Conserving Coherence Under Constraint

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Abstract

Across biology, organisms facing energy shortage, time pressure, or threat narrow their range of activity: they lower metabolic demand, restrict behaviour to a few coordinated patterns, or move in close synchrony with their neighbours. These responses are strikingly similar across otherwise unrelated systems, yet they are studied in separate literatures, and their resemblance is usually attributed to convergent selection. Accounts of the convergence have been offered within particular lineages. What remains open is one that yields a common signature and a shared way to test it. We propose that these responses reflect a single principle, the conservation of coherence: when the demand to coordinate exceeds the capacity to do so, a biological system preserves coordinated function by shedding variables that were varying independently and reorganizing the coupling among those that remain, while defending the variables most critical to viability and retaining the machinery needed to re-expand. This transition should leave a common four-part signature wherever it occurs, and the claim is not that each element occurs, which is largely known, but that they occur together as one transition. From that principle we derive four testable hypotheses covering the joint signature itself, the threshold at which systems simplify, the asymmetry between entry and recovery, and the relation between simplification at one organizational level and coordination at another. Because coherence is inferred from convergent, system-specific measurements while the signature stays fixed, the principle applies from cells to social groups and is falsifiable in each, and existing continuous-monitoring datasets already permit direct tests. We build on a recent cross-taxonomic framework for animal dormancy, extending its scope beyond programmed dormancy to acute defensive states and collective behaviour, and identify where current evidence is strong and where it remains to be gathered.

Keywords: collective behaviour, diapause, dimensionality reduction, dormancy, hysteresis, regime shift, tonic immobility, torpor

A common response to being overwhelmed

When constraints are low, a broad behavioural repertoire can enhance fitness. Under energy shortage, extreme conditions, or predation, many organisms instead narrow that repertoire: they enter torpor or dormancy [1], arrest development (diapause) [2], freeze or become immobile [3], or synchronize closely with their neighbours [4]. New tracking and machine-learning tools now make these shifts measurable across scales [5].

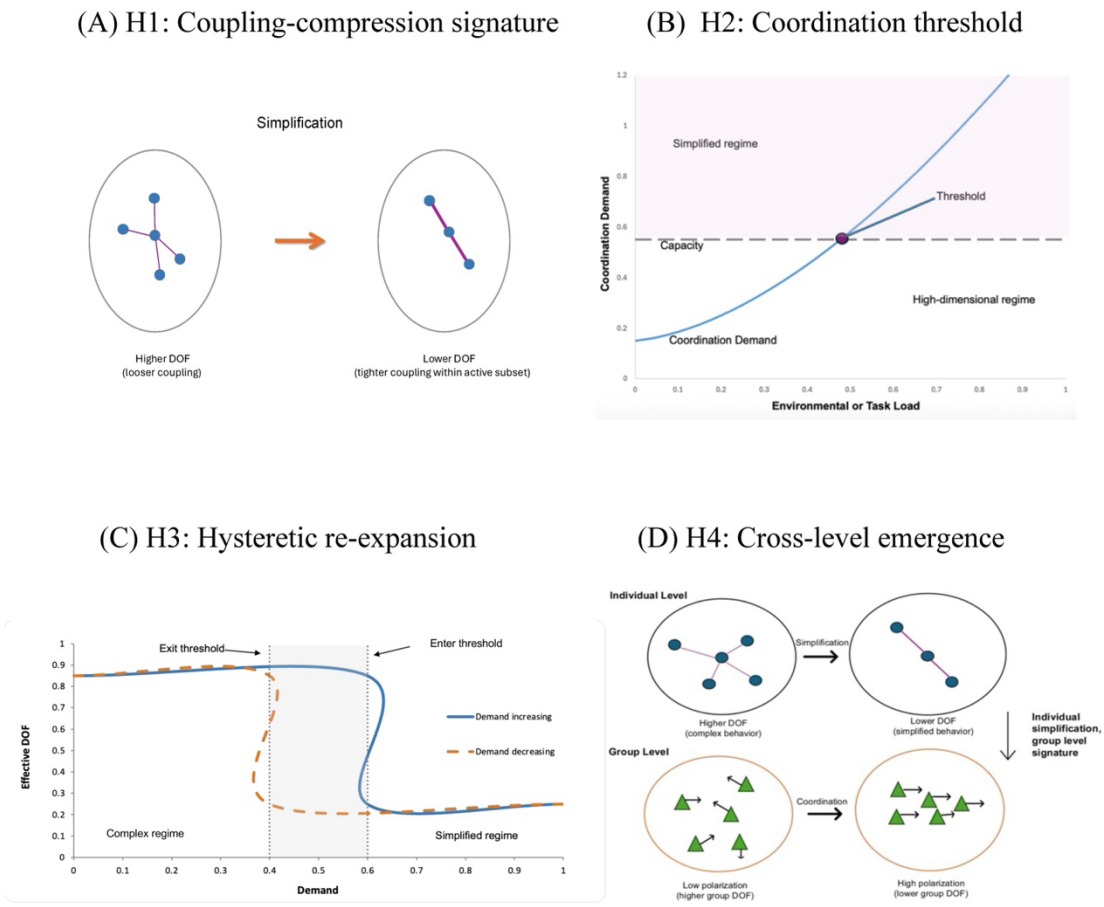
States of this kind were long treated as passive shutdown or suspended animation, and generally simplification is easily read as impairment [6]. We argue instead that, across many biological systems, functional simplification can act as a regulated survival mechanism that keeps organisms viable near the boundaries of their capacity to coordinate. The problem there is holding the components that remain in register, not keeping as many as possible in independent

operation. We refer to this trade-off between complexity and coordinated function as the conservation of coherence.

Stating this precisely requires a few defined terms. Components are the variables or latent modes that make up a system's state, whether behavioural, physiological or interactional depending on the level described. Coherence is the latent coordination state of a biological system, the degree to which its components act together in real time to support continued function. Coherence is not conserved as a physical quantity; it is preserved by active reorganization at a cost, and it can fail. Coordination demand is what needs to be coordinated at a given moment to sustain function, and increases with the number, speed, interdependence and uncertainty of the variables involved. Coordination capacity comprises the partially substitutable energetic, signalling or information-processing, and temporal budgets available to a system for coordinating its activity. A capacity-demand mismatch is the condition in which no allocation across those budgets can hold every component in coordination. Complexity here operationally refers to effective dimensionality, the number of components varying independently at a given time, not biological sophistication. Effective degrees of freedom are the number of components varying independently at a given time; effective dimensionality is the estimate of that number recovered from the covariance structure of a system's observed variables, which is scale-dependent, so the scale of observation must be stated when levels are compared [7]. A regime is a configuration of which components are coordinated and how tightly; a regime shift is a rapid switch between two such configurations, into a simplified regime or back out of one [8,9]. Fuller definitions are provided in the electronic supplementary material.

With these terms in place, we can state the core prediction of the conservation of coherence. Adaptive simplification should exhibit a joint signature across the transition into a simplified regime (Figure 1): a decrease in effective degrees of freedom (behavioural, physiological, interactional), reorganization of coupling (tightening of coordination within the remaining active components while others are down-regulated or decoupled), stabilization of key protected variables, and retained re-expansion capacity. Re-expansion capacity is the machinery that remains in place, letting the system register conditions bearing on exit and rebuild coordination when that becomes possible or necessary. This fourth element is what distinguishes adaptive simplification from terminal collapse: both may involve reduced activity or dimensionality, but only adaptive simplification preserves the capacity for coordinated recovery. Exit is itself a regime shift with its own signature, in which dimensionality rises, coupling reorganizes as suppressed dimensions re-engage, and the defended range of the protected variable shifts again.

Figure 1. Coherence-conserving simplification under a capacity-demand mismatch
(A) Dimensionality compression and coupling reorganization: effective degrees of freedom fall while coupling among the remaining active components tightens, and others are suppressed or decoupled (H1). (B) When coordination demand is greater than coordination capacity, the system should transition into a simplified regime (H2). (C) Where switching and rebuilding create costs, entry and exit thresholds should differ, producing hysteresis (recovery requires greater available capacity, a stronger or more sustained cue or more time than entry) (H3). (D) As individuals simplify, group-level effective degrees of freedom fall while polarization and synchrony rise and cohesion is maintained (H4). DOF, degrees of freedom.



The costs of coordination

Coordination does not occur for free. Monitoring components, signalling between components, and computing adjustments require energy, time, and information-processing capacity. These costs rise with the number of dimensions that must be independently managed [10,11]. What an organism can afford to coordinate depends on the cost of coordination in each of these currencies and on the availability of each. Of these, energy is the most studied. From cells to brains, metabolic supply constrains how much sensing, signalling, and computation can be sustained. The cost of neural signalling is significant, requiring continued expenditure of ATP to maintain ion gradients, generate action potentials, and send synaptic signals [12,13]. When resources are limited, animals alter movement, exploration, social coordination, and defensive responses. The energetic landscape framework shows that animals travelling with limited resources will either reduce how far they travel or use a form of locomotion that requires significantly less energy [14,15,16]. For instance, soaring birds reduce the energetic cost of travel by gliding on rising air currents, saving energy that would otherwise go to continuous wing beating.

Time is a second currency. Coordinating multiple components to sense, integrate, and adjust takes time, so a shorter response window reduces how much coordination is affordable regardless of how much energy is available. Under imminent threat, defensive responses often

shift towards fewer, tightly coordinated modes, prioritizing coherence of action over breadth of response to avoid catastrophic error [17,18].

Group coordination increases these costs and therefore favours simpler rules of interaction in larger groups. In fish schools or flocks of birds, each member monitors only a few immediate neighbours rather than all members, which decreases the coordination each must perform [4,19]. When group coordination costs exceed the benefits, groups may align more tightly into cohesive, polarized movement, or may disperse, with each member reallocating its coordination to individual escape [4,19]. In framework terms, aligning preserves coordination at the group level over fewer effective dimensions, while dispersal preserves it at the individual level. Both conserve coherence, at different levels of organization. At either level, coordination costs rise with the number of components held in register.

Simplified states are actively held, not switched off

Simplified regimes are not passive. Freezing is a preparatory state for rapid action rather than a suspension of it, sustained by active autonomic and central regulation [17,18]. Torpor is imposed and sustained by identified neural circuits [20]. Dormant microorganisms maintain viable cell function at reduced activity [21,22]. Each is an alternative mode of regulation, not a failure of one. Whether that regulation also preserves the capacity to leave the state is a separate question, taken up below.

Regime shifts also carry recovery costs. Entering a simplified regime can incur switching costs (lost time, missed opportunities, physiological reconfiguration), and exiting may require rebuilding capacity. Arousal from torpor is metabolically expensive and must be funded by reserves the constraint has already depleted [1]. A system may enter a simplified mode at a higher demand than the demand at which it re-expands, making the state resistant to reversal and delaying recovery after a prolonged disturbance.

A simplified regime may also accrue costs it cannot itself discharge. Where the regime suspends a restorative process, capacity declines while the regime is held. In hibernation, torpor's low body temperature precludes sleep, and the resulting sleep debt accumulates with bout duration, so animals arouse periodically to euthermy, when they can sleep, to discharge it [23,24]. The debt is measured as slow-wave activity during subsequent euthermy rather than inferred from arousal timing. A parallel, long-standing proposal holds that some substrate depleted during torpor can be replenished only in euthermia, though that substrate has not been identified [25]. Where such a debt accumulates it sets a ceiling on how long a regime can be held, and exit may be forced by declining capacity rather than triggered by improving conditions. Cycles of this kind are best known in rodent hibernators but also occur in insects, fish, lizards, and birds [6]. A debt ceiling offers a candidate account of why such cycling recurs across lineages that share no common mechanism for it.

Recognizing conservation of coherence and ruling out alternatives

Conservation of coherence must be distinguished from several patterns it superficially resembles as it is not the only way that biological systems maintain function under stress. Robustness, for example, can be supported by modularity and partial decoupling, which limit the spread of perturbations [26]. Conservation of coherence describes a different pattern, in which coupling

tightens within a narrowed active set of components while the remaining components are decoupled or suppressed. One instance is a fish school, where individuals coordinate their movement by interacting with their immediate neighbours through local interaction rules [27]; when the group is threatened, each individual's range of independent movement narrows and the group's movement collapses to a few coordinated patterns.

Reduced activity is the pattern most often mistaken for conservation of coherence. What matters is not whether activity falls but whether the components that remain couple more tightly, whether a protected variable such as body temperature in a torpid mammal is held within bounds, and whether the shed options become jointly unavailable rather than merely unused. That distinction is testable: ordinary task selection leaves unused options readily available, whereas in a regime shift the suppressed dimensions go together, are not individually retrievable, and return together as the capacity-demand balance improves. Under acute stress, neural representations of action outcomes weaken while those of habitual responses strengthen [28], consistent with the broader repertoire becoming less accessible rather than merely unselected.

Two more alternatives are disruption and collapse. The framework applies when a stable simplified regime exists to which the system can converge; stressors that are novel, severe, or poorly matched may instead produce disrupted, non-equilibrium dynamics. Responses to novel or stressful conditions are frequently non-adaptive, displacing the mean response from the favoured optimum or inflating variance around it [29]. These can involve stochastic responses, heterogeneous relaxation, decoupling of processes, disorganized rather than coordinated changes in dimensionality, or failure to hold protected variables within bounds. Such dynamics might be expected, for instance, in microorganisms exposed to atypical sublethal stresses for which no coordinated response has evolved, where the system becomes simpler only through a failure of coordination rather than a conservation of coherence. These cases are better described as stress-induced disruption, shutdown, or collapse, which the diagnostic matrix distinguishes (Table 1). Entry-exit asymmetry alone is also not diagnostic: in ecosystem regime shifts, feedback structure can produce different entry and exit thresholds with no regulation involved [8,30].

Table 1. Diagnostic matrix for distinguishing conservation of coherence from other responses to constraint

Pattern	Dimensionality reduction	Coupling change/reorganization	Protected Variables Stabilized	Re-expansion capacity retained	Interpretation
Conservation of Coherence	Yes	Yes, coordinated with compression	Yes	Yes	Adaptive Simplification
Stress/load response without simplification	No	Possible, but non-diagnostic	May be defended initially	Usually yes	Load response, not conservation of coherence
Behavioural suppression or shutdown	Yes/No	No coherent reorganization	Variable	Variable	Reduced activity without the full coherence-preserving signature
Stress-induced disruption/frustrated Dynamics	Variable or disorganized	Disorganized or lost	Variable	Variable	Novel or severe stress exceeding coordination capacity; full signature absent
Terminal Collapse	Yes or disorganized loss	Disorganized or lost	No	No	Pathology, failure, collapse
Maladaptive lock-in	Yes	Yes	Yes	No	Signature is present at simplification, but the

					recovery machinery is compromised; it is distinguished from conservation only by recovery data (see H3)
Indeterminate Case	Yes	Yes	Yes	Unknown	Requires recovery data to distinguish adaptive simplification from lock-in; a confirmed re-expansion failure indicates the latter

Assessing any of these distinctions requires estimating coherence, which is inferred rather than measured directly, from behavioural, physiological, or interaction time series. The measurements are therefore system-specific while the signature is not, which is what allows one framework to be applied from cells to social groups and tested separately in each. Inferring coherence in this way makes the framework vulnerable to circular reasoning, and guarding against it requires discipline in how a test is constructed. Coordination demand, candidate capacity limits, protected variables, and transition criteria should be specified before the regime shift is examined: demand estimated from task structure or manipulated experimentally, capacity indexed independently, and protected variables nominated from prior physiological, functional, or fitness evidence. The set of measures and the time window over which the signature is assessed should likewise be stated in advance, since compression in one measurement domain or over one timescale need not appear in another. The joint signature is then the predicted response, not the basis for retrospectively defining the mismatch. Exploratory identification remains appropriate for generating candidate protected variables and capacity limits, provided the confirmatory test uses data that played no part in generating them, whether a held-out sample, an independent dataset, or a different system. The electronic supplementary material sets out candidate measures for each construct (box S1).

Four testable hypotheses

Conservation of coherence yields four testable hypotheses. Electronic supplementary material, table S2 lists, for each hypothesis, the measurements or manipulations needed, candidate analyses, the systems in which the test could be run, and the results that would support or refute it.

H1 (Coupling–Compression Signature Hypothesis): When coordination demand exceeds coordination capacity, four things should occur together: effective degrees of freedom fall, coupling among the remaining active components reorganizes (Figure 1A), the critical protected variables remain stable, and re-expansion capacity is retained throughout. Testing H1 therefore requires indexing retained recovery infrastructure, such as residual sensory responsiveness, regulatory control, or energetic reserves, alongside dimensionality and coupling.

H2 (Coordination Threshold Hypothesis): Simplification should be triggered not by any single stressor but by a capacity-demand mismatch (Figure 1B). Stress and energy shortage can contribute to that mismatch but are not required. The demand that crosses the threshold may also be projected rather than current: where a reliable cue signals imminent mismatch, simplification is expected in advance of it. Entry on a predictive cue can be distinguished experimentally from entry on the current capacity-demand balance, as in the established distinction between diapause

and quiescence [2]. In *Wyeomyia smithii* short days initiate and maintain diapause independently of temperature [31], so entry there is cue-driven rather than a response to conditions already deteriorating. In either case, increased coordination demand should drive simplification even when energy savings are small, while greater capacity should allow coordination to be sustained longer. The latter has been measured in breath-hold diving, where the aerobic dive limit predicted from independently measured oxygen stores matches the observed lactate threshold and scales with body size in Weddell seals [32,33].
Coordination demand and stressor intensity can be varied independently and crossed factorially so their contributions separate, with a predictive cue included as a third factor to test whether entry tracks projected rather than current demand. At constant stressor intensity, the number of inputs to integrate, the sensory noise to filter, the density of the surrounding group, or the time available to respond can each be manipulated. Systems facing higher coordination demand should then simplify earlier and more deeply than systems facing lower demand at matched stressor intensity. This relationship should hold until demand outstrips the capacity for any viable coordinated response, at which point the system should show disruption rather than deeper simplification.

H3 (Hysteretic Re-expansion Hypothesis): Switching costs alone do not imply asymmetry, since entry and exit may be equally costly. Asymmetry arises when exit is more demanding than entry, whether because it involves processes that entry did not require or because shared processes cost more in the exit direction. Candidate exit-side processes include restoration of suppressed degrees of freedom, replenishment of depleted reserves, restoration of coordination machinery, and reversal of feedback loops that actively maintain the simplified state. Because capacity comprises several partially substitutable budgets, the cost comparison must be made within a stated budget, and the threshold comparison on the dimension that governed entry (Figure 1C). Where asymmetry arises from rebuilding costs, it should grow with the depth and duration of an episode: momentary freezing should show little hysteresis, extended torpor substantially more.

H3's premise is already documented. Diapause termination depends on processes that induction did not require [2], and in torpor the shared processes cost more in the exit direction [34]. Where both cues have been titrated the outcome varies, with threshold asymmetry in two insect species and coincident thresholds in a third (see below). That variation should track what exit requires beyond entry. Where termination demands nothing beyond reversal of the entry cue, thresholds should coincide. Where it demands accumulated exposure, as in Wyeomyia smithii, in which about three long days are needed for half a cohort to terminate [31], the asymmetry should appear in cue persistence rather than cue value. What has not been done is the paired comparison within individuals, or alongside dimensionality and coupling. Individual exit thresholds are measurable in Wyeomyia smithii, where diapausing larvae exposed to incrementing day lengths reveal a critical photoperiod for each animal [35], but the entry threshold in the same individuals is not recorded. Neither has been attempted in torpor at either level, the individual bout or the hibernation season. Depletion accounts of arousal timing [25] locate the trigger in an internal quantity rather than in the entry cue, so they are not rivals to H3 but do bear on where it can be tested: wherever exit is internally triggered, the entry-cue comparison is unavailable and only the cost comparison applies.

H3 predicts in the same individual, exit on the dimension that governed entry is more demanding than entry was, requiring greater available capacity, a higher cue value, or more time. Exit triggered on other dimensions, such as disturbance, is not a counterexample: there the threshold should be set by the risk of remaining in the simplified state rather than by rebuilding costs.

H4 (Cross-level Emergence Hypothesis): During a demand transition, simplification at one organizational level should coincide with the joint signature at an adjacent level, and simplifying a level does not mean its coherence is lost. Emergence here means the joint signature appearing at one level in coordination with simplification at another and tied to it, not the creation of coordination that was previously absent. An individual that compresses its behavioural repertoire remains coordinated, but over fewer dimensions. When individuals simplify, the group may itself show the joint signature: effective degrees of freedom at the group level fall as individual trajectories become less independent, coupling among neighbours tightens, a group-level protected variable such as cohesion is maintained, and the tightening remains reversible rather than locked in (Figure 1D). A valid test must specify both levels and their state variables in advance, and must estimate dimensionality, coupling, protected variables, and retained re-expansion capacity separately for individuals and for the group, simultaneously, with the same metrics and at a stated scale of observation [7] (see electronic supplementary material, table S2). Since local neighbour coupling and group polarization measure the same underlying alignment, group-level effective dimensionality provides the independent test. That pattern must then be compared against null models based on common external forcing or simple aggregation. H4 is supported only where individual-level compression is temporally associated with an independently measured group-level joint signature; increased polarization alone is insufficient. Failure at the pre-specified levels challenges that application rather than licensing a search across other scales.

H1 tests the framework directly: if the joint signature does not occur as a coordinated transition, the account fails. H2 carries the account itself: if simplification proves to be driven by something other than a demand-capacity mismatch, the joint signature would stand without the reason offered for it. H3 and H4 test the exit and generality across levels; either could fail while leaving the framework narrower in scope rather than refuted.

These hypotheses are stated verbally, but each connects to established mathematical traditions that offer formal grounding: dynamical-systems accounts of how many coordinated variables collapse to few near a transition, control-theoretic treatments of regulation under limited capacity, and information-theoretic treatments of what a system retains when it must compress. None is adopted here as the model, and a complete formalization would need to reproduce the full joint signature as a single coordinated transition rather than any one element in isolation. We set out these candidate formalizations, and their correspondences to each hypothesis, in the electronic supplementary material. The present contribution is the framework and its disconfirming conditions; the formal development is a direction it invites.

Where the evidence stands

Systems across biological domains appear to converge on lower-dimensional stable states at capacity limits (see electronic supplementary material, table S3), but evidence for the complete joint signature varies across scales. We do not claim a single underlying mechanism: physical

processes, neural control, and simple interaction rules are convergent functional solutions shaped by similar constraints, not mechanistic homologies.

In plant and invertebrate diapause and dormancy, development and activity arrest while resources are redirected to protective structures [2,36]. Tonic immobility in invertebrates collapses the behavioural repertoire to a single defensive state [37,38]. Both are consistent with dimensionality reduction, but coupling reorganization hasn't been explicitly measured, and protected variable stabilization (structural integrity, metabolic viability) is implied rather than quantified. Diapause, however, is defined partly by a difference between entry and exit: shortening days induce it ahead of adverse conditions, and it does not terminate when favourable conditions return but requires a separate terminating cue, in many species a longer photoperiod than the one that induced it [2]. The dormancy literature measures resistance to that resumption as recalcitrance, the time or proportion of individuals resuming active-season physiology under permissive conditions [6]. Because those conditions are chosen to support active-season function rather than by measuring what exit requires, the measure assumes rather than tests that any of them suffices to release the animal. Titrating the inducing and terminating cues separately gives the comparison recalcitrance cannot, and the outcome varies. In the linden bug *Pyrrhocoris apterus* the critical daylength is 15.75 h for induction against 16.75 h for termination, stable from four to fourteen weeks in diapause [39]; about 1.2 h separates them in *Pieris brassicae* [40]; in the pitcher-plant mosquito *Wyeomyia smithii* they coincide in unchilled larvae [31]. Where they differ, a photoperiod between them lies above the induction threshold but below the one for termination, so animals held there resume more slowly or in smaller proportion, which is what the standard measure scores as recalcitrance [6]. That a termination threshold stays detectable across the tested interval shows the machinery for re-expansion is retained, as does the responsiveness of diapausing *W. smithii* larvae to photoperiod [31]. In many temperate species termination requires accumulated chilling rather than photoperiod alone [2], so the threshold comparison is available only where a photoperiodic exit cue suffices.

Torpor and hibernation offer the most tractable test of the joint signature, since one individual undergoes repeated discrete transitions across a season. During torpor, metabolic rate, body temperature and heart rate become tightly coupled [1]. Geiser et al. [34] distinguished torpor from pathological hypothermia: torpor reduced metabolic rate and body temperature together, defending body temperature at a lowered set point, while hypothermia reached an indistinguishable minimum body temperature with metabolic rate about sevenfold higher. The same study found that metabolic rate and body temperature trace different paths on entry and arousal, rewarming being more costly at any given body temperature, and termed that loop hysteresis. That is hysteresis in the physiological trajectory, and it is the cost asymmetry H3 requires. Hysteresis in the triggering conditions, where the environmental value that ends a bout or a season differs from the one that began it, has not been reported in torpor. Nor do we know of a test of whether behavioural and physiological repertoires lose dimensionality at the same transition point.

During tonic immobility and freezing in vertebrates, the behavioural repertoire narrows to a few coordinated defensive responses [18,41], while autonomic function becomes tightly coupled around threat monitoring [3,18]. What is undocumented is whether a protected variable is defended, whether re-expansion capacity is retained across the episode, and whether the changes

occur together rather than separately. Little hysteresis is expected here in any case, since episodes are brief and exit is triggered on the threat dimension rather than on the one that produced entry.

Groups under predator attack show increased polarization and synchronization [4,19,27], both consistent with tighter coupling, though neither establishes it. Storms et al. [42] catalogued several distinct escape patterns in starling flocks, which could be read as a maintained repertoire rather than dimensionality compression. That ambiguity is why the test must estimate the effective dimensionality of the ensemble of individual trajectories rather than group-level polarization. Diversity across escape patterns is compatible with the framework; what matters is whether, within a pattern, group-level dimensionality falls and coupling tightens while a protected variable such as cohesion is held within bounds and the capacity to re-expand is retained.

Global suppression of biosynthetic activity and priming for stress tolerance are well documented in microbial persistence and dormancy [21,22,43,44]. Multivariate analyses of coupling reorganization across the dormancy transition remain rare, however, and we have not found a formal test of threshold asymmetry between active and dormant states. Transcriptomic and metabolomic time series would support both.

Retained re-expansion capacity is documented across biological scales. Neuronal activity tracks both entry into and exit from torpor [20]. Dormant microorganisms retain sensory capacity sufficient to detect improving conditions and reactivate [21]. Freezing vertebrates monitor the threat environment throughout the episode [3]. In some systems that machinery is not merely retained but defended. Hibernating mammals resist the muscle loss that comparable disuse produces in non-hibernators, maintaining mass and fibre cross-sectional area across months of torpor in ground squirrels and black bears [45,46,47]. Whether the basis is maintained protein synthesis, suppressed degradation, or both remains open, but the phenotype indicates that re-expansion capacity is preserved actively rather than as a by-product of inactivity. Where re-expansion capacity is lost, whether because the system can no longer register conditions bearing on exit or because it can no longer rebuild coordination, the state is better described as maladaptive lock-in than as conservation of coherence.

A worked example: applying the hypotheses to torpor

Continuous physiological monitoring is feasible in small endotherms, and each animal supplies many transitions. Testing H1 requires continuous multivariate recording across the transition into torpor: body temperature, heart rate, breathing rate, and activity from implanted loggers, metabolic rate from respirometry, with effective dimensionality read from the eigenvalue spectrum of their covariance and coupling from the pattern of pairwise dependence. Capacity should be indexed independently over the same period, for example from fat stores, and body temperature nominated in advance as the protected variable on physiological grounds. On entry, the number of latent modes needed to represent physiological state should fall, coupling among the remaining active variables should redistribute rather than simply rise, and body temperature should be defended at a lower set point. Retained re-expansion capacity should be indexed alongside these, from the arousal machinery that returns the animal to euthermy [1,34]. The framework would be challenged if metabolic rate fell without the accompanying fall in

dimensionality, reorganization of coupling, and defence of body temperature, or if re-expansion capacity were not retained. Finally, the signature is nested: a torpor bout is one regime, entered and left repeatedly, and the hibernation season another, entered and left once. Each must be scored at its own level, since arousal restores what the bout suppressed and not what the season did, and each level has its own entry and exit conditions.

Testing H2 requires manipulating coordination demand independently of energetic state and threat. Barratt et al. [48] found that alarm-call playback deepened and lengthened subsequent rest-phase torpor bouts in wild superb fairy-wrens, with no manipulation of food supply. That result does not separate the coordination-demand mechanism proposed here from a general stress response or from a direct anti-predator adaptation such as reduced detectability: all three predict deeper torpor under predation risk, and anti-predator behaviour itself reduces energy intake. Separating them requires varying coordination demand while holding threat intensity constant.

Testing H3 requires comparing entry and exit on the same measures: the conditions at which each occurs, the capacity each requires, and the cost and time each takes. Arousal should require greater available capacity, a stronger or more sustained cue, or more time than entry did, and the asymmetry should grow as bouts become longer or deeper. Public datasets allow an immediate test. The Chmura et al. [49] arctic ground squirrel archive holds 306 hibernation seasons from 199 individuals, with body temperature and with soil temperature logged at one metre depth near burrow locations across the same seasons. Those records support the comparison at both levels: within the season, whether the ambient temperature at which a bout is entered differs from that at which arousal begins; and across the season, whether the temperature at which hibernation is entered differs from that at which it is terminated. Each level has its own confound. At the bout level, exit may be forced by accumulated debt rather than by temperature: torpor spares energy while sleep debt accumulates [23], and an animal leaving on a spent budget was not responding to conditions. At the season level, terminal arousal may be set by circannual timing rather than by temperature. Neither confound is directly measurable in free-living records, where slow-wave activity and endogenous phase cannot be recorded, but both have proxies. Debt accumulates with bout duration [24], so temperature can be tested for variance in arousal timing beyond that explained by elapsed duration. Date stands in for endogenous phase, which the record's warming trend partly separates from temperature across years. Female emergence advanced with earlier thaw over the period while male emergence did not [49], giving a contrast within one dataset between exit that tracks conditions and exit that does not. Separately, where a triggering event damages the coordination apparatus itself, a large recovery gap appears irrespective of episode length; that is reduced re-expansion capacity rather than adaptive hysteresis, and the scaling prediction detects it (Table 1).

What would falsify the framework and how it relates to existing ideas

Two scenarios would falsify the framework. The first: organisms routinely exceed their coordination capacity with no increase in failure rates and no reduction in complexity. The second: systems that simplify under a capacity-demand mismatch and later recover are consistently found to have compressed, reorganized and stabilized separately rather than as one transition. Where coupling is inferred from covariance rather than measured as connection strength, it must be scored as change in the pattern of dependence, since a rise in average dependence follows from compression alone.

Reduced activity, metabolic rate, or behavioural diversity without coupling reorganization, a defended protected variable, or retained re-expansion capacity is not evidence of conserved coherence. Coherence can also be lost by routes external to the coordination dynamics: physical disruption, damage, or acute insult can degrade coordinated function with no regulated simplification having occurred. The framework concerns coherence conserved or lost through a system's own coordination under constraint, so neither counts as an instance or a failure of coherence-preserving simplification. Table 1 distinguishes conservation of coherence from other patterns arising under constraint.

Several frameworks address how organisms maintain stability under increasing demand. Allostasis emphasizes controlled adjustments to mediators or set points, which provide short-term stability at cumulative cost when prolonged [50,51]. Robustness and resilience concern the ability to withstand disturbance and recover, typically through modularity and redundancy [26,52]. Critical transition theory addresses abrupt nonlinear switching between states, the processes driving it, and its early warning signs [8,9,30]. State-dependent decision theory models threshold-dependent behavioural switches as a function of resource state, risk, and expected fitness returns [53,54]. Predictive processing and the free energy principle treat perception and action as inference that minimizes prediction error under time and energy constraints [55,56,57]. Phenotypic plasticity describes environment-dependent expression of alternative phenotypes, covering torpor, diapause, dormancy, and defensive immobility, but specifies that the phenotype tracks the environment rather than what form the response takes [58]. A cross-taxonomic framework for animal dormancy classifies dormancies along axes of induction, recalcitrance, and magnitude, and tracks core traits (metabolism, activity, reproduction, energy storage) through sequential phases [6]. Those core traits are measured variable by variable rather than as dependence structure, and coupling reorganization is not among them. Two of its constructs do anticipate the present account. Recalcitrance measures resistance to resumption, though not the entry-exit comparison itself. Potentiation, the phase during which responsiveness to terminating cues is progressively restored, describes the recovery of re-expansion capacity. That framework locates the trigger in seasonality and its fitness consequences rather than in a mismatch between coordination demand and capacity. Each of these frameworks accommodates one or more elements of the proposed pattern; conservation of coherence differs in making their coordinated temporal organization the primary prediction, and so testable against shutdown or a general stress response (electronic supplementary material, table S1).

Discussion

We have proposed that simplification under constraint is a coherence-preserving regime shift with a four-part joint signature. When an organism's capacity to coordinate is exceeded, it reduces its effective degrees of freedom and reorganizes coupling among the remaining components, while protecting key variables and retaining the capacity to recover. This may explain why structurally similar responses appear across systems as diverse as bacterial dormancy, freezing, torpor, and flocking.

What distinguishes the account is not any single element but their organization in time. All four should hold across one transition, with the first three changing together and the fourth retained throughout and demonstrable during recovery. Whether that holds is testable now, in continuous-monitoring archives that already exist.

If conserving coherence is adaptive, selection should act on the threshold at which systems simplify and on coordination capacity itself. Thresholds should track internal state and external conditions [53,54], while capacity is built only where it is cheap enough to be worth holding in reserve [58]. Lineages that differ in what capacity costs should therefore differ in whether they absorb recurrent demand or simplify earlier when it arrives, and individuals within a population should differ for the same reasons.

Treating simplification as regulated rather than pathological raises questions about when a simplified regime becomes too restrictive, when recovery occurs, and when repeated entry becomes costly. These matter most under novel anthropogenic stressors, which fall outside the distribution of demand under which thresholds and capacities evolved and can force sustained vigilance that limits foraging and reproduction [59]. Recovery may then slow or fail, whether because accumulated allostatic load degrades the structures re-expansion requires [50,60,61] or because persistent cues prevent the system from registering that conditions have improved [62]. Direct tests of hysteresis in behavioural dimensionality would identify when adaptive simplification becomes an ecological trap [63]. For conservation, this suggests that management should preserve recovery windows rather than only minimize disturbance intensity.

Ethics
This work did not involve human participants or the collection of data from live animals, and no ethical approval was required.

Data accessibility
No new data were generated or analysed for this review. The arctic ground squirrel hibernation dataset identified as a candidate test of H3 is publicly available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.pzgmsbcqq. Supplementary material is provided in the electronic supplementary material.

Authors' contributions
Both authors contributed equally to this work, gave final approval for publication and agree to be held accountable for the work performed therein.

Conflict of interest declaration
We declare we have no competing interests.

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AI was used to improve readability, grammar, and language of the work- used in conversion of American English to British English.

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