

Conserving Coherence Under Constraint

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Abstract

Organisms often respond to energy constraints, time pressure, or imminent threat by limiting behavioral options, lowering metabolic demands, and increasing their level of coordinated action. Although these responses can be framed as impairment, we argue they can be adaptive responses that occur as the costs of coordinating complexity exceed an organism's capabilities. As such, selection favors mechanisms that conserve the coherence of function by reducing control inputs and reorganizing coupling among remaining components. We propose these transitions share a diagnostic signature that encompasses reduced degrees of freedom, reorganized coupling, and stabilization of protected variables. This perspective generates testable predictions about threshold-driven emergency modes, asymmetric recovery, and anthropogenic disturbance driving functional simplification.

Keywords: adaptive simplification, energetic constraint, dormancy, torpor, collective behavior, tonic immobility, regime shift, coherence, dimensionality reduction

Key Terms Box

Conservation of coherence: when demand on an organism exceeds its coordination capacity, the organism maintains coherent function by reducing its degrees of freedom and tightening coordination among the remaining active components.

Coordination Capacity: the energetic, information processing/neural, and temporal resources available to an organism for coordinating its behavior at any given point in time.

Coupling: The strength of the interaction between components of a system. An organism maintains its coherence by increasing the connection between active components and decreasing or eliminating the connection to other less important components; thus, changing their stability and interdependence.

Degrees of freedom: the number of independent ways a system can vary. Effective degrees of freedom decrease under constraint as components become more tightly coupled.

Hysteresis: an asymmetry between entry and exit conditions, such that the demand or capacity required to enter a regime differs from that required to leave it.

Protected variables: variables maintained within a narrow range during a regime shift (e.g., body temperature, oxygen delivery, spatial position), often at the expense of other degrees of freedom.

Regime shift: a rapid, nonlinear transition between distinct states of organization. This transition is triggered when a system crosses a critical threshold.

When complexity is unaffordable

When constraints are low, flexibility can enhance fitness/performance. However, under constraints (e.g., food shortages, extreme environmental conditions and/or predation) many organisms will reduce complexity by adopting fixed behavioral patterns and/or becoming immobile (quiescent) or will become highly synchronized with one another (collective). New

tracking and machine-learning tools now make these shifts measurable across scales (Pereira et al. 2022).

Historically, simplification is often considered to be a dysfunction. However, across many biological systems, simplification in function can act as a regulated survival mechanism that allows organisms to remain viable near the boundaries of their functional capacities. The primary issue confronting an organism when functioning near the boundary of its functional capacity is maintaining coordination among components, not maximizing its operational complexity. Sampling the environment extensively when energy is very low can lead to starvation. Delaying response to an immediate threat can result in death. Therefore, the goal is to have enough coordination among the components of an organism to permit it to survive.

We refer to this pattern as the conservation of coherence (see Key Terms Box). When coordination capacity is limited, selection should favor mechanisms to preserve coordinated function and thereby limit the degrees of freedom that need to be managed at one time (even at the expense of flexibility). This affords a simple evolutionary prediction which can be applied to all levels of biological organization and across all taxonomic groups. When demands exceed capacity, biological systems will tend to simplify to maintain coherent function because incoherence can be acutely lethal.

Related frameworks

There are several other theoretical frameworks which have explored how organisms maintain stability and act under uncertainty as demand increases. Allostasis emphasizes regulated shifts in mediators or set points. These changes help organisms cope with acute challenges and support short term stability. However, repeated activation carries cumulative costs (McEwen and Wingfield 2003, Word et al. 2022). Robustness/resilience refers to how well an organism can buffer against disturbances and recover from them, often underscoring aspects such as modularity and redundancy (Kitano 2004, Crespi et al. 2021). Critical transition theory examines how nonlinear systems can shift abruptly between different states, including what triggers these shifts and what warning signs precede them (Scheffer et al. 2001, Scheffer et al. 2009, Dakos et al. 2024). Predictive Processing and the Free Energy Principle afford a complementary computational perspective on how organisms make perceptions and actions (framed as inference) based upon minimizing prediction errors (free energy) within specific limits (energetic and temporal) (Rao and Ballard 1999, Friston et al. 2010, Friston 2010a, Hodson et al. 2024). Box 1 shows how these concepts relate to the conservation of coherence and highlights its unique observable predictions.

Box 1: Related frameworks for stability and control under constraint

Box 1 compares conservation of coherence with related theories of stability and control under constraint.

Allostasis: describes how organisms regulate their stability through internal mediator and/or set point adjustments to meet varying demands. While these adjustment mechanisms can be beneficial in the short-term (e.g., allow an organism to survive), repeated activation of this type of regulation can result in an accumulation of physiological cost that is commonly referred to as allostatic load (McEwen and Wingfield 2003, Word et al. 2022).

Resilience and Robustness: focus on how systems remain functional and recover from disturbances. Robustness and resilience provide ways for systems to buffer, have redundant parts/modules, and be organized into modules so that when a component of the system fails it will only minimally affect the rest of the system, thus limiting the effects of perturbations (Kitano 2004, Crespi et al. 2021).

Critical Transition Theory: examines how nonlinear systems can transition between different states once certain thresholds have been reached. Early warning signals and hysteresis have been observed in some systems near transition points; illustrating the possibility of rapid changes in system states (Scheffer et al. 2001, Scheffer et al. 2009, Dakos et al. 2024).

Predictive Processing and the Free Energy Principle: considers both perception and action as forms of inference that are based on minimizing prediction error or free energy. Constraints such as time or energy will cause the system to favor less exploratory policy choices; therefore, the system will rely more heavily on prior experiences or habitual response mechanisms (Rao and Ballard 1999, Cohen et al. 2007, Friston et al. 2010, Friston 2010a, Meier et al. 2022, Hodson et al. 2024, Rae et al. 2024). While the FEP predicts reduced model complexity under constraint, it does not make specific predictions about the pattern of coupling reorganization among biological system components or about hysteresis in recovery at the organismal and group levels.

Conservation of Coherence: in contrast, provides for a capacity-demand trigger for the emergence of simplified patterns. It gives emphasis to observable coordination patterns, such as reduced dimensionality and coupling reorganization (tightening within an active subset alongside suppression/decoupling elsewhere), and stabilization of protected variables (Bernstein 1967, Bialek 2022). Unlike the above frameworks, conservation of coherence specifies a joint signature (dimensionality reduction together with coupling reorganization and variable protection) that can distinguish coherence-preserving simplification from mere behavioral suppression or general stress responses. In many cases, these patterns appear to be associated with hysteresis (Scheffer et al. 2001, Scheffer et al. 2009, Dakos et al. 2024).

When demand exceeds capacity

We do not suggest that there is only one mechanism of preserving coherence – whether through physical processes, neural control, or simple interaction rules. These examples represent convergent functional solutions shaped by similar constraints and thus are not examples of mechanistic homologies. The framework would be challenged if systems routinely remained complex after coordination limits were exceeded without a rise in coordination failures, or if simplification occurred without a detectable drop in degrees of freedom and a reorganization of coupling that stabilizes key interactions while others are suppressed. Importantly, conservation of coherence does not predict that all stress responses involve simplification; systems with sufficient reserve capacity, redundant modules, or low coordination costs may buffer perturbations without reducing dimensionality. Furthermore, a mere reduction in activity level without restructuring of component interactions would not constitute evidence for this framework.

The conservation of coherence framework adds a clear operational prediction to existing frameworks. Near switching points, there should be a reduction in effective degrees of freedom (behavioral, physiological, interactional) accompanied by a reorganization of coupling (tightening coordination within the remaining active components while other degrees of freedom are down-regulated or decoupled), and stabilization of key protected variables. This can occur even when energy savings are small and coordination or information processing is the main constraint (Bialek 2022).

The pattern of simplified, tightly coordinated behavior predicted by this framework can be seen in the collective escape behavior in starlings when under attack by peregrine falcons. Starlings will revert to a small number of coordinated escape modes (e.g., flash expansions, blackening, splits, waves). Whether these modes also involve moment-to-moment reductions in the dimensionality of individual trajectories remains an open and testable question (Storms et al. 2019). A direct test would track individual bird movements in three dimensions before and during predator attacks, then measure whether the flock's effective dimensionality drops as inter-individual coupling tightens.

Why coherence is important

We define coherence as the ability of functioning elements (e.g., cells, organs, behavioral components, or groups) to work together in real time in order to support continued function. Coherence is determined by relationships among parts (timing and coupling) and not by the performance of any single part in isolation. Biological robustness relies on decoupling and modularity to buffer against perturbation (Kitano 2004). In contrast, conserving coherence involves the opposite: reducing active components and increasing coupling among those that remain.

Coherence can be described in terms of degrees of freedom, defined as the number of semi-independent variables a system needs to coordinate to function effectively. While higher degrees of freedom may afford more complex and flexible performance, they also require more sensors, computation, and control (Bernstein 1967, Bialek 2022). This challenge is formally recognized in motor coordination research as the degrees of freedom problem (Morasso 2022), where biological systems routinely reduce effective dimensionality through functional coupling of components to achieve reliable performance under constraint (Latash 2024). The degree of coherence is reflected in the data by changes in the dimensionality of an organism's behavior such as its postural movements, movement patterns, or interaction patterns (Bialek 2022) (see Box 2).

Box 2: A diagnostic checklist for identifying coherence-preserving regime shifts

Box 2 outlines the process for identifying regime shifts based on analyzing the levels of complexity and coordination close to threshold values.

Dimensionality: determine the number of dimensions required to describe organisms' behaviors or physiological states within a particular time scale (e.g., principal component analysis of animal movement, covariance or factor structure of physiological states, order or dispersion of subjects in groups).

Coupling: examine if there is a reorganization of the coupling structure of a system undergoing a simplification regime shift (i.e., which links strengthen/weaken), including stronger coordination among elements of the active subset, and/or suppression/loosening of other linkages.

Variables protected during regime shift: determine which variables remain within a narrow range during a regime shift (for example, body temperature maintains its range; position does not significantly move).

Thresholds/hysteresis: use change point methods or segmented regression to identify the thresholds where regime shift occurs and where there are different thresholds for entry vs exit from a given regime (Scheffer et al. 2001, Dakos et al. 2024).

Inter-scale comparisons: measuring with the same methods at both the individual and group scales to see if coherence is moved to higher regime scales rather than lost (e.g., individual freezing reduces personal degrees of freedom, but the group becomes more polarized suggesting coordination shifts upward rather than disappearing).

When coherence is maintained by reducing complexity, effective dimensionality is reduced and the coupling structure reorganizes: coordination tightens within the remaining active components (often becoming more synchronized), while other processes are suppressed or decoupled. Animals may limit their movement to a few stereotyped patterns, reduce head and body motion, or they may use a limited number of habitual reflexes (Roelofs 2017, Meier et al. 2022, Taylor et al. 2023). Groups of animals can align in terms of speed and direction to facilitate group coordination (Storms et al. 2019). Such adjustments are typically temporary and reversible; however, if the cost of switching between behaviors is high, then recovery time will be longer than expected, exhibiting a form of hysteresis (Scheffer et al. 2001).

What are the economic costs of coordination?

Maintaining coherence is governed by available resources. From cells to brains, metabolic supply constrains how much sensing, signaling, and computation can be sustained. The cost of neural signaling is significant as it requires a continued expenditure of ATP to maintain ion gradients, generate action potentials, and send synaptic signals (Levy and Calvert 2021, Li and Sheng 2022, Padamsey and Rochefort 2023, Rae et al. 2024).

When resources are limited, animals alter movement, exploration, social coordination, and defensive responses. The energetic landscape framework shows that animals traveling with limited resources will either reduce how far they travel or utilize a form of locomotion that uses significantly less energy than other forms of locomotion (Wilson et al. 2012, Shepard et al. 2013, Gallagher et al. 2017, Cordes et al. 2025).

Time is another constraint. There is little time to compute flexible, context-sensitive responses when faced with imminent threat. Under imminent threat, defensive responses often shift toward fewer, tightly coordinated modes. Each stage prioritizes coherence of action/function to avoid catastrophic error (Mobbs et al. 2007, Mobbs et al. 2015, Roelofs 2017, Roelofs and Dayan 2022).

Group coordination increases the costs associated with coordination and therefore favors the utilization of simpler rules of interaction in larger groups of animals, and results in tighter group cohesion or dispersal when the cost of flexible coordination of the behaviors of individual members of the group exceeds the benefits. This allows group members to avoid collisions,

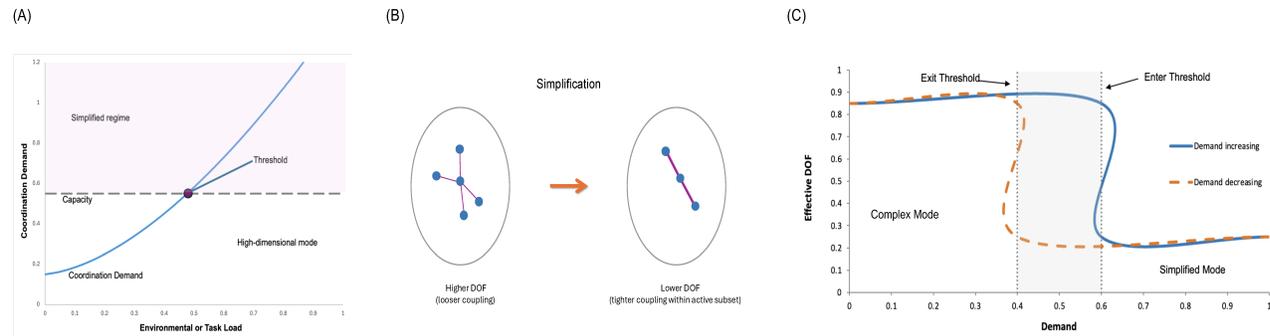
maintain cohesion, and to track neighbors. However, responses can also include fission or dispersal when alignment costs exceed benefits. This shows that groups can preserve coherence either by aligning more tightly or dispersing when coordination costs are too high (Couzin 2009, Sumpter 2010).

Simplification as a regime shift

A regime shift is a rapid switch in how an organism regulates its function. This occurs when coordination demand exceeds coordination capacity. In this new mode of operation, there will be fewer degrees of freedom and a reorganization of coupling that helps preserve important protected variables including body temperature or available oxygen (Figure 1). However, this often occurs at the expense of higher complexity behaviors like reproduction or exploration. Behavioral ecologists have documented numerous examples of state-dependent thresholds in the literature (Ydenberg and Dill 1986, Lima and Bednekoff 1999). The idea of coherence conservation adds a unique 'signature' to this study area: a coordinated reduction in effective degrees of freedom together with coupling reorganization and stabilization of protected variables. Simply decreasing the amount of behavior or energy usage does not indicate a system is displaying this signature (Bialek 2022).

Figure 1 The mismatch in capacity–demand driving simplification

- (A) Coordination capacity is constrained by energy, time, and control. A threshold is crossed when demand exceeds capacity. Environmental or task load increases coordination demand.
 (B) Illustration of biological systems maintaining coherence through a reduction in the available degrees of freedom along with reorganization of coupling (often tighter within the remaining active subset).
 (C) Entry and exit thresholds can differ and thereby produce hysteresis. DOF, degrees of freedom.



Simpler systems of organization do not equate to being passive systems. Freezing can allow for greater operational efficiency and preparation for an activity. Torpor states have active regulation through the use of neural circuitry. Dormant microorganisms retain the ability to maintain viable cell function at a reduced level of activity and continue to possess enough sensory capacity to activate an action when reactivated (Roelofs 2017, Hrvatin et al. 2020, Geiser 2021, Bradley 2025). These are simply alternative control methods, not malfunctions.

Additionally, regime shifts typically have recovery costs associated with them. Entering a simplified regime can have switching costs (lost time, missed opportunities, physiological reconfiguration), and exiting may require rebuilding capacity. Within a given episode, entry and exit thresholds can differ (e.g., hysteresis). Systems can enter the simplified mode at higher demand than the demand level at which they re-expand (Geiser et al. 2014). Hysteresis can

provide stability for behaviors but it can also delay recovery after extended periods of disturbance (Scheffer et al. 2001, Dakos et al. 2024).

Common signatures across biological systems

The same pattern emerges across biological domains. Often systems will transition to lower cost and lower dimensional stable states for the most critical variables when their capacity limits are reached (see Table 1).

Table 1. How constrained regimes simplify

Biological Level	Common constraints	Coherence preserving regime	How the regime simplifies	Example Studies
Cells / Microbes	Starvation, antibiotics, oxidative stress	Dormant states, quiescent states, persister states	Biosynthetic activity and growth decrease; remaining metabolism consolidates around survival functions	Bradley 2025, Hossain et al. 2023, Niu et al. 2024, McDonald et al. 2024
Plants / Invertebrates	Seasonal changes, desiccation or drought, low temp	Seed dormancy, diapause, tonic immobility	Development and activity arrested; resources directed to protective structures or states. Under threat, behavioral repertoire collapses to a single defensive state	Taylor et al. 2023, Baskin and Baskin 2014, Denlinger 2002, Sakai 2021
Endotherms	Food shortage, cold temp, energetic deficit	Torpor, hibernation	Metabolic rate and body temperature reduced; thermoregulation narrows to a defended setpoint	Hrvatin et al. 2020, Geiser 2021, Shankar et al. 2023
Vertebrates	Immediate danger with limited time to respond	Freezing, tonic immobility	Behavioral repertoire narrows to a few defensive responses; coordination tightens around threat monitoring	Roelofs 2017, Mobbs et al. 2015, Roelofs and Dayan 2022, Carli and Farabollini 2022
Animal groups	Predation, external disruption, social information overload	Alignment, clustering, reduction in task repertoire	Individual behavioral variability decreases; synchrony and polarization increase among group members	Couzin 2009, Sumpter 2010, Herbert-Read et al. 2011

The lower dimensional state can occur at many scales. Cells become dormant or persistent; plants, insects and other invertebrates cease development, and endotherms will decrease their metabolic activity by entering torpor or hibernation (Denlinger 2002, Baskin and Baskin 2014, Hrvatin et al. 2020, Geiser 2021, Hossain et al. 2023, Shankar et al. 2023, Letten et al. 2024, McDonald et al. 2024, Niu et al. 2024, Bradley 2025). Invertebrates also display defensive states such as tonic immobility (Sakai 2021, Taylor et al. 2023). Vertebrates defend against predators through freezing and tonic immobility (Roelofs 2017, Carli and Farabollini 2022, Roelofs and Dayan 2022). In addition, all members in a group will define tighter rules of interaction with each other and subsequently cluster or polarize (Couzin 2009, Sumpter 2010, Herbert-Read et al. 2011). All of these states will share at least one common trait; that is reduced effective degrees of freedom with reorganization of coupling (tighter coordination within the active subset) (Table 1).

Evolutionary consequences

If conserving coherence is adaptive, selection should influence both entry into simplified states and recovery from them. Thus, the threshold for entering simplified states should vary with internal state (e.g., energy, health, developmental stage) and external conditions (e.g., threat level, temperature, group density). Populations should evolve differences in when they simplify and how extreme those simplified states become, based on how often demand exceeds capacity (Auld et al. 2010, Piersma and van Gils 2010). This reframes behavioral flexibility to being beneficial yet costly (Auld et al. 2010, Rae et al. 2024). Organisms that are near their energetic limits may opt for quick entry into simple states (e.g., torpor or habitual behavior), while less constrained organisms will have sufficient energy resources to allow them to spend longer amounts of time learning or exploring.

The conservation of coherence also predicts individual differences. Regime thresholds and switching rates depend on both coordination capacity and coordination demand, including energetic reserves, environmental volatility, and individual differences in stress sensitivity/risk tolerance. These differences can be viewed as reflecting alternative coherence-management strategies shaped by environmental variability, rather than being characterized as noise (Dall et al. 2004, Sih et al. 2004, Biro and Stamps 2010).

Anthropogenic disturbances can interfere with the natural processes involved in the dynamics described above. Human disruption of the natural environment can force other species into states of heightened vigilance which can limit their ability to find food and reproduce (Smith et al. 2021, Rahman and Candolin 2022). While some studies have demonstrated that chronic anthropogenic disturbance can cause long-term changes in the behavior of some non-human species (Gaynor et al. 2019, Lee et al. 2024), direct empirical tests of hysteresis in behavioral dimensionality (where the threshold for entering a simplified regime differs from the threshold for re-expanding) are currently outstanding. Such tests would help identify when adaptive simplification becomes an ecological trap (Schlaepfer et al. 2002, Robertson and Hutto 2006).

Additionally, under chronic anthropogenic stress, recovery may become slower or fail altogether through several plausible mechanisms: accumulated allostatic load may degrade the physiological capacity to re-expand behavioral complexity (McEwen and Wingfield 2003), persistent environmental cues may prevent organisms from detecting that conditions have improved, or the chronic stress that drives prolonged simplification may simultaneously degrade the neural and social structures needed to re-expand (Woo et al. 2021, Girotti et al. 2024). As a result, systems may remain in low-flexibility states, which can have subsequent impacts on their mobility, learning, social interactions, and ultimately on the larger ecological dynamics (Gaynor et al. 2019, Sih et al. 2023, Lee et al. 2024, Uchida et al. 2024).

Testing coherence conservation

The concept of coherence is dependent on interactions among the components of the system. Rather than focusing on single traits, empirical study should emphasize changes in effective dimensionality, coupling structure (which links, strengthens, or weakens), and protected variables.

Box 2 summarizes measures for movement, physiology, and social interaction data.

Conservation of coherence yields several testable predictions:

- (i) Dimensionality should decline nonlinearly as demand increases.
- (ii) Thresholds and hysteresis are suggested based upon the existence of switching costs. These may be detectable via heightened sensitivity to small perturbations near switching points (Scheffer et al. 2001, Scheffer et al. 2009, Dakos et al. 2024).
- (iii) Organisms that have reserve capacity or have lower levels of baseline demand are suggested to delay the process of simplification.
- (iv) When demand decreases, regimes can potentially once again be complex, although this potential can be asymmetric.
- (v) Moving from a simple regime to a more complex one takes time. The speed of recovery is influenced by the recovery of physiology and learning.

Conservation of coherence makes independent predictions at each organizational level. The absence of the signature at one scale does not indicate its absence at another. Instead, it reveals where coordination costs are most limiting.

Conclusions

We have suggested that "emergency modes" across biology may be viewed as coherence-preserving regime shifts. When an organism's ability to coordinate complex behavior is limited, it reduces the number of possible options for action and reorganizes coupling among the remaining options. This may explain why structurally similar emergency responses appear across such diverse biological systems, e.g., bacterial dormant states, freezing, torpor, habitual control, and flocking.

Considering emergency responses as regulated rather than pathological creates new considerations regarding when limits become too restrictive, when recovery occurs, and when repetitive activation of emergency responses could be detrimental. For conservation practitioners, this framework suggests that management strategies should aim to preserve recovery windows rather than simply minimizing disturbance intensity, because even moderate chronic stressors may prevent the re-expansion of complexity if they eliminate the time or energy required for recovery. Answering these questions will require an integration of ecological contexts into dimensionality assessments (see Box 2) and cross-scale comparisons (see Table 1). Understanding how organisms maintain coherence while constrained by environmental conditions may therefore be central to both ecology and evolutionary studies as they relate to our current rapidly changing world. Future work should clarify when hysteresis shifts from an adaptive buffer to an evolutionary constraint. It remains to be determined how selection distributes coherence across organizational levels during simplification. Additionally, individual variation in energy reserves and experience may shape both the onset and recovery of simplified states, particularly under novel anthropogenic stressors that may suppress the recovery windows on which these evolved mechanisms depend.

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