *regime interiority*. Where ***R***, ***M***, and ***P*** are not merely nonzero but mutually sustaining, the conditions under which selection operates are themselves self-maintaining through the system's own organized activity (Fig. 1). The structure of this mutual sustenance is specific, and takes the form of a causal loop. ***R*** maintains the counterfactual availability of alternative organizational roles, which allows ***P***-driven reorganizations to remain internal to the regime rather than dissolving it. ***P*** generates structured responses to perturbation that feed into ***M***, because the system's reorganizations under challenge become part of what is retained. ***M*** reshapes the transition space in ways that preserve ***R***, because accumulated constraint maintains the repertoire of roles through which the system can reorganize. The three conditions close on each other, and when they close reciprocally, the regime becomes self-maintaining through turnover (Fig. 1).

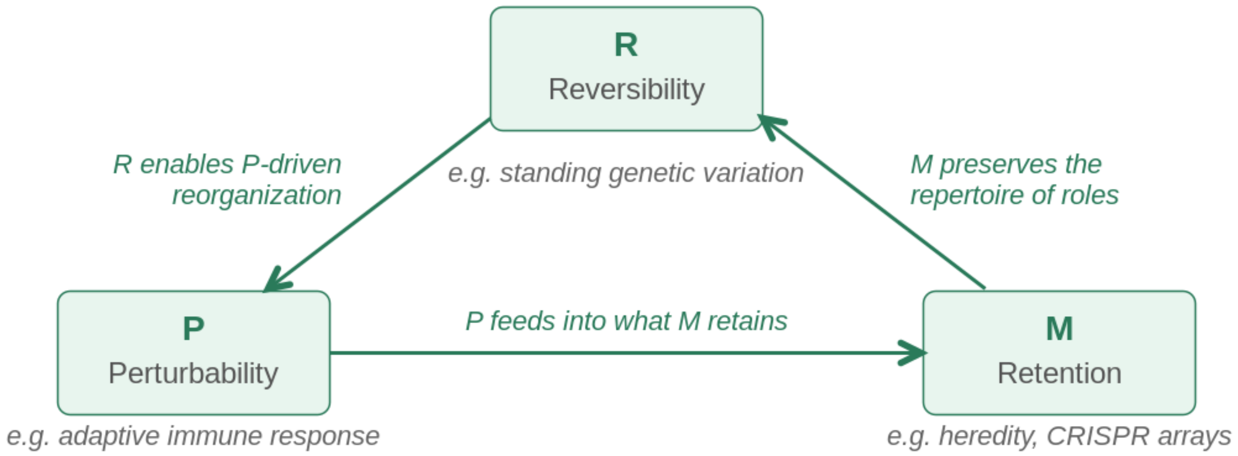

Fig. 1 The causal loop defining *regime interiority*. Reversibility (***R***) enables perturbability-driven reorganizations to remain internal to the regime. Perturbability (***P***) generates structured responses that feed into what retention (***M***) carries forward. Retention preserves the repertoire of organizational roles through which the system can reorganize, completing the loop. When ***R***, ***M***, and ***P*** close reciprocally, the conditions under which selection operates are self-maintaining.

The distinction between these two conditions is what the framework diagnoses. A system in which ***R***, ***M***, and ***P*** are all nonzero but vary independently, each degrading on its own trajectory without affecting the others, satisfies the first condition but not the second. Selection operates, but on an eroding substrate. It consumes its own prerequisites. What is absent in such a system is not any individual condition but the closure among the conditions. *Regime interiority* is therefore a higher-order organizational closure, a closure of the conditions that diagnose closure. Section 4 provides detailed empirical evidence for this distinction.

This higher-order closure is analyzable rather than primitive. Mutual sustenance has a specific empirical signature. Perturbation of any one criterion elicits compensatory response in at least one other, producing dependent covariance among ***R***, ***M***, and ***P***. Where mutual sustenance is absent, the criteria vary independently. The distinction between dependent and independent covariance is testable using standard multivariate methods, as discussed in Section 4.3. *Regime interiority* can be formally stated as:

Regime interiority is present in a system when and only when

*(1) reversibility (**R**), retention (**M**), and perturbability (**P**) are each nonzero, indicating departure from the null condition,*

and

(2) ***R****,* ***M****, and* ***P*** *are mutually sustaining, each contributing to the persistence of the others across turnover.* *The first condition is necessary for selection to operate. The second is necessary for the conditions under which selection operates to be self-maintaining.*

A natural concern is that ***R***, ***M***, and ***P*** simply restate properties already captured by constraint closure in a different vocabulary (*cf.* Montévil and Mossio 2015). They do not, though the distinction requires care. ***R*** introduces something genuinely absent from the closure tradition, namely the counterfactual availability of alternative organizational configurations. ***M*** goes beyond the cyclic regeneration that closure requires by asking whether a system accumulates constraint from its history. ***P*** draws on the concept of regulation but converts it from a characterization of what the capacity is into a diagnostic for whether it is present. The relationship between the two frameworks is that ***R***, ***M***, and ***P*** operationalize the question of whether the closure that Moreno and Mossio characterize is in fact being sustained by a given system's own organized activity, a question their framework raises but does not provide the tools to answer.

R, ***M***, and ***P*** do not restate variation, heredity, and differential fitness. Those describe distributions of variants and their transmission within an already established regime. The present criteria diagnose whether such a regime exists and is being sustained. Reversibility concerns the counterfactual availability of alternative organizational roles, not the presence of phenotypic variation. Retention concerns whether past transitions durably restructure future possibilities, not merely whether traits are inherited. Perturbability concerns whether perturbations elicit internal reorganization that preserves the regime, not whether some variants leave more offspring than others. The distinction is therefore between conditions for selection and the outcomes selection produces.

Section 3.2. The Null Condition

Establishing that ***R***, ***M***, and ***P*** are jointly satisfied requires a baseline specification of what dynamics look like when *regime interiority* is absent. Without such a baseline, attributing *regime interiority* risks becoming an exercise in redescription, where any sufficiently complex system is declared to possess it because the observer sees organizational features worth naming (*cf.* Cusimano and Sterner 2020).

Under the *null condition*, a system's future transitions are fully determined by its current state and external inputs, with no system-generated constraints carried forward as part of the transition structure itself. The austerity of this definition is deliberate. The *null condition* specifies the absence of retained internal references across transitions, not the absence of activity, complexity, or organization. Systems that satisfy the *null condition* may be stable, regulated, and indispensable to organismal or ecological function. What they lack is internal ownership of their transitions. Under the *null condition*, regulation restores predefined state variables rather than preserving a history-dependent space of alternative future roles. Perturbation of a system that conforms to the *null condition* either shifts parameters within the same dynamics or exceeds tolerance and results in system failure. The system does not reorganize.

Deviation from the *null condition* is assessed by examining whether ***R***, ***M***, and ***P*** are jointly satisfied at the organizational level under investigation. The conditions defined in Section 3.1 translate into three diagnostic questions. For ***R***: do prior organizational roles remain counterfactually available across component turnover? For ***M***: do past transitions continue to constrain present dynamics in a way that persists through turnover, rather than being erased when conditions normalize? For ***P***: do perturbations elicit internal reorganization that preserves organizational unity, rather than passive absorption or dissolution?

These questions do not require the introduction of novel observables. They formalize distinctions that biologists already make implicitly when they distinguish adaptive reorganization from degradation, lineage continuity from mere survival, and regulated persistence from passive equilibrium. The questions can be addressed using existing experimental, ecological, genetic, and comparative data by examining how systems respond to disturbance, turnover, and variation. Any assessment of *regime interiority* will therefore be composite, comparative, and system-specific rather than derived from a universal formula. The framework specifies what must be established for attribution of *regime interiority* to be warranted.

Glycolysis illustrates what this looks like in biological terms. Glycolysis responds to perturbation through mass-action kinetics. When ATP is consumed, ADP concentration rises and flux accelerates. But the constraints governing this response, enzyme kinetics and substrate affinities, are not themselves regenerated by the pathway and do not accumulate organizational history. Glycolysis does not carry forward constraint from past perturbations in a way that reshapes what future transitions are available. It fails ***M***. Nor does it reorganize under perturbation in a way that preserves organizational unity through novel configurations; it absorbs perturbation or collapses. It fails ***P***. The pathway is biologically essential and thermodynamically sophisticated, but it satisfies the *null condition*. Describing it as lacking *regime interiority* is not a judgment of importance but a diagnostic finding about the appropriate kind of explanation. Selection-based explanation does not apply to glycolytic flux at the level of the pathway's own dynamics.

A candle flame provides a complementary test from outside of biology. Cusimano and Sterner (2020) showed that a candle flame can be redescribed to satisfy the formal definition of organizational closure. By merging certain chemical processes into a single constraint, the indirect dependency relations become direct, and closure obtains. Their point is that closure attribution depends on how the investigator carves up the causal structure. The flame case is therefore a direct challenge to any framework that relies on closure alone. Diagnosed against ***R***, ***M***, and ***P***, however, the flame fails decisively regardless of how its constraint network is described. Retention is absent. Past flame configurations do not constrain future transitions in a role-preserving way. A flame that has burned for an hour is organizationally indistinguishable from one that has burned for a minute. Reversibility is absent. Extinguished configurations are not retained as available organizational roles. Perturbability fails in any diagnostic sense. Perturbations alter flame shape or intensity, but do not elicit reorganization that preserves a structured transition space. The flame either adjusts parametrically to current boundary conditions or extinguishes. It does not carry forward a history that shapes future possibilities. The *null condition* therefore resolves the ambiguity that Cusimano and Sterner identified. Formal closure may be redescription-dependent, but the diagnostic criteria are not.

The logic of the *null condition* parallels, in a restricted but important sense, the role played by the Hardy-Weinberg principle in population genetics. In the absence of selection, mutation, migration, and drift, allele frequencies remain stable across generations. Deviations from this equilibrium do not imply purpose or direction; they indicate the presence of additional forces. Selection is not inferred because populations "try" to adapt, but because distributions fail to remain invariant under known conditions (Hardy 1908; Weinberg 1908; Kimura 1968; King and Jukes 1969). The *null condition* introduced here follows the same diagnostic logic, specifying conditions under which attribution of *regime interiority* is unwarranted. The parallel is in structure of inference, not in the mathematics. Hardy-Weinberg makes precise quantitative predictions about allele frequency distributions; the *null condition* does not. It does not predict the trajectory of a system lacking *regime interiority*, any more than Lewontin's (1970) conditions for selection predict the trajectory of populations that satisfy them. What it provides is an explicit diagnostic baseline that makes attribution principled rather than *ad hoc*, something the closure tradition has not provided (Moreno and Mossio 2015, p. 145, n. 4). The parallel is limited, however. Hardy-Weinberg diagnoses the absence of evolutionary forces within a population whose coherence is already established (Sober 1984). The *null condition* developed here asks a logically prior question, whether any unified transition structure exists at all. It addresses what Hardy-Weinberg takes as already answered.

One further clarification concerns organizational level. The diagnostic applies at whatever level of organization is under investigation. A population, an organism, a cell lineage, and an immune repertoire may each be assessed for *regime interiority* at their respective levels, and the answer need not be the same at every level. An individual organism may exhibit *regime interiority* at the organismal level while being part of a population that has lost it at the population-level. The diagnostic criteria are the same at every level, ***R***, ***M***, and ***P***, but what counts as a "transition," a "role," and a "perturbation" will differ depending on the organizational level at which the question is posed. The material mechanisms differ. The diagnostic structure does not.

Section 3.3. Relationship to Existing Frameworks

With the full diagnostic apparatus now in place, the relationship between the three frameworks can be stated precisely. Each addresses a distinct question. Moreno and Mossio (2015) answer a constitutive question. *What must a system be for it to count as autonomously organized?* Their framework specifies the architecture of mutual constraint dependency that defines autonomy, and argues (chapter 5) that this architecture must precede natural selection rather than being its product. Godfrey-Smith (2009) answers a grading question. *Given that a population is Darwinian, how Darwinian is it?* His parameter space allows populations to be located along a continuum from marginal to paradigm cases. The present framework answers a threshold question, one that is logically prior to Godfrey-Smith's and diagnostically downstream of Moreno and Mossio's. *Does a given system currently sustain the structural conditions under which selection-based explanation is applicable at all?* This is neither a question about what a system must be nor about how well a Darwinian population performs. It is a question about whether the threshold has been crossed, in either direction.

To see why this third question is needed, consider first what the closure tradition can and cannot provide. It operates at the level of the individual organism and its constitutive constraints. Rosen's β function, which Letelier and colleagues (2006) interpret as "organizational invariance," captures part of what is needed here, namely that something must persist that ensures the regeneration of the system's functional organization. But the closure network loops; retention accumulates. Each organism in a population may be individually intact, with closure holding at the organismal level. But the question of whether a collection of organisms retains the structural conditions under which selection can do adaptive work is not a question the closure framework addresses.

Now consider the same question from the Darwinian population side. Take any small, isolated population undergoing mutational meltdown (Lynch *et al*. 1993; Gabriel *et al*. 1993). Such a population qualifies as a Darwinian population and can be located in Godfrey-Smith's parameter space. *V* (abundance of variation) is not low, because deleterious mutations are generating abundant variation. *H* (fidelity of heredity) remains high, because heredity faithfully transmits what it has, including accumulating load. *S* (dependence of reproductive differences on intrinsic character) is locally nonzero, because purifying selection is still removing the worst variants. *C* (continuity between phenotypic variation and fitness variation) may be unchanged. The population scores adequately on every parameter. But genetic diversity has been irreversibly lost, and deleterious mutations are accumulating faster than selection can purge them (Muller 1964; Felsenstein 1974). What heredity carries forward is increasingly genetic load rather than organizational constraint. Selection is running, but it is running on an eroding substrate. The parameters describe what selection is currently doing. They do not diagnose whether the structural conditions sustaining selection's effectiveness remain intact.

Regime interiority provides the diagnostic link between the two. It asks whether the organizational closure that Moreno and Mossio characterize is currently being sustained at the level of organization under investigation, and whether the structural conditions under which Godfrey-Smith's parameters become explanatorily consequential are met. The three frameworks are complementary. The closure tradition specifies what it means to be self-maintaining through mutual constraint dependency. The Darwinian population framework characterizes evolutionary dynamics once selection-based explanation already applies. *Regime interiority* provides the diagnostic threshold between them, specifying when a system enters or exits that domain.

Although the *regime interiority* threshold is categorical, the framework introduces a three-category distinction within the space of biological systems that clarifies where that threshold falls (Fig. 2). The regimes are defined structurally, by the configuration of ***R***, ***M***, and ***P***, not by evolutionary outcomes. Under the *null condition* no unified transition structure exists to carry variants forward across time. ***R***, ***M***, and ***P*** are each zero because there is no organized transition structure from which they could arise. Selection is inapplicable, not because it is weak, but because there is no regime on which it could operate. Between the *null condition* and *regime interiority* lies a structural category that this paper calls the *minimal Darwinian regime* (Fig. 2). Under the *minimal Darwinian regime*, a minimal Darwinian population exists in the sense analyzed by Godfrey-Smith (2009). A collection of causally connected individual things exhibits variation, heredity, and differential reproduction. ***R***, ***M***, and ***P*** may each be nonzero, because the population retains some reversibility, some retention, and some perturbation response. But the criteria are not mutually sustaining. Each may degrade or persist on its own trajectory without eliciting compensatory response in the others. *Regime interiority* is absent. The meltdown case described above is precisely such a population. It scores adequately on every Darwinian parameter while the diagnostic criteria degrade independently, with erosion in one failing to elicit compensation in the others. Selection operates under the *minimal Darwinian regime*, but on an eroding substrate. Purifying selection may continue to remove the worst variants, drift may sort among the rest, and heredity faithfully transmits what remains. But the structural conditions that would sustain selection's capacity to do adaptive work are not being maintained through the system's own organized activity. In the terms of the formal definition stated above, the minimal Darwinian regime satisfies condition (1) but not condition (2).

Where *regime interiority* is present, ***R***, ***M***, and ***P*** are not merely simultaneously nonzero but mutually sustaining. Each criterion supports the conditions under which the others persist, so that perturbation of one elicits compensatory responses in the others rather than independent decline. *Regime interiority* is present. The distinction between the *minimal Darwinian regime* and *regime interiority* is categorical. Either the criteria are in a mutually sustaining configuration or they are not. This is a structural threshold, not a graded continuum, because mutual sustenance is itself a closure, a higher-order organizational property that either obtains or does not. The threshold is categorical in structure, not in the underlying variables, which vary continuously. But because each criterion varies continuously, the distinction is in principle empirically testable. Mutual sustenance predicts dependent covariance among ***R***, ***M***, and ***P***, while independent degradation predicts that the criteria vary independently of one another. Section 4 illustrates this distinction empirically; the development of formal statistical tests is a task for future work. The threshold therefore separates the *minimal Darwinian regime* from *regime interiority*. The *null condition* and *the minimal Darwinian regime* both lack *regime interiority*, for different structural reasons. Under the *null condition*, there is no transition structure to diagnose. Under the *minimal Darwinian regime*, the transition structure exists but is not self-maintaining. Godfrey-Smith's parameters describe what selection is doing under both the *minimal Darwinian regime* and *regime interiority*. The three-category distinction specifies the structural conditions under which selection can be sustained (Fig. 2).

Fig. 2 The three-category distinction and two diagnostic thresholds. Under the *null condition*, ***R***, ***M***, and ***P*** are zero and selection is inapplicable. Under the *minimal Darwinian regime*, ***R***, ***M***, and ***P*** are each non-zero but not mutually sustaining; selection operates on an eroding substrate. Where *regime interiority* is present, ***R***, ***M***, and ***P*** are mutually sustaining and the conditions under which selection operates are self-maintaining. Threshold 1 marks departure from the *null condition*. Threshold 2 marks the onset of *regime interiority*.

Existing frameworks can describe loss of variation, accumulation of genetic load, or reduced fitness, and can track how selection operates under such conditions. What they do not provide is a criterion for distinguishing whether these changes occur within a regime in which selection-based explanation remains applicable, or reflect the erosion of the regime that makes such explanation meaningful in the first place. The distinction matters because the same population-genetic signatures, reduced heterozygosity, elevated load, continued purifying selection, can arise in both cases. Because population-genetic parameters alone do not draw this distinction, the present framework introduces a diagnostic layer that complements, rather than competes with, existing accounts.

Section 4. Diagnosing *Regime Interiority*: Case Studies

The preceding section specified three diagnostic criteria whose joint closure indicates *regime interiority*, developed a null condition against which that closure can be diagnosed, and distinguished three structural categories bearing different relationships to selection-based explanation. This section applies the diagnostic to populations whose genomic histories are thoroughly documented, permitting ***R***, ***M***, and ***P*** to be assessed against specific empirical evidence rather than schematic descriptions. The cases are not presented as definitive tests, but as empirically grounded demonstrations of how the diagnostic organizes existing evidence. Their role is to render the structural distinction empirically legible rather than to establish its generality. Throughout this section, "independent degradation" means that decline in one criterion does not elicit compensatory response in the others, regardless of whether the criteria share a common upstream cause such as demographic restriction. Section 4.1 examines Wrangel Island mammoths as a case of progressive regime collapse, in which each diagnostic criterion degraded independently and the population fell from *regime interiority* to the *minimal Darwinian regime* while remaining a Darwinian population. Section 4.2 examines cheetahs as a case of attenuated but preserved *regime interiority*, in which the diagnostic criteria remained mutually sustaining despite severe demographic restriction. Section 4.3 addresses what the diagnostic adds beyond what population-genetic methods already provide.

Section 4.1. Regime Collapse: Wrangel Island Mammoths

The Wrangel Island mammoth case illustrates what happens when the conditions required for *regime interiority* progressively fail. The case is diagnostic because the population continued to exist demographically for thousands of years after the conditions for *regime interiority* had begun to erode, demonstrating that genealogical persistence and regime persistence are distinct.

Following post-glacial isolation approximately 10,000 years before present (ybp), a relict population of woolly mammoths (*Mammuthus primigenius*) persisted on Wrangel Island, an Arctic landmass off the northeast coast of Siberia, for approximately six millennia before going extinct around 4,000 ybp (Vartanyan *et al*. 1993; Palkopoulou *et al*. 2015). The founding population consisted of as few as eight individuals, though it recovered to an estimated 200–300 within approximately 20 generations and remained demographically stable throughout its subsequent history (Dehasque *et al*. 2024). Genomic analyses of Wrangel Island mammoth remains reveal progressive accumulation of deleterious mutations affecting olfactory receptors, sperm development, insulin signaling, coat morphology, and immune function, accompanied by elevated inbreeding and widespread loss of heterozygosity (Rogers and Slatkin 2017). A subsequent temporal genomic analysis complicates but does not overturn this picture. Dehasque and coworkers (2024) showed that while mildly deleterious mutations accumulated gradually throughout the island period, highly deleterious mutations were purged. Purifying selection continued to operate against the most severe variants. The authors concluded that the population's extinction was unlikely to have been caused by genomic erosion alone, since no decline in population size was detected prior to extinction. This mixed pattern of continued purging alongside gradual accumulation of mildly deleterious variants is precisely the kind of case the three-category distinction is designed to address. The question for the present framework is not whether any selection occurred, but whether the structural conditions for selection to do adaptive work remained intact.

Reversibility (***R***) was progressively lost. The founding bottleneck represented a 43-fold reduction in effective population size relative to mainland populations (Rogers and Slatkin 2017). Post-glacial sea level rise eliminated any possibility of gene flow from the mainland (Vartanyan *et al*. 1993). Palkopoulou and coworkers (2015) found a 20 percent reduction in heterozygosity relative to a mainland specimen, accompanied by a 28-fold increase in runs of homozygosity. At the major histocompatibility complex (MHC) class DQA locus, mean allelic diversity was 37 percent lower than on the mainland, and coalescent simulations found no evidence that balancing selection had maintained diversity during the final six millennia (Pečnerová *et al*. 2016). Rogers and Slatkin (2017) identified 819 premature stop codons in the island genome compared to 503 in a mainland specimen, including pseudogenization of 85 olfactory receptor genes and 3 vomeronasal receptor genes. Lynch and coworkers (2015) confirmed loss of function in mammoth genes associated with development (HYLS1), male fertility (NKD1), metabolic regulation (NEUROG3), and olfaction (OR5A1) by expressing synthetic mammoth-specific variants in African elephant (*Loxodonta* africana) fibroblasts and frog (*Xenopus laevis)* embryos. Organizational roles that were counterfactually accessible for mainland populations were irreversibly foreclosed, with no mechanism for recovery. This loss did not elicit compensatory response in the population's retention or perturbation capacity; as the following paragraphs document, those criteria degraded on their own trajectories.

Retention (***M***) underwent a qualitative shift. In a functioning regime, heredity carries forward constraint that preserves alternative future possibilities. In the Wrangel Island population, what was increasingly carried forward was genetic load rather than organizational constraint. The 28-fold increase in runs of homozygosity indicates that inbreeding was being faithfully transmitted across generations, progressively converting masked deleterious load into realized load as heterozygous variants became homozygous (Dehasque *et al*. 2024). The functional consequences are visible in the systems documented by Lynch and coworkers (2015). The compromised male fertility, disrupted metabolic regulation, and developmental defects that they found were not transient injuries but heritable degradation carried forward through each generation. The population retained its history, but that history constrained future transitions by narrowing them rather than by preserving viable alternatives.

Perturbability (***P***) became increasingly terminal rather than regulative. The 37 percent reduction in MHC DQA allelic diversity (Pečnerová *et al*. 2016), combined with the absence of balancing selection maintaining immune diversity during the final six millennia, meant that the population's capacity to mount adaptive immune responses to novel pathogens was structurally diminished. That the population remained demographically stable for six millennia despite these accumulating compromises illustrates that a stable environment can sustain a population long after its capacity to reorganize under novel challenge has eroded.

The signature of the Wrangel case is that each diagnostic criterion degraded independently of the others. The progressive loss of reversibility did not elicit compensatory retention of organized constraint. Instead, ***M*** independently shifted from role-preserving to damage-accumulating. The shift in retention did not trigger reorganization of perturbation response; instead, ***P*** independently became terminal as the immune, reproductive, and developmental systems required for reorganization degraded on their own trajectories. The criteria were all nonzero throughout the island period, but they were not mutually sustaining. This is the structural signature of the *minimal Darwinian regime*. The population remained a minimal Darwinian population and could still be located in Godfrey-Smith's parameter space: *V* was not low (deleterious mutations generated abundant variation), *H* remained high (heredity faithfully transmitted what it had, including accumulating load), *S* was locally nonzero (purifying selection continued to remove the worst variants). But the structural conditions that define *regime interiority* had eroded. Regime collapse preceded demographic extinction by hundreds of generations.

Section 4.2. Attenuated Regime Interiority: Cheetah Population Bottleneck

In contrast to Wrangel Island mammoths, cheetahs (*Acinonyx jubatus*) illustrate a population that experienced comparable demographic restriction but did not cross the threshold from *regime interiority* to the *minimal Darwinian regime*. The diagnostic question is what structural difference accounts for the divergent outcomes.

The well-documented bottleneck experienced by modern cheetahs resulted in extreme loss of genetic diversity across two successive events approximately 100,000 and 10,000-12,000 ybp (O'Brien *et al*. 1983; Menotti-Raymond and O'Brien 1993; Dobrynin *et al*. 2015). MHC diversity collapsed to near-uniformity, to the point that unrelated individuals accept reciprocal skin grafts (O'Brien *et al*. 1985). Approximately 70 percent of spermatozoa are morphologically abnormal across the species (Wildt *et al*. 1993), and genome-wide heterozygosity is among the lowest of any large felid (Prost *et al*. 2022). Despite this impoverishment, the cheetah population did not follow the trajectory diagnosed in the mammoth case.

Reversibility (***R***) persists in attenuated form. Many organizational roles associated with alternative MHC haplotypes have been permanently eliminated and cannot be recovered through recombination or standing variation. However, the picture is not one of simple loss. Castro-Prieto and coworkers (2011) detected 10 MHC class I alleles across 4 putative loci in 149 Namibian cheetahs, more than earlier small-sample studies had found, and positive selection was detected at both class I and class II loci, indicating that what diversity remains is actively maintained. Cheetahs also compensate for reduced adaptive immune breadth through constitutive innate immunity. In bacterial killing assays across six sympatric free-ranging carnivore species, cheetahs showed the highest killing capacity, at least an order of magnitude above the caniform jackal (*Lupulella mesomelas*; Heinrich *et al*. 2016). Diagnosed through the framework, this compensatory innate channel constitutes an alternative route through which immune function remains accessible even though the MHC-mediated adaptive route has narrowed.

Retention (***M***) continues to carry constraint forward in a role-preserving manner rather than accumulating damage. The cheetah genome is 93 percent homozygous and carries 90 percent fewer single-nucleotide variants than comparable mammals (Dobrynin *et al*. 2015), and this genetic impoverishment reflects bottlenecks after which coalescent demographic analysis indicates population expansion rather than continued decline. Positive selection was detected across close to 1,000 genes, with 11 candidate genes showing strong signatures in muscle contraction, stress response, and catabolic regulation (Dobrynin *et al*. 2015). Those results indicated that deleterious alleles have been purged rather than allowed to accumulate. What heredity carries forward in the cheetah is reduced but operative functional constraint, not damage that compounds across generations.

Perturbability (***P***) remains operative but fragile, and this is where the empirical uncertainty concentrates. Free-ranging cheetahs absorb familiar pathogenic challenges without regime disruption (Munson *et al*. 2008; Thalwitzer *et al*. 2010). But when a feline coronavirus was introduced to the Wildlife Safari breeding facility in Oregon in 1982, all 60 cheetahs seroconverted within six months, 90 percent developed disease, and 60 percent died within two years (Heeney *et al*. 1990). In domestic cats the same virus causes fatal disease in only 5 to 10 percent of infected individuals, and lions housed in the same facility were infected simultaneously but did not succumb (Pearks Wilkerson *et al*. 2004). The outbreak identifies the boundary of the compensatory innate channel diagnosed above under ***R***. The regime can reorganize around perturbations that fall within its narrowed range, but perturbations that overwhelm innate compensation expose the absence of MHC-mediated adaptive breadth and may prove irreversible.

The signature of the cheetah case is that the diagnostic criteria are mutually sustaining despite their attenuation. When ***R*** narrowed through loss of MHC diversity, the population did not simply lose perturbability as the mammoths did.

Instead, constitutive innate immunity compensated, maintaining ***P*** through an alternative route where the primary route had narrowed. The regime's perturbation response co-varied with its reversibility structure rather than degrading independently. Retention continued to carry forward organized constraint that had been shaped by active purifying selection, maintaining the functional architecture on which both ***R*** and ***P*** depend. The criteria are diminished, but they form a mutually sustaining configuration that supports the conditions under which the others persist. This is the structural signature of *regime interiority*, attenuated but intact. The population continues to sustain its transitions through its own organized activity, but the transition space within which those transitions occur has narrowed, and the compensatory mechanisms that sustain current function may not generalize to novel challenges.

Section 4.3. What the Diagnostic Adds

The mammoth and cheetah cases raise an obvious question: if the diagnosis depends on genomic data, and population genetics already provides methods for interpreting that data, then what does the ***R***, ***M***, ***P*** framework contribute? Consider the two cases as population genetics would encounter them. The Wrangel Island mammoth population experienced a 43-fold reduction in effective population size, a 20 percent decline in heterozygosity, a 28-fold increase in runs of homozygosity, and 63 percent more premature stop codons than documented in a mainland specimen (Rogers and Slatkin 2017; Palkopoulou *et al*. 2015; Pečnerová *et al*. 2016). Purifying selection continued, and the population remained demographically stable for six millennia (Dehasque *et al*. 2024). The cheetah population experienced two severe bottlenecks, MHC collapse to near-uniformity, 70 percent sperm abnormality, and genome-wide heterozygosity among the lowest of any large felid (O'Brien *et al*. 1983; Dobrynin *et al*. 2015; Wildt *et al*. 1993; Prost *et al*. 2022). Positive selection on muscle contraction and stress metabolism genes was detected, and free-ranging populations show robust health (Dobrynin *et al*. 2015; Munson *et al*. 2008; Thalwitzer *et al*. 2010). Population-genetic methods characterize both cases with precision. But the structural significance of that impoverishment, whether the population has stabilized at a reduced but self-maintaining level or entered a trajectory where the conditions for selection are themselves degrading, is not a question the metrics themselves are designed to answer.

R, ***M***, and ***P*** ask different questions of the same data. Applied to the mammoth and cheetah evidence, they yield structurally different diagnoses that correspond to different regimes (Fig. 3). In the mammoth, the three criteria degraded independently. Organizational roles were irreversibly foreclosed without compensatory retention of organized constraint, and perturbation became terminal without eliciting reorganization. This is the *minimal Darwinian regime*. In the cheetah, the criteria co-varied. Narrowing of reversibility elicited compensatory perturbation response through innate immunity, and retention continued to carry forward functional constraint shaped by active selection. This is *regime interiority*. Two populations with comparably reduced heterozygosity occupy different sides of the boundary between the *minimal Darwinian regime* and *regime interiority*, and the framework identifies which side each occupies.

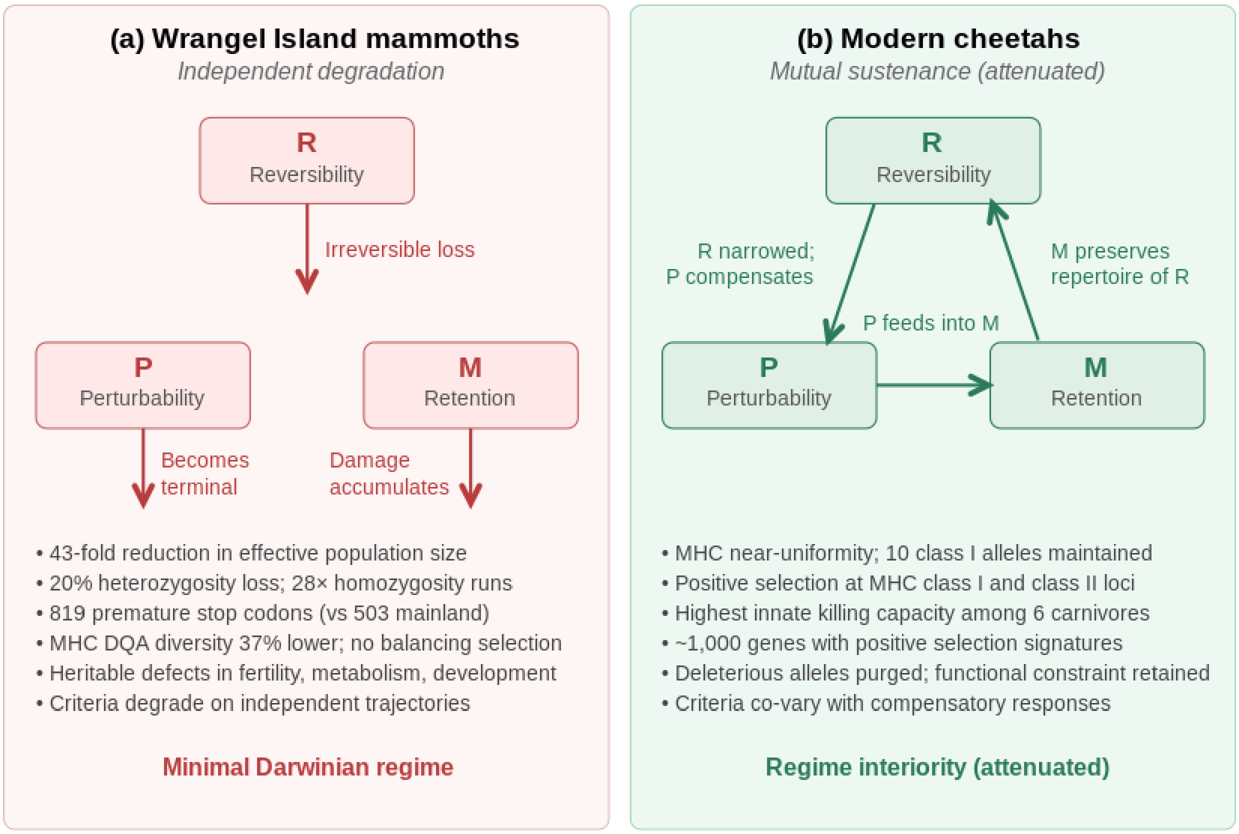

Fig. 3 Diagnostic comparison of two populations with comparably reduced genetic diversity. (a) Wrangel Island mammoths: ***R***, ***M***, and ***P*** each degrade on independent trajectories with no compensatory response among them. The population occupies the *minimal Darwinian regime*. (b) Modern cheetahs: ***R***, ***M***, and ***P*** form a mutually sustaining loop. Narrowing of ***R*** elicits compensatory response in ***P***; ***P*** feeds into what ***M*** retains; ***M*** preserves the repertoire of roles available to ***R***. The population retains *regime interiority*, though attenuated. Key empirical findings supporting each diagnosis are listed below the diagrams.

The distinction is not merely qualitative. Because ***R***, ***M***, and ***P*** are continuous variables, the difference between mutual sustenance and independent degradation is in principle empirically testable. Mutual sustenance predicts dependent covariance among the criteria, while independent degradation predicts that they vary on their own trajectories. The development of formal statistical tests for this dependence structure is a task for future work. The statistical methods required, including partial correlations, mutual information measures, and covariance structure tests, are standard tools of multivariate analysis (Lande and Arnold 1983). What is novel is the question. Neither multivariate quantitative genetics nor population viability analysis asks whether the structural conditions for selection are themselves in a mutually sustaining or independently degrading configuration. Operationalizing this test requires quantifying ***R***, ***M***, and ***P*** as continuous variables. The case studies presented here demonstrate which existing empirical measures bear on each criterion; the development of formal quantification procedures, particularly in experimental systems where the relevant variables can be directly manipulated, is a companion objective.

The regimes connect directly to the frameworks established in Section 2. Godfrey-Smith's parameters describe what selection is doing. The three-category distinction specifies the structural conditions under which what it is doing can be sustained. Under the *minimal Darwinian regime*, the parameters remain applicable but are increasingly hollow. In Thompson's (2007) terms, the distinction is between operational and organizational closure. Population-genetic methods track operational closure: the continuation of processes such as reproduction, selection, and drift. ***R***, ***M***, and ***P*** diagnose organizational closure: the persistence of the relational structure that defines which roles are available and which constraints preserve which other constraints. The *regime interiority* framework does not replace or compete with population-genetic analysis. It depends on it. What ***R***, ***M***, and ***P*** provide is a set of structurally specific questions that organize genomic evidence into a diagnosis of regime status, distinguishing cases where selection can still do adaptive work from cases where the structural conditions for selection have themselves eroded.

Section 5. Objections and Clarifications

The preceding section illustrated the three-category distinction empirically, using two population-level cases where severe demographic restriction produced diagnostically distinct outcomes. The framework as presented invites several objections. This section addresses three. First, that *regime interiority* merely redescribes natural selection using unfamiliar terminology (Section 5.1). Second, that the language of "ownership" and "organized transitions" imports cognition or teleology (Section 5.2). Third, that the distinction between regime-preserving and regime-dissolving transitions introduces evaluative normativity (Section 5.3).

Section 5.1. Regime Interiority is not Selection Redescribed

The most immediate objection from biologists is likely to be that reversibility (***R***), retention (***M***), and perturbability (***P***) merely redescribe variation, inheritance, and differential survival using unfamiliar terminology, and that *regime interiority* therefore collapses into selection "all the way down." This reading places the explanatory order differently. Natural selection presupposes the existence of entities whose transitions belong to a unified regime. Selection does not explain how such unity arises; it operates only once unity is already present. *Regime interiority* therefore occupies a logically prior position. It identifies the structural conditions that must hold for selection-based explanation to be applicable, rather than redescribing what selection does once those conditions are met. The Wrangel Island mammoth case (Section 4.1) makes this clear. Throughout the island period, selection was running. Purifying selection removed catastrophic variants, deleterious mutations generated variation for selection to act on, heredity faithfully transmitted what it had. The population scored adequately on every Darwinian parameter. Yet the structural substrate on which selection depends was progressively eroding. ***R***, ***M***, and ***P*** were degrading independently rather than sustaining one another. The framework did not redescribe the selection that was occurring. It diagnosed that the conditions under which selection could do adaptive work had deteriorated, a determination that the selection-based description alone could not deliver. Selection is one mechanism through which *regime interiority* is sustained at the population level, but the framework diagnoses structural conditions, not the mechanisms that maintain them.

Section 5.2. Regime Interiority is not Cognition, teleology, or Goal-Directedness

The language of "ownership" and "organized transitions" may invite the impression that *regime interiority* attributes awareness, purpose, or goal-directed behavior to biological systems. It does not. *Regime interiority* is a structural condition diagnosed by deviation from the *null condition*. A system either sustains organizational closure through its own transitions or it does not. No appeal is made to what a system "intends," "knows," or "aims at." The diagnostic criteria, ***R***, ***M***, and ***P***, are assessed through empirical measures of the kind documented in Section 4, not through ascriptions of agency or purpose.

Section 5.3. Normativity Without Norms

The framework relies on a distinction between transitions that preserve regime unity and transitions that dissolve it. This distinction may appear to import evaluative normativity, as though the system follows norms or pursues goals. The normativity involved is strictly structural. Once ***R***, ***M***, and ***P*** jointly close, a boundary between regime-preserving and regime-dissolving transitions necessarily exists, enforced by the system's own organization. But the system does not classify transitions as acceptable or unacceptable. It does not sort them, evaluate them, or direct itself toward preferred outcomes. What happens is that the system's own architecture makes certain trajectories structurally incompatible with that architecture's continued existence. Collapse becomes a distinct event rather than merely another state, not because the system recognizes it as such, but because the relational structure that defines the regime cannot persist through those particular transitions. The analogy is to the spandrels of San Marco in Gould and Lewontin's (1979) analysis. Once you mount a dome on rounded arches, spandrels necessarily exist, but they are not designed features. Joint closure similarly generates a boundary between viable and not-viable transitions as a structural byproduct, not as a goal. Under the *null condition*, no such boundary exists. All transitions are equivalent in kind. A chemical reaction that proceeds to equilibrium does not fail. Normativity in the sense employed here arises only when the *null condition* is escaped and the system's architecture makes certain trajectories untenable as continuations of the same regime. This form of normativity is immanent rather than imposed (Moreno and Mossio 2015), and does not require external evaluation, semantic interpretation, or representation of future states.

None of these objections undermines the framework's central claim. *Regime interiority* diagnoses structural conditions for selection-based explanation, not selection itself, not cognition, and not evaluative norms. The concluding section summarizes what has been established and identifies the empirical work that remains.

Section 6. Conclusion

This paper began from a simple observation. If organizational closure must precede natural selection, then selection-based explanation has structural prerequisites that can be present or absent. The *regime interiority* framework provides a diagnostic for determining whether those prerequisites currently hold. The *null condition* specifies the baseline. Three criteria, reversibility (***R***), retention (***M***), and perturbability (***P***), must each be nonzero for selection to operate and must be mutually sustaining for the conditions under which selection operates to be self-maintaining. The Wrangel Island mammoth and cheetah cases demonstrate that populations with comparably reduced genetic diversity can occupy different sides of this threshold, a distinction that population-genetic metrics alone do not draw.

The diagnostic bears on questions beyond the two cases examined here. Conservation biology routinely distinguishes threatened from viable populations using genetic metrics, but the structural distinction between populations that have stabilized at reduced diversity and populations whose conditions for selection are actively eroding currently depends on expert interpretation rather than a systematic diagnostic. Evolutionary transitions research asks when a new level of organization becomes a unit of selection, a question that requires diagnosing whether Darwinian properties at that level are externally scaffolded or internally sustained. The framework provides operational criteria for drawing these distinctions.

Several empirical tasks remain. Formal quantification of ***R***, ***M***, and ***P*** as continuous variables has not been attempted. The central empirical prediction, that mutual sustenance produces dependent covariance among the criteria while independent degradation produces independent variation, is testable using standard multivariate methods, but the development of specific statistical protocols is a companion objective not undertaken here.

The *regime interiority* framework does not replace existing approaches but isolates a specific diagnostic question that they leave open. Natural selection is not in question. What is in question is how to determine when the conditions for its explanatory applicability are met.

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