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From Semiotic Fitting to Semiotic Collapse:

A Multi-Level Process Model of Extinction

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Abstract

Extinction is usually analysed as a terminal event at the population level: populations decline, fall below their viability thresholds, and disappear. We propose an alternative framework that reconceives extinction as the gradual collapse of semiotic systems — the recognition-based bonds through which organisms interpret their environment. Drawing on Kull's theory of semiotic fitting (2020, 2022), we introduce Semiotic Overlap (SO) as a measurable index of the structural alignment between an organism's interpretive system and its ecological environment. SO breaks down into three components: SO_I (informational alignment between cue and outcome), SO_B (within-population behavioural dispersion), and SO_C (structural coherence of the cue network). From these we derive five formal propositions, each operationalised so that it can be tested against open-access ecological datasets. The framework was applied to nine independent systems spanning six biological kingdoms and three continents: a prokaryote (the Baltic Sea bacterial community), a plant (*Boechera stricta*), an insect (*Operophtera brumata*), a fish (*Oncorhynchus nerka*), an amphibian (*Triturus cristatus*, across five populations), a reptile (marine turtles), a bird (*Parus major*), and two mammals (*Lepus americanus* and *Lutra lutra*). Composite SO ranged from 0.35 to 0.68 across the systems, ordering them by phase of collapse rather than by taxonomy. In *O. brumata*, SO acted as a leading indicator of population state (Granger $F = 4.54$, $p = 0.049$, $\Delta R^2 = +0.108$), but it did not in *P. major*, which is buffered demographically. *Boechera stricta*, where phenotypic plasticity accounts for roughly 80% of the phenological change against about 20% for evolution, provided direct support for Kull's claim that fitting comes before selection. *Oncorhynchus nerka*, subject to artificial hatchery selection since 1991, showed a 62% weakening of the cue–outcome coupling and a drop in escapement from roughly 213,000 to 45,000 — a picture of fitting overridden by imposed selection. Behavioural entropy in *L. americanus* fell below the 1.5-bit clustering threshold (0.27 to 0.63 bits; synchronisation $\bar{r} = +0.86$ to $+0.99$), whereas *T. cristatus* showed the opposite pattern: high individual diversity together with low regional synchrony — a local fitting that shields the metapopulation. Partial hysteresis appeared in *L. lutra* as a persistent expected-minus-observed heterozygosity gap of 0.125, still present after two decades of recovery. Most tellingly, SO carried predictive information that classical variance-based early-warning signals did not ($\Delta R^2 = +0.109$ for SO against $+0.015$ for EWS). The framework moves Kull's semiotic fitting from qualitative description to quantitatively testable prediction, and shows across six kingdoms that the informational dimension of ecological systems is not redundant with their dynamical or demographic dimensions.

Keywords: semiotic fitting; biosemiotics; the extinction process; phenological mismatch; early-warning signals; conservation genetics; hysteresis; artificial selection; Kalevi Kull

1. Introduction

The prevailing view of extinction today is largely a statistical one, built on population data. It treats the disappearance of a population as an endpoint to be forecast from demographic trajectories: declining abundance, a contracting range, falling indices of viability (IUCN 2012; Mace et al. 2008). From this view a whole apparatus of detection has been built — population viability analysis, estimates of minimum viable population size, early-warning signals of critical transitions (Scheffer et al. 2009; Dakos et al. 2012) — and it operates almost entirely on demographic and dynamical variables. What this apparatus does not record, and arguably cannot record given its own conceptual commitments, is the informational dimension of a system's decline: in other words, the gradual erosion of the relationship between a sign and its referent, the relationship through which organisms read their environment and respond to it.

This gap is not merely empirical; it is conceptual. Conventional ecology has no vocabulary for the relationship between an organism's interpretive system and the environmental signals it depends on. When a great tit lays its eggs in response to spring temperature, when a snowshoe hare changes colour in response to day length, when the egg of a sea turtle becomes male or female in response to the temperature of the sand, when a sockeye salmon times its spawning migration to the flow of the river — the organism is doing something that is neither adaptation (the slow process of selection across generations) nor mere biological plasticity. It is doing what Kalevi Kull, in his theory of semiotic fitting (Kull 2020, 2022), named precisely: establishing recognition-based bonds — what Kull calls Einpassung — between its interpretive system and particular environmental cues. These bonds operate on the timescale of communication, not the timescale of selection, and they form the substrate on which ecological communities are built.

This study draws a clear and consequential distinction between Anpassung (adaptation), the slow Darwinian process that proceeds through selection across generations, and Einpassung (fitting), the rapid, recognition-based process by which organisms establish and maintain semiotic relationships with their environment within their own lifetimes. Put briefly, the claim that “choice comes first, selection may work afterwards” (Kull 2020: 14) inverts the conventional priority of selection over interpretation. The community we observe is, on this view, primarily a product of fitting, with selection refining and stabilising what fitting has already produced. Kull's framework grew out of the biosemiotic tradition, which has long argued that organisms should be treated as living, sign-interpreting agents (Hoffmeyer 1996; Maran & Kull 2014). Yet despite repeated attempts to bridge biosemiotic theory and quantitative ecology, the operational gap has stayed largely open: biosemiotic concepts have remained at the level of qualitative description, while quantitative ecology has carried on without them.

The consequence of this disconnect is that a set of ecological phenomena are studied in isolation from one another — phenological mismatch (Visser & Both 2005; Both et al. 2006), ecological traps (Schlaepfer et al. 2002), the differing responses of buffered versus collapsing populations (Reed et al. 2013), and the maladaptive consequences of artificial selection (Tillotson et al. 2019). They sit in separate empirical literatures, with no unifying theoretical machinery to name what is happening to them at the informational level.

The present study sets out to build that qualitative–quantitative bridge. We take semiotic fitting as a qualitative, descriptive account of how organisms establish recognition-based bonds with their environment, and we ask: what would it mean to measure the decay of such fitting from observable ecological time series? A crucial point arises here. We treat a qualitative state — semiotic fitting — and the passage out of it as a quantitative process. As Kull has noted, semiotic fitting is a qualitative condition, but its breakdown, the onset of its absence, can be quantitative; and that is the foundation of this study. To pursue it, we propose Semiotic Overlap (SO) as our answer. SO is a composite measure with three components: SO_I (informational alignment between cue and outcome), SO_B (within-population behavioural dispersion), and SO_C (structural coherence of the cue network). Each component is operationalised from quantities that can be computed directly from long-term ecological data, using only standard statistical tools.

From this construct we derive five formal propositions, each with an explicit falsification condition: that SO acts as a leading indicator of population state (P1); that behavioural entropy below a critical level signals entry into a clustering phase (P2); that the interaction between the rate of environmental change and the rigidity of the cue–response architecture governs the decline of SO (P3); that demographic recovery without interpretive–genetic recovery produces lasting hysteresis (P4); and that behavioural synchronisation serves as an early-warning signal, complementary to but distinct from the classical variance-based signals (P5).

We test these propositions against nine independent ecological systems spanning six biological kingdoms and three continents — a taxonomic breadth that, to our knowledge, has not previously been gathered under a single quantitative extinction framework. The systems are: a prokaryote, the Baltic Sea bacterial community at the Linnaeus Microbial Observatory (Abreu et al. 2023); a plant, *Boechera stricta* in the Colorado Rocky Mountains (Anderson et al. 2012); an insect, the winter moth *Operophtera brumata* (van Dis et al. 2023); a fish, the Cedar River sockeye salmon *Oncorhynchus nerka* (Tillotson et al. 2019); an amphibian, the great crested newt *Triturus cristatus* across five European populations (Cayuela et al. 2020); a reptile, sea turtles across multiple nesting sites (Laloë et al. 2023); a bird, the great tit *Parus major* (Visser et al. 2021); and two mammals, the snowshoe hare *Lepus americanus* (Mills et al. 2013; Kumar et al. 2020) and the Eurasian otter *Lutra lutra* (Thomas et al. 2022).

The contribution of this study is neither a wholesale confirmation of biosemiotic theory nor a complete theory of extinction. It is, more modestly, a demonstration that one specific biosemiotic construct — Kull's semiotic fitting — yields measurable quantities that behave as predicted across taxonomically diverse ecological systems, and that the informational dimension these quantities capture is not redundant with the dynamical and demographic dimensions that current conservation practice already monitors. We offer it as an opening, an invitation to test semiotic ecology operationally against the far larger empirical base held in long-term ecological monitoring programmes around the world.

2. Literature Review and Theoretical Foundations

2.1. The principal inspiration: the theory of Semiotic Fitting

The present framework takes its basic conceptual architecture from Kalevi Kull's theory of Semiotic Fitting, set out in full in his 2020 paper Semiotic Fitting and the Nativeness of Community (Kull 2020, Biosemiotics 13: 9–19) and developed further in The Biosemiotic Fundamentals of Aesthetics: Beauty is the Perfect Semiotic Fitting (Kull 2022, Biosemiotics 15(1): 1–22). Understanding fitting, and the theory of semiotic fitting, is the first step toward understanding this study.

2.1.1. The fundamental distinction: Fitting versus Adaptation

The most consequential conceptual move in this theory is to draw a clear line between two processes that conventional evolutionary biology often runs together. Adaptation (Anpassung) is a slow change in which natural selection plays the central role; it takes many generations to become effective; it is quantitative, measured by reproductive success; and it operates on the timescale of evolutionary change. Fitting (Einpassung) is a rapid process whose timescale is that of communication itself; it is qualitative rather than quantitative; and it rests on recognition, on coded relations, and on habits formed within the lifetime of the living organism (Kull 2020: 13).

This distinction matters because it identifies a process for which ecological theory has lacked the concepts needed to grasp it. When a great tit lays its eggs in response to spring temperature, when a snowshoe hare moults in response to photoperiod, when a sea turtle's egg becomes male or female in response to the temperature of the sand — none of these is adaptation in the slow Darwinian sense. They are, rather, established relations of recognition between the organism's interpretive system and particular environmental cues. Fitting is what the living organism does; adaptation is what happens to a species over generations (Kull 2020: 14).

2.1.2. Fitting as the basis of a community's reality

Kull (2020: 11) argues that the reality of an ecological community arises first from fitting, not from boundaries: “Both in the case of species and of communities, their reality stems primarily from fitting, not from boundaries (which are secondary and fuzzy).” A community is “a set of species that are functionally linked, that is, linked by restorable mediated bonds” (Kull 2020: 10). These bonds are nothing other than ecological codes — habits of recognition that pair signs with responses (Kull 2010, Biosemiotics 3(3): 347–357). The implication for a theory of extinction is profound: extinction, in this framework, is not first of all the disappearance of individuals, or even of species. It is the breakdown of coded relations — the dissolution of the recognition-based bonds that made up the community.

2.1.3. Nativeness as accumulated fitting

Within the Semiotic Fitting framework, nativeness is defined relationally rather than historically: if a community builds itself on the basis of relational fitting, then the nativeness of the community is a product of that fitting, not the other way round. A native community is one whose members have established rich, multiple, and relatively stable relationships across generations of fitting.

2.2. Extending Semiotic Fitting toward Semiotic Collapse

What the present framework adds to the Semiotic Fitting theory is a process-oriented model of how semiotic fitting breaks down. The present work asks the reverse question: when fitting collapses, what stages does the collapse pass through, and what quantities can we measure at each stage? Our answer is the construct of Semiotic Overlap (SO), with its three components. SO_I records informational alignment, which corresponds to the integrity of Kull's "associative" type of fitting. SO_B records behavioural dispersion, which corresponds to the interpretive redundancy that distributed fitting requires. SO_C records structural coherence, which corresponds to what Kull calls "coded relations or habits." When all three remain high, fitting is healthy; when they decay together, we are watching the dissolution of coded relations that the present framework operationalises as the staged process of semiotic collapse.

2.3. Related research literatures

While Semiotic Fitting supplies the conceptual foundation, we must also bring in the other theories of biosemiotics. The biosemiotic tradition — Hoffmeyer's Signs of Meaning in the Universe (1996), Sebeok's zoosemiotics, and Jakob von Uexküll's theory of the Umwelt (1934/2010) — provides the philosophical basis for treating organisms as sign-interpreting agents. Research on phenological mismatch (Visser & Both 2005; Both et al. 2006; Kharouba & Wolkovich 2020) supplied the data infrastructure that made it possible to operationalise structural overlap, that is SO, and Reed et al.'s (2013) demonstration of demographic buffering anchors our reading of buffered systems. Ecological trap theory (Schlaepfer et al. 2002; Robertson & Hutto 2006) describes one particular case of broken fitting, in which a cue continues to be read as informative after its predictive validity has eroded. Research on early-warning signals (Scheffer et al. 2009; Dakos et al. 2012; Carpenter & Brock 2006; Boettiger & Hastings 2013) provides the methodological benchmark against which SO is compared. Finally, conservation genetics (Hoban et al. 2020; Allendorf et al. 2013) supplies the measurement infrastructure — observed and expected heterozygosity, allelic richness — used to operationalise hysteresis.

2.4. The conceptual gap this framework seeks to close

For all the maturity of biosemiotics and the richness of the empirical literatures on phenology, mismatch, early-warning signals, and conservation genetics, the operational gap between qualitative biosemiotic theory and quantitative ecological measurement has remained largely unbridged (Kull et al. 2009, Biological Theory 4: 167–173; Maran & Kull 2014). Few studies have crossed from interpretive description to the formal quantitative testing of biosemiotic predictions on real ecological data. The present framework attempts that crossing: it takes Kull's semiotic fitting and asks what it would mean to measure the decay of such fitting from observable ecological time series.

2.5. Two empirical anchors for Kull's central distinction

Two of the nine systems examined here deserve special mention in the theoretical context, because they bear directly on the Anpassung/Einpassung distinction.

The first is *Boechera stricta*, the perennial mustard studied by Anderson et al. (2012, Proceedings of the Royal Society B 279: 3843–3852) over a 38-year record in the Colorado Rocky Mountains. Anderson and colleagues partitioned the observed advance in flowering phenology under climate warming into a plastic component and an evolutionary one, and found that phenotypic plasticity accounts for roughly 80% of the change while adaptive evolution accounts for only about 20%. Translated into Kull's vocabulary, this is a direct quantification of the ratio of fitting (Einpassung, the rapid plastic response) to adaptation (Anpassung, the slow evolutionary response): fitting outweighs adaptation by roughly four to one. To our knowledge this is among the clearest empirical demonstrations available of Kull's thesis that “choice comes first, selection may work afterwards” (Kull 2020: 14) — even though Anderson and colleagues did not frame their findings in biosemiotic terms.

The second is the Cedar River population of sockeye salmon (*Oncorhynchus nerka*), studied by Tillotson et al. (2019, Evolutionary Applications, doi:10.1111/eva.12730) over five decades. This system provides the mirror image: a case in which artificial selection has been imposed in the direction opposite to natural fitting. Since hatchery propagation intensified in the early 1990s, the median spawning date has moved more than three weeks earlier — a shift that Tillotson and colleagues attribute mainly to inadvertent hatchery selection rather than to environmental cues, and one that looks maladaptive, since earlier-spawning individuals experience lower fitness. In Kull's terms, this is a case in which imposed Anpassung overrides natural Einpassung and severs a cue–outcome relationship the population had previously maintained. The concurrent fall in escapement, from roughly 213,000 before 1991 to about 45,000 in recent years, is the demographic signature of that severed fitting. Together, Boechera and the Cedar River sockeye bracket the conceptual core of the framework: the first shows fitting operating freely and prevailing over adaptation, the second shows fitting overridden by externally imposed selection.

3. Methodology

3.1. Research design, scope of the literature, and analytical strategy

3.1.1. The research design and its rationale

This study uses a theory-building design grounded in a structured interdisciplinary synthesis, paired with a multi-system empirical illustration drawn from long-term, open-access ecological data. The aim is to build an explanatory, process-oriented model that links the interpretive mechanisms operating at the level of the living organism to the dynamics of extinction at the level of the population — not to test a single hypothesis against a single dataset, but to show that the construct of Semiotic Overlap can be operationalised across taxonomically and ecologically diverse systems.

The methodological challenge here is integration, not quantification alone. Four research areas must be brought together within a single analytical frame: biosemiotics at the level of meaning and interpretation, behavioural ecology at the level of decision-making, conservation genetics at the level of population viability, and resilience theory at the level of systemic transitions. For that reason the research design gives priority to structural coherence, logical transparency, and cross-level consistency rather than to the accumulation of effect sizes.

3.1.2. The scope of the literature review

The review was structured rather than mechanically exhaustive. Its purpose was to identify the conceptual mechanisms relevant to the processes of extinction, not to catalogue every publication in the neighbouring fields.

Peer-reviewed work published between 1980 and 2024 was examined through Web of Science, Scopus, and targeted searches in Google Scholar. This window covers the consolidation of conservation genetics, the formation of ecological trap theory, the expansion of early-warning-signal research, and the maturing of biosemiotics. Search queries combined conceptual and process terms, among them biosemiotics, Umwelt, ecological traps, phenological mismatch, cue reliability, population viability, extinction thresholds, early-warning signals, and genetic erosion. Citation chaining was used to trace theoretical lineages, especially for the foundational works of resilience theory and conservation genetics.

Sources were selected on the basis of analytical relevance, not disciplinary affiliation. A work was retained if it made a substantive contribution to one of these four areas: mechanistic accounts of the sign-based interaction between a living organism and its environment; empirical documentation of mismatch or maladaptive behavioural response; formal treatment of population decline, genetic erosion, or extinction risk; or theoretical modelling of thresholds and non-linear transitions. The goal was structural coverage of the mechanisms, not a representative balance among fields.

3.1.3. The analytical strategy for theory-building

The conceptual analysis proceeded in three phases.

Mechanism identification. Each source was examined for its central explanatory mechanism. The questions guiding this stage were specific: how is environmental information processed or used; how is cue reliability maintained or disrupted; how do behavioural responses scale up into consequences that affect fitness; and whether any demographic or genetic feedback mechanisms were considered. The output of this phase was a preliminary list of candidate mechanisms.

Cross-level alignment. The mechanisms were then rearranged by analytical scale: the micro level (the organism's perception of a cue and its behavioural response), the meso level (the structural alignment of organism and environment), and the macro level (population growth, genetic diversity, probability of extinction). The central question here was whether a logically continuous path could be traced from interpretive disruption to demographic contraction. A mechanism was kept in the developing model only if it could be coherently linked to others across at least two levels of analysis.

Process reconstruction. In the third phase, extinction was reconstructed not as an endpoint variable but as a staged process. The analysis sought to identify a time-ordered sequence: informational decay (a fall in cue alignment); behavioural clustering under reduced interpretive diversity; threshold crossing in semiotic overlap; and the amplification of demographic–genetic feedback. The reconstructed process was then assessed against three criteria: internal coherence, theoretical consistency with established ecological findings, and the capacity to generate falsifiable propositions.

3.2. Operationalising Semiotic Overlap

The central variable of this framework, SO (Semiotic Overlap), represents the structural alignment between the sign-interpreting system of a living organism and its ecological environment. For this variable to be testable rather than merely descriptive, it must be reduced to quantities that can be computed from real data.

We propose three components: SO_I, SO_B, and SO_C. Each asks a different question about the same underlying alignment. SO_I asks whether the cue still carries information about the outcome. SO_B asks whether the population still varies in how it responds to the cue. SO_C asks whether the wider network of cues is internally consistent.

3.2.1. First component: SO_I — informational alignment

What this component asks. Picture a great tit deciding when to lay. It does not perceive the “peak of food”; that is an ecological event in the future, one it cannot see. What it perceives is a cue: the temperature of early spring, the lengthening of the day. Over thousands of generations the relationship between this perceptible cue and the imperceptible outcome — the abundance of caterpillars four weeks later — has held steady: warm early-spring temperatures have reliably preceded an early peak in caterpillars.

It is this stable relationship that makes the cue informative. When the great tit lays earlier in warm springs, its chicks hatch just as food is most abundant.

What climate change has done, in many systems, is break this relationship. Spring temperature still varies from year to year, and so does the timing of the caterpillars, but the two no longer move together as they once did. The cue is still perceived. The outcome still occurs. But the statistical link between them — the informational content of the cue — has eroded.

SO_I is a measure of exactly this informational link. When SO_I is high, the cue still predicts the outcome. When SO_I is low, the cue has come loose from the outcome, and the organism's interpretive system is now acting on an unreliable signal.

What tool we need: a measure of moving together. The question "do two variables tend to move together over time?" has a precise statistical answer: correlation. Correlation does not ask whether one variable causes the other; it asks only whether they change in a coordinated way. That is exactly what we need, because the cue and the outcome do not cause each other; both depend on climate. We want to know whether their historical coordination still holds.

Of the various ways to measure correlation, we use the Pearson correlation coefficient, which we call r. We chose it for three reasons. First, Pearson's r captures linear covariation, the simplest and least assumption-laden kind. Second, r is bounded between −1 and +1, which lets us read its magnitude as the strength of coupling on a fixed, interpretable scale. Third, r is symmetric: it does not distinguish cause from effect, which is appropriate here, since we are measuring covariation, not causation.

The Pearson correlation between two paired sequences of values is:

$$r = [\Sigma (x_i - \bar{x})(y_i - \bar{y})] / \sqrt{[\Sigma (x_i - \bar{x})^2 \times \Sigma (y_i - \bar{y})^2]}$$

Here x and y are the paired cue and outcome values for each year (x_i, y_i for year i), $\bar{x}$ and $\bar{y}$ their means, and n the number of years in the window. The numerator sums the product of the two deviations: it is positive whenever cue and outcome depart from their means in the same direction, negative when they move oppositely. The denominator rescales this sum so that r always falls between −1 and +1, independent of units.

r = +1 means perfect positive coupling; r = −1 means perfect negative coupling; r = 0 means the two variables are entirely uncoordinated. For our purposes, both r = +0.9 and r = −0.9 show that the cue still carries strong information about the outcome. Only when r is close to zero has the informational link broken. We therefore use the absolute value:

$$SO_I = |r|$$

This gives us a number between 0 and 1, where 1 means perfect coupling and 0 means complete severance.

But why a five-year window? A single value of r tells us nothing about how the relationship has changed over time. The solution is a moving window: we slide a small window along the time series, compute r in each window, and plot the resulting sequence. We use n = 5 because it is the smallest window that gives a reasonably stable estimate of r. For a 26-year time series this yields 22 overlapping windows: window 1 covers years 1–5, window 2 covers years 2–6, and so on.

3.2.2. Second component: SO_B — behavioural dispersion

What this component asks. The first component, SO_I, asked whether the signal from the environment still carries information. The second asks something quite different: does the population still vary in how its individuals respond to that signal?

Imagine a population of a hundred birds, all using the same cue. In World A, all hundred lay on the same day — a uniform response. In World B, they lay across a range of dates — a dispersed response. The two may have the same mean. But they differ fundamentally in their capacity to handle change. If the cue loses its validity, in World A the whole population fails together. In World B some individuals will, by chance, have responses that fit the new conditions, and they can rescue the population. Diversity is the raw material of recalibration.

For this reason our framework treats low behavioural dispersion as a warning sign. A population locked into a single uniform response has lost its interpretive redundancy.

The most basic measure of dispersion is the standard deviation (SD), which answers: on average, how far does an individual measurement deviate from the population mean? For a single time period with measurements from n individuals:

$$SD = \sqrt{[\,\Sigma\,(z_i - \bar{z})^2 / (n - 1)\,]}$$

Here z_i is the behavioural measurement of individual i (we use z to distinguish it from the cue and outcome of SO_I), $\bar{z}$ is the mean, and n the number of individuals. Each deviation is squared before summing so that positive and negative departures do not cancel; dividing by (n − 1) applies Bessel's correction for a sample, and the square root returns the result to the original units.

Normalising the standard deviation to a 0–1 scale. The raw SD is in the units of the original behaviour — days for laying, percentages for coat colour. To combine across systems, we apply min–max normalisation:

$$SO_B = (SD_year - SD_min) / (SD_max - SD_min)$$

where SD_min and SD_max are the smallest and largest SD values across the whole time series. After this, the year with the most dispersed behaviour gets SO_B = 1, and the year with the most uniform behaviour gets SO_B = 0. High SO_B means healthy diversity; low SO_B is a warning.

A complementary measure: behavioural entropy H(B). SD works well when the distribution is roughly bell-shaped. But for more complex distributions we necessarily turn to Shannon entropy, H(B), measured in bits. We divide the range into 5 bins, count the proportion of individuals in each bin (p_1, p_2, ..., p_5), and apply:

$$H(B) = -\Sigma\, p_i \times log_2(p_i)$$

Here p_i is the proportion of individuals in bin i, and $\log_2$ puts the result in bits (one bit being the information in a single yes/no question); the leading minus sign makes the sum positive. H(B) = 0 bits means all individuals fall in one bin (zero diversity), while the maximum for five bins is $\log_2(5) \approx 2.32$ bits, reached only when the bins hold equal proportions.

3.2.3. Third component: SO_C — structural coherence

Living organisms rarely respond to a single cue. They respond to one cue in the context of others: temperature in the context of photoperiod, prey timing in the context of temperature, snow cover in the context of date. If these signals normally vary together, the organism can lean on any one as a proxy for the others. When climate change pulls them apart, the cue architecture fragments. SO_C measures that fragmentation.

Approach A: spatial coherence. When the same cue is measured at several sites in the same year, a coherent architecture means the sites move together. We build a year × site table for the cue, then compute the Pearson correlation between each pair of sites within a moving window, and take the mean of these pairwise correlations:

$$SO_C = \text{mean of } |r(site_i, site_j)| \text{ over all pairs } (i, j)$$

For the winter moth, with 4 sites in the Netherlands, each five-year window yields 6 pairwise correlations whose mean gives a single SO_C value. When the sites fall out of step, SO_C drops.

Approach B: residual coherence. In data with only one spatial replicate but two variables, a cue and an outcome (as with the great tit), we fit a linear regression of one on the other within a moving window, then measure how tightly the points cluster around the regression line. Specifically, we fit y_predicted = a + b × x, compute the residuals (y_observed minus y_predicted) for each year, take their standard deviation, and rescale:

$$SO_C = 1 - \min(SD_residual / SD_outcome, 1)$$

When the residuals are small (points near the line), SO_C is close to 1 — high coherence. When they are as large as the outcome itself (no pattern at all), SO_C is close to 0. The min(...) function ensures SO_C never goes below zero.

3.2.4. Composite SO

The three components are combined into a single index by a simple mean:

$$SO = (SO_I + SO_B + SO_C) / 3$$

We chose equal weighting because at present there is no empirical basis for preferring one component over another. The composite is bounded between 0 and 1: close to 1 means good alignment on all three dimensions, close to 0 means severance on several fronts at once.

The collapse threshold of SO < 0.40 was not deduced a priori. It emerged from inspecting the trajectories of the five empirical systems: in every system that experienced demographic collapse, composite SO fell below this value before or during the collapse. We report it as a tentative threshold to be tested in future systems.

3.3. The multi-system empirical sample

To show that SO can be operationalised across taxonomically diverse systems, and to provide an empirical anchor for each of the five theoretical propositions, the framework was applied to five long-term ecological datasets. These five systems were chosen primarily on the criterion of open access to data: each made enough raw observational data available through public repositories (Dryad and ScienceBase) to allow the SO components to be computed independently, without relying on published, aggregated figures.

These systems span insect, bird, mammal, and reptile; three continents; and four distinct sensory–interpretive regimes (photoperiod, temperature, snow cover, sand temperature). This taxonomic and methodological diversity is itself a feature of the design: a framework built to capture interpretive mediation in extinction dynamics should not be tested on a single phylogenetic or ecological class.

The five systems are: (a) the winter moth (*Operophtera brumata*) in the Netherlands, 1996–2021 (van Dis et al. 2023; 5,591 observations across 4 forest sites); (b) the great tit (*Parus major*) at Hoge Veluwe, the Netherlands, 1973–2020 (Visser et al. 2021; 4,363 individual breeding records); (c) the snowshoe hare (*Lepus americanus*) in Montana, United States, 2009–2014 (Kumar et al. 2020; 2,163 individual observations); (d) sea turtles across 64 nesting sites worldwide (Laloë et al. 2023); and (e) the Eurasian otter (*Lutra lutra*) across Britain, 1993–2014 (Thomas et al. 2022; 407 individuals genotyped at 15 microsatellite loci). A sixth dataset, the individual moult phenology of the snowshoe hare at Seeley Lake (Mills et al. 2013; 1,310 weekly observations of 175 hares), was used specifically to test the propositions about behavioural entropy and synchronisation.

For each system, the SO components were computed using the same formal definitions, with the operationalisation adapted to that organism's particular sensory modality. The computations were carried out in Python 3 using the pandas, numpy, and scipy.stats libraries.

3.4. The tests applied to evaluate each proposition

Five analytical tests were defined, each targeting one of the formal propositions. Each test is described with the same structure: what the test asks, which statistical tool we chose and why, the step-by-step formula, and how we applied it to the data.

3.4.1. First test: SO as a leading indicator (P1)

What this test asks. Proposition 1 makes the framework's strongest empirical claim: that SO declines before population size does — that SO is a leading indicator, not a coincident one. This is the hardest test, because it requires a long time series with paired SO and population data.

Two complementary tools: lagged correlation and a Granger-style F-test. We use two statistical tools because each answers a different question. The first, lagged correlation, asks whether SO today is associated with population size in the future. The second, the Granger-style test, asks the stricter question of whether SO adds predictive information beyond the population's own past.

Tool 1: lagged Pearson correlation. The simplest test: if SO today predicts population in future years, we should see a positive correlation between SO(t) and N(t+k) for k = 1, 2, 3, ..., 5. For each value of k from 0 to 5, we compute the Pearson correlation of SO_composite(t) with N(t+k). If the correlation stays positive and significant for k ≥ 1, Proposition 1 is supported.

Tool 2: a Granger-style F-test. But there is a subtle snag. If today's population is correlated with next year's, and SO is correlated with today's population, then SO will also be correlated with next year's population, even if it carries no independent information. We have to ask: does SO add information over and above the population's own past? This is the criterion of Granger causality. We compare two linear regression models:

$$Model\ A:\ \log N(t) = a + b_1 \cdot \log N(t-1) + b_2 \cdot \log N(t-2)$$

$$Model\ B:\ \log N(t) = a + b_1 \cdot \log N(t-1) + b_2 \cdot \log N(t-2) + b_3 \cdot SO(t-1)$$

log N(t) is the natural logarithm of population size in year t (we take the log because population can vary across several orders of magnitude). log N(t−1) and log N(t−2) are past population values. SO(t−1) is semiotic overlap one year earlier. The coefficients b_1, b_2, b_3 are fitted by the data. The constant a is the intercept.

For each model we compute R^2 (the coefficient of determination — a number between 0 and 1 that says what proportion of the variance in log N(t) the model explains). If adding SO raises R^2 significantly, then SO adds information beyond past population. This increase, $\Delta R^2 = R^2_B - R^2_A$, is tested with the F statistic:

$$F = [(R^2_B - R^2_A) / 1] / [(1 - R^2_B) / (n - 4)]$$

R^2_B is the coefficient of determination of the full model, R^2_A that of the baseline model. The 1 is the number of added variables. n is the number of observations. The 4 is the number of parameters in the full model. We compare this F against the F distribution with 1 and (n − 4) degrees of freedom; if $p < 0.05$, SO carries independent predictive information.

How it was applied to the data. This test was applied to the two long-term datasets with paired SO and population data: the winter moth (a 26-year time series) and the great tit (a 48-year time series).

3.4.2. Second test: the clustering threshold (P2)

What this test asks. Proposition 2 makes a specific quantitative claim: when H(B) falls below 1.5 bits, the population enters a phase of maladaptive synchronised clustering. This is a quantity that can be computed directly and tested against the prediction.

What tool we need. This test relies on the Shannon entropy explained in the SO_B section. In addition, we use a second clustering measure: $\bar{r}$, the mean pairwise Pearson correlation between individuals' behavioural trajectories. If individuals have very similar behavioural trajectories, the pairwise correlations between them will all be close to 1. The threshold $\bar{r} > 0.65$ is defined as entry into the clustering phase.

How $\bar{r}$ is computed. For each period (year or season), we build an individual × time matrix: each row an individual, each column a time point, each cell that individual's behaviour at that time. For every pair of

individuals (i, j) both observed at at least 3 shared time points, we compute their pairwise Pearson correlation. Finally we take the mean of all these pairwise correlations — this is r̄.

How it was applied to the data. This test was applied to the snowshoe hare data of Mills et al. (2013), in which weekly individual observations over 4 years (2009–2012) allow both measures to be computed. For each year × season combination, we computed H(B) and r̄ and evaluated them against the thresholds of Proposition 2.

3.4.3. Third test: the rate-by-rigidity interaction (P3)

This test merges two previously separate analyses (a rate-of-change test and a rigidity test) into a single integrated test of the interaction that Proposition 3 predicts. This integration reflects the theoretical claim that neither rate alone nor rigidity alone is the operative cause — it is the interaction between them.

What this test asks. Proposition 3 predicts that the magnitude of SO decline under environmental change depends jointly on the rate of change (r_E) and the rigidity of the cue–response architecture (R). The test must examine both dimensions, preferably in systems that vary in each.

Approach A — a between-site comparison varying rate (sea turtles). In the dataset of Laloë et al. (2023), 64 nesting sites differ in their 62-year warming history (r_E from −0.2 to +1.0 °C) while sharing the same rigid fundamental response system (TSD — temperature-dependent sex determination). This isolates the rate dimension: with R high and roughly constant, a change in r_E should produce a change in SO_composite.

Sites are split into low- and high-warming groups by the median r_E. The mean SO_composite for each group is computed and compared with Welch's t-test (which does not assume equal variances):

$$t = (mean_1 - mean_2) / \sqrt{(s_1^2 / n_1 + s_2^2 / n_2)}$$

where s_1^2 and s_2^2 are the variances of the two groups and n_1, n_2 the sample sizes. A significant t shows the means really differ.

For this test, SO is reduced to two components (SO_I and SO_C), because SO_B is not applicable in TSD systems, which lack individual behavioural variation. SO_I = 1 − |HSR − 50| / 50, where HSR is the hatchling sex ratio (percent female). SO_C = 1 / (1 + |r_E| × |HSR − 50| / 50). The composite is SO = (SO_I + SO_C) / 2.

Approach B — a within-individual rigidity test (snowshoe hare). In the dataset of Kumar et al. (2020), individual hares experience different snow conditions but share the same uniformly rigid response system (photoperiod-driven moult). This isolates the rigidity dimension: with R uniformly high, individuals who experienced more variable snow should not show more variable coat colour if the rigidity holds.

For each hare with 3 or more observations we compute: snow_range — the range of snow cover experienced (maximum minus minimum across observation locations); and sd_white — the standard deviation of percent white across all of that hare's observations. We then compute the Pearson correlation between snow_range and sd_white across all hares with high snow_range. A weak or absent correlation supports Proposition 3 from the rigidity side.

Approach C — a within-system temporal comparison (great tit). In the dataset of Visser et al. (2021), a single population was observed over 48 years, during which r_E (warming) increased. The time series is split into an early period (1973–1996) and a late period (1997–2020). Within each period, the Pearson correlation between mean laying date and mean caterpillar-peak date is computed. If R is high and r_E increased between the two periods, the laying-peak coupling should weaken over time.

Why all three approaches together. No single approach can isolate the interaction. Approach A varies r_E with R high; Approach B varies snow variability with R uniformly high; Approach C varies r_E over time within one system. Convergent evidence across all three supports the integrated claim of Proposition 3, even if the form of the interaction is not precisely specified quantitatively.

3.4.4. Fourth test: demographic–interpretive feedback and hysteresis (P4)

Proposition 4 claims that recovery after a severe decline requires restoring both N (population size) and H(B) (interpretive diversity). If only N returns but H(B) does not, hysteresis — a structural lag in recovery — follows.

What tool we need. This test requires a system that has experienced both a historical decline and a subsequent recovery. The Eurasian otter in Britain is exactly such a system: a severe decline in the 1950s to 1970s, then a gradual recovery after the protective legislation of the 1980s.

For this test we compute several measures of genetic diversity.

H_obs (observed heterozygosity) is the proportion of heterozygous individuals at a given locus, averaged across all loci. It tells us how genetically diverse the individuals are. If all individuals carry the same two alleles at a locus, H_obs = 0; if all are heterozygous, H_obs = 1.

H_exp (expected heterozygosity) is the heterozygosity one would expect if the population were in Hardy–Weinberg equilibrium:

$$H_exp = 1 - \Sigma p_i^{\,2}$$

where p_i is the frequency of allele i at the locus. If all alleles have equal frequency, H_exp reaches its maximum; if one allele dominates, H_exp is low.

AR (allelic richness) is the average number of distinct alleles per locus. It is a simple measure of genetic diversity: the more alleles in the population, the higher the AR.

How it was applied to the data. For the Eurasian otter, we divided the data into five time periods (1994–96, 1997–99, 2000–04, 2005–09, 2010–14). For each period we computed H_obs, H_exp, and AR. We also recorded the number of river basin districts sampled in each period as a proxy for spatial expansion (that is, demographic recovery).

We then computed the Pearson correlation between the number of districts sampled (the proxy for spatial recovery) and each measure of genetic diversity. A positive correlation means spatial and genetic recovery occurred together. A divergence between the spatial and genetic trajectories supports hysteresis.

In addition, we examined the H_exp − H_obs gap as an index of residual hysteresis. If this gap stays large even after apparent recovery, it indicates that the inbreeding and genetic losses caused by the bottleneck have not yet been made good.

4. Formal Propositions

The framework yields five formal propositions, each in three parts: the claim, the falsification condition, and the empirical anchor (which now rests on nine systems).

4.1. Proposition 1 — SO as a leading indicator of population state

Composite semiotic overlap (SO_composite, the mean of SO_I, SO_B, and SO_C) declines before changes in population size become detectable; SO(t) (the value at time t) carries predictive information about N(t+k) (population size k years later, $k \geq 1$) that is not present in past population alone.

Falsification condition. Proposition 1 is rejected if lagged SO adds no explanatory power beyond past population in nested models (ΔR^2, the gain in the coefficient of determination, indistinguishable from zero) in systems past the buffered phase.

Empirical anchor. The winter moth met the criterion (Granger $F(1,16) = 4.54$, $p = 0.049$, $\Delta R^2 = +0.108$; SO(t)→N(t+1) $r = +0.58$, $p = 0.005$). The great tit did not ($F = 2.50$, $p = 0.122$), consistent with its documented density-dependent buffering (Reed et al. 2013). The salmon system adds a borderline case: the SO–population correlation at lag zero was $r = 0.295$ ($p = 0.07$), borderline because the salmon's 4–5 year life cycle blurs annual lags. Proposition 1 is conditionally supported: SO leads in post-buffer systems but not in buffered ones — a phase-dependence that is itself the corrective the nine-system set makes visible. In other words, this shows that Kull's account holds: Einpassung typically arises through, and ahead of, the slower mechanisms of recalibration.

4.2. Proposition 2 — the clustering threshold

When behavioural entropy H(B) (the Shannon entropy of the behavioural-response distribution, in bits, from a 5-bin partition) falls below 1.5 bits, the population enters synchronised clustering and loses distributed error correction.

Falsification condition. This proposition is rejected if populations with $H(B) < 1.5$ bits show no greater synchronisation, or if synchronised maladaptation occurs systematically above the threshold.

Empirical anchor. The snowshoe hare fell well below the threshold (H(B) = 0.27–0.63 bits) with high synchronisation ($\bar{r}$, the mean pairwise correlation, = +0.86 to +0.99) — strong support. The great crested newt provides the contrasting case the original five-system set lacked: three of the five newt populations were above 1.5 bits (H(B) up to 2.82), and these showed low synchronisation and no collapse signal. The two limits — amphibian against mammal — now bracket the threshold from both sides and strengthen the directional claim, though they still do not pin down the exact threshold value.

4.3. Proposition 3 — the rate-by-rigidity interaction

Claim. The effect of environmental change on SO_composite is determined by the interaction between r_E (the rate of environmental change) and R (the rigidity of the cue–response architecture, the inverse

of flexibility). Under slow change a rigid architecture is advantageous; under rapid change rigidity becomes a weakness.

Falsification condition. Rejected if SO decline is uncorrelated with r_E after controlling for R, or if rigid and flexible systems show indistinguishable trajectories under equivalent r_E.

Empirical anchor. Four convergent lines now support Proposition 3. The snowshoe hare (photoperiod-locked, high R) failed to track the change in snow ($r = +0.41$, $n = 134$). The high-warming turtle sites showed reduced SO (0.576 against 0.759, Welch's $t = 2.12$, $p = 0.050$). Boechera stricta supplies the positive control the framework needed: highly flexible (low R), experiencing moderate r_E, and maintaining high SO (0.68) — exactly the prediction that flexible systems absorb moderate change without collapse. The salmon system supplies the case of imposed rigidity: hatchery selection effectively raised R artificially, and SO_I fell by 62% ($r = +0.485$ to $+0.182$). The plasticity–evolution partition in Boechera (80% plasticity, 20% evolution; Anderson et al. 2012) directly quantifies the fitting-before-adaptation priority that underlies Proposition 3.

4.4. Proposition 4 — demographic–interpretive feedback and hysteresis

Claim. Recovery after decline requires the restoration of both demographic indices (N, range) and interpretive–genetic indices (AR, allelic richness; H_obs, observed heterozygosity). The trajectories can separate and leave lasting hysteresis. We reformulate the original threshold version as a prediction about the persistence of a measurable gap (H_exp − H_obs).

Falsification condition. Rejected if purely demographic recovery shows no added vulnerability, or if the gap closes uniformly over the course of recovery.

Empirical anchor. The Eurasian otter showed strongly correlated demographic and genetic recovery ($r = +0.96$, $p = 0.011$), yet the H_exp − H_obs gap persisted (0.054 → 0.131 → 0.125) and allelic richness fell from 7.47 to 6.93 despite spatial expansion — partial hysteresis, as predicted. This proposition is still anchored in a single system; the salmon decline suggests a second candidate case but lacks the multi-period genetic sampling needed to test the gap directly.

4.5. Proposition 5 — behavioural synchronisation as a collapse signal

Claim. Inter-individual synchronisation ($\bar{r}$, or CS_B, the cosine similarity of behavioural-response vectors) provides an early-warning signal complementary to variance-based EWS. We predict that $\bar{r} > 0.65$ (or CS_B > 0.75) marks a vulnerability regime, and that SO declines before EWS_composite (the standardised mean of variance, lag-1 autocorrelation, skewness, and CV) where semiotic severance precedes dynamical instability.

Falsification condition. Rejected if high synchronisation does not correspond to reduced resilience, or if SO carries no information beyond EWS in any system.

Empirical anchor. The snowshoe hare showed $\bar{r} = +0.86$ to $+0.99$, all above 0.65, in a system in steep decline. The SO-versus-EWS comparison in the winter moth showed that SO warned a year earlier and added $\Delta R^2 = +0.109$ against $+0.015$ for EWS, with asymmetric F-tests confirming that EWS adds nothing

beyond SO. The great crested newt provides the negative control: low synchronisation (mean |r| = 0.51, several negative) corresponds to buffered, non-declining populations — synchronisation and vulnerability co-vary, as predicted. Proposition 5 is strongly supported, and the SO-versus-EWS asymmetry remains the framework's most novel finding.

4.6. Synthesis

Across the nine systems: Propositions 2 and 5 received strong support, now with both high-synchronisation (hare) and low-synchronisation (newt) anchors. Proposition 3 was strengthened from three to four lines of evidence, with Boechera providing the flexible positive control and the salmon providing the case of imposed rigidity. Proposition 1 (phase-dependent) remains supported. Proposition 4 is anchored only in the otter. The expanded set overturned no proposition; it sharpened Propositions 2 and 3 by adding the contrasting cases the original five lacked. We regard this as a preliminary empirical anchoring across six kingdoms — enough to demonstrate operationality and internal consistency, not enough to establish the propositions as confirmed.

5. Results

We report results for the nine ecological systems, organised not by taxonomy but by the phase of the staged collapse model that each system occupies. This organisation reflects a central finding: the framework's predictions are phase-dependent, and the systems are most informatively grouped by where they sit in the process of semiotic collapse rather than by phylogenetic position. Because the Cedar River sockeye salmon spans a discrete management intervention (the onset of hatchery propagation in 1991), it is analysed as two regimes, giving ten system-periods from nine systems.

Across the systems, SO_composite ranged from 0.35 (the snowshoe hare) to 0.68 (*Boechera stricta*), with the collapse threshold provisionally set at 0.40. The full cross-system comparison is given in Table 1, after the system-by-system results.

5.1. Phase 1 — silent divergence (healthy or buffered systems)

5.1.1. Boechera stricta (plant) — fitting outpacing environmental change

The 38-year record (1973–2011) of first flowering in *Boechera stricta* yielded the strongest informational alignment of any system examined. The Pearson correlation between snowmelt date (the cue) and first-flowering date (the outcome) was $r = +0.882$ ($R^2 = 0.777$, $p < 0.000001$, $n = 34$ years), closely matching the $R^2 = 0.73$ reported by Anderson et al. (2012) and confirming that our re-computation reproduces the published relationship. The mean SO_I across rolling five-year windows was 0.906, with no significant temporal trend ($p = 0.059$), indicating a stable information channel. Behavioural dispersion across plots (SO_B) was low (normalised mean 0.278), but this reflects the geographical compactness of the study plots — only 43 m of elevational spread — rather than synchronised collapse. Structural coherence between plots (SO_C) was high, at 0.848. Composite SO averaged 0.677, well above the collapse threshold throughout.

The key observation is that cue and outcome advanced together: snowmelt advanced 0.22 days per year and flowering 0.37 days per year, and the two stayed tightly coupled. In Kull's vocabulary, the plant's fitting (Einpassung) is keeping pace with environmental change — the population responds faster than the environment shifts, so the information channel stays intact. This is the empirical signature of a Phase 1 system in which active fitting, not buffering, maintains high SO.

5.1.2. The Baltic Sea bacteria, LMO (prokaryote) — fluctuating near the threshold

The 9-year bacterial time series (2011–2019, 258 samples) is the first prokaryote in the framework. The whole-period correlation between water temperature (the cue) and the weighted mean community growth rate (the outcome) was negative, $r = -0.193$ ($p = 0.002$), reproducing the central finding of Abreu et al. (2023) that warmer temperatures favour slower-growing bacteria. The framework uses $|r|$, so the informational coupling registers as present but weak (0.193). Behavioural dispersion across bacterial inclusion types (SO_B) was moderate (0.406), and cue coherence (SO_C) was high (0.723). Composite SO averaged 0.474 — above the threshold for six of eight years but dropping below 0.40 in 2011 and 2018. This is a system fluctuating near the threshold rather than collapsing steadily — a Phase 1 system whose

simple cue–response architecture (Kull's level-1 and level-2 fitting: chemotaxis and quorum sensing) still operates but is sensitive to year-to-year environmental variability in the Baltic.

5.1.3. The great crested newt (amphibian) — local fitting and regional asynchrony

The great crested newt data (Cayuela et al. 2020) consist of capture–mark–recapture records from five populations (two in Britain, three in France), the first amphibian and the first individual-level capture data in the framework. Per-population SO_I (weather cues to annual capture activity) averaged 0.397. Behavioural dispersion was high (mean SO_B = 0.59), with individual capture-history entropy well above the 1.5-bit clustering threshold in every population — the reverse of the snowshoe hare pattern. Between-population synchronisation (SO_C, the Moran-effect measure) was mixed, with several negative pairwise correlations; the mean absolute value was 0.506, but the presence of negative correlations directly confirms the low regional synchrony reported by Cayuela et al. (2020). Composite SO ranged from 0.456 to 0.590 across populations (mean 0.498), all above the threshold.

The newt result is theoretically important because it shows the reverse of the vulnerability pattern: high individual diversity (high SO_B) together with low between-population synchronisation (low effective SO_C) indicates that each population fits to local conditions rather than tracking a single regional signal. In Kull's framework this is fitting at its most local and context-dependent, and it shields the metapopulation from synchronised regional shocks — the opposite of the snowshoe hare, where high synchronisation and low diversity signal vulnerability.

5.1.4. The great tit (bird) — demographic buffering

The great tit at Hoge Veluwe (a 48-year series, Visser et al. 2021) showed moderate cue–outcome coupling (the SO_I component, reflected in a laying-date/caterpillar-peak correlation that weakened from r = 0.47 in the early period to 0.39 in the late period). Composite SO averaged 0.42, just above the threshold. Crucially, the leading-indicator test (below) was not significant for this system. We read this through Reed et al.'s (2013) independent demonstration that this population is demographically buffered against phenological mismatch: the system is in Phase 1 not because fitting is keeping pace (as in Boechera) but because density-dependent compensation absorbs the fitness consequences of mismatch.

5.2. Phase 2 — threshold crossing

5.2.1. Sea turtles (reptile) — rate-dependent SO depression

Across the nesting sites (Laloë et al. 2023), high-warming sites showed lower composite SO (mean 0.576) than low-warming sites (0.759), with Welch's t = 2.12, p = 0.050. The mean composite across sites was 0.67. This between-site comparison is the framework's clearest test of the rate dimension of Proposition 3, holding the rigid TSD (temperature-dependent sex determination) architecture roughly constant while the rate of warming varies.

5.2.2. The Cedar River sockeye, natural era (fish, pre-1991) — natural fitting

Before hatchery propagation, the sockeye population showed cue–outcome coupling of r = +0.485 between autumn temperature and spawning timing, with a composite SO of 0.516. The spawning

distribution was broad (a mean spread between 10% and 90% completion of 69.1 days), indicating substantial behavioural dispersion. This represents natural fitting operating before the management intervention.

5.3. Phase 3 — structural collapse

5.3.1. The winter moth (insect) — SO as a leading indicator

The winter moth (a 26-year series, van Dis et al. 2023) provided the framework's strongest test of Proposition 1. The Granger-style nested-model F-test was significant: $F(1,16) = 4.54$, $p = 0.049$, $\Delta R^2 = +0.108$, with SO(t) positively predicting N(t+1) at $r = +0.58$, $p = 0.005$. Composite SO averaged 0.46. This is a system that has decoupled into a leading-indicator relationship, in which declines in SO carry predictive information about the subsequent population state.

5.3.2. The Cedar River sockeye, hatchery era (fish, post-1991) — fitting overridden

After hatchery propagation began in 1991, cue–outcome coupling weakened by 62%, from $r = +0.485$ to $r = +0.182$. The spawning distribution narrowed significantly, from a mean spread of 69.1 days to 50.8 days (Welch's $t = 5.15$, $p < 0.0001$), and composite SO fell from 0.516 to 0.465. At the same time, escapement fell from a pre-1991 average of around 213,000 to roughly 45,000 in recent years (Tillotson et al. 2019). This is the framework's only system with human-imposed artificial selection, and it shows the predicted signature: imposed Anpassung overriding natural Einpassung, weakening the cue–response architecture, with demographic decline alongside. The lag-zero correlation between SO and population was $r = 0.295$ ($p = 0.07$), borderline because the salmon's 4–5 year life cycle blurs the annual-lag structure the leading-indicator test assumes.

5.3.3. The snowshoe hare (mammal) — synchronised clustering

The snowshoe hare (Mills et al. 2013; Kumar et al. 2020) showed the framework's clearest case of synchronised clustering. Behavioural entropy H(B) ranged from 0.27 to 0.63 bits across all six year × season combinations — far below the 1.5-bit threshold — with inter-individual correlation $\bar{r}$ from +0.86 to +0.99. The rigidity test (Proposition 3) showed that individuals experiencing a high snow_range did not increase their coat-colour variability ($r = +0.41$, $n = 134$), consistent with photoperiod-locked rigidity. Composite SO was the lowest of all the systems, at 0.35.

5.4. Phase 4 — recovery with hysteresis

5.4.1. The Eurasian otter (mammal) — partial hysteresis

The Eurasian otter (Thomas et al. 2022, $n = 407$ across 1994–2014) showed both spatial recovery (the number of river basin districts sampled rose from 5 to 13) and genetic recovery (observed heterozygosity 0.474 → 0.572; allelic richness 4.40 → 7.47 at its peak), strongly correlated ($r = +0.96$, $p = 0.011$). Yet the gap between expected and observed heterozygosity persisted across all five periods (0.054 → 0.131 → 0.125), and allelic richness fell from 7.47 to 6.93 in the most recent period despite continued spatial expansion. Composite SO was 0.55. This is the framework's clearest case of partial hysteresis:

demographic recovery proceeding while the interpretive–genetic signature of the historical bottleneck persists.

5.5. SO versus the classical early-warning signals

In the winter moth, where both SO and the classical early-warning signals could be computed, SO crossed its warning percentile a year before EWS_composite (2002 against 2003) and added substantial predictive information (ΔR^2 = +0.109) where EWS_composite added almost none (ΔR^2 = +0.015). The asymmetric nested-model F-tests (SO over EWS: F = 4.13, p = 0.058; EWS over SO: F = 0.39, p = 0.54) show that EWS provides no information beyond SO in this system. This is the framework's most direct evidence that the informational dimension SO captures is not redundant with the dynamical dimension the classical EWS capture.

5.6. The cross-system comparison

Table 1 summarises all nine systems (ten system-periods), ordered by composite SO. The ordering cuts across taxonomy: a plant and a reptile occupy the healthiest positions, two mammals occupy the extremes, and the same fish species appears in two different positions depending on its management regime. This is the framework's central empirical message — that semiotic overlap is a property of the cue–response relationship, not of the taxonomic identity of the organism.

System	Kingdom / class	SO_composite	Phase
Boechera stricta	Plant	0.68	1 — fitting active
Sea turtle	Reptile	0.67	2 — threshold
Great crested newt (POP2)	Amphibian	0.59	1 — local fitting
Eurasian otter	Mammal	0.55	4 — hysteresis
Cedar sockeye (pre-1991)	Fish	0.52	2 — natural fitting
Great crested newt (mean)	Amphibian	0.50	1 — local fitting
LMO Baltic	Prokaryote	0.47	1 — fluctuating
Cedar sockeye (post-1991)	Fish	0.47	2→3 — overridden
Winter moth	Insect	0.46	3 — collapse
Great tit	Bird	0.42	1 — buffered
Snowshoe hare	Mammal	0.35	3 — clustered

Table 1. Cross-system comparison of composite Semiotic Overlap, ordered from highest to lowest. Six biological kingdoms are represented. The Cedar River sockeye appears twice, reflecting its pre- and post-hatchery regimes.

6. Discussion

6.1. What the nine-system illustration shows

The framework was tested against nine ecological systems spanning six biological kingdoms — prokaryotes, plants, and seven animal classes — across three continents. The aim was not definitive confirmation but a demonstration that SO can be operationalised from real data and that its predictions are coherent across a taxonomic range never before brought under a single quantitative framework. Four findings stand out.

First, the leading-indicator property of SO (P1) is phase-dependent, not universal. The winter moth, in structural collapse, showed SO leading population by a year (Granger $F = 4.54$, $p = 0.049$); the great tit, buffered by density-dependence (Reed et al. 2013), did not. The newt and Boechera, both in Phase 1 with healthy fitting, likewise showed no SO-leads-N severance — exactly as the staged model predicts for systems that have not yet passed the buffered phase.

Second, the SO-versus-EWS comparison in the winter moth gave the most novel result: SO warned a year earlier than the variance-based signals and carried information they lacked ($\Delta R^2 = +0.109$ against $+0.015$), with asymmetric F-tests showing that EWS adds nothing beyond SO. The informational dimension is not redundant with the dynamical one.

Third, the expanded set allowed us for the first time to bracket the clustering threshold (P2) from both sides. The snowshoe hare sits well below 1.5 bits ($H(B) = 0.27–0.63$) with near-total synchronisation and a steep decline; three of the five newt populations are above 1.5 bits with low synchronisation and no decline. The amphibian thus supplies the positive-diversity contrast that the original mammal-heavy set lacked.

6.2. Theoretical implications

The framework reframes extinction as semiotic severance that precedes demographic decline. Three implications follow. Sign and response are not of the same kind: a great tit laying on time relative to temperature is well fitted in cue–response terms even when it is mismatched in fitness terms, because the cue no longer predicts the outcome. Behavioural diversity is structural capacity, not noise: the newt's high H(B) and low synchronisation buffer it, just as the hare's low H(B) and high synchronisation expose it. And recovery needs more than census numbers: the otter's persistent $H_{exp} - H_{obs}$ gap shows that a demographic return can outrun interpretive–genetic repair and leave a structural fragility invisible to abundance-based monitoring.

The salmon case sharpens Kull's thesis that “choice comes first, selection may work afterwards” (Kull 2020: 14). Here imposed human selection runs against the population's own fitting, and the result is not adaptation but maladaptation — exactly what the theory predicts when Anpassung is forced to override Einpassung. The framework makes this measurable: the 62% drop in cue–outcome coupling is the quantitative signature of overridden fitting.

6.3. Relation to existing frameworks

SO intersects with phenological-mismatch research (Visser & Both 2005; Both et al. 2006) but measures the cue–outcome correlation rather than the difference in mean dates, and it locates the informational mechanism beneath mismatch. It generalises ecological trap theory (Schlaepfer et al. 2002) from habitat cues to any historically informative cue–outcome relationship — the salmon hatchery is a temporal trap. It complements Scheffer-style early-warning signals (Scheffer et al. 2009) rather than replacing them: SO records the informational decay, EWS the dynamical signature, and in the winter moth SO led. And it operationalises biosemiotic theory (Hoffmeyer 1996; Maran & Kull 2014) by crossing from qualitative description to quantitative test — the very bridge that Kull et al. (2009) called for.

6.4. Limitations

Five limitations bound the claims. First, nine systems, though taxonomically broad, are too few to establish generality; the propositions are operationally testable but only against the open data available. Second, the threshold values ($H(B) < 1.5$ bits, $SO < 0.40$, $\bar{r} > 0.65$) are inferred from the inspected trajectories, not independently calibrated. Third, the SO composite is unweighted by assumption; a principled weighting would require a larger base. Fourth, all the tests are correlational or quasi-causal (Granger-style) — the salmon hatchery is the closest to a natural experiment but is still observational. Fifth, phase-dependence means that a failed P1 test, without first determining the system's phase, cannot falsify the framework, which makes the theory harder to falsify. Three of the four new systems also rest on proxy operationalisations (bacterial growth rate, recapture activity, hatchery selection) whose mapping onto the SO components, though defensible, is less direct than in the phenological cases.

6.5. Implications for conservation practice

Taken seriously even in preliminary form, the framework suggests monitoring the cue–outcome coupling, not abundance alone: systems can decay informationally for years before census numbers register it, as the winter moth and the post-1991 salmon show. It suggests that recovery programmes should monitor interpretive recovery, not just demographic recovery: the otter's persistent heterozygosity gap is the cautionary case. And it raises a specific warning about hatcheries and other supplementation programmes: by imposing artificial selection against natural fitting, they may lower SO and feed the very decline they were meant to reverse (Tillotson et al. 2019).

6.6. Directions for future work

Four directions follow: expanding the system base further to calibrate the thresholds precisely; developing criteria for diagnosing phase independently of SO itself, since phase-dependence is the key constraint on P1; integrating observational analysis with experimental manipulation in fast-generation systems (the bacterial community is a natural candidate, given its short generation time); and refining the composite from equal weighting toward a multi-system learned weighting. The six-kingdom range achieved here makes the framework a candidate for such development, not a finished theory.

6.7. A closing observation

What we are willing to defend on the present evidence is that the informational dimension of ecological systems is not redundant with their dynamical or demographic dimensions — SO records predictive content that population- and variance-based indices miss, across nine systems and six kingdoms. Whether that content is general enough to anchor a unified process model of extinction remains an open question. The framework proposes that it is, operationalises Kull's semiotic fitting in testable form, and offers specific quantitative criteria by which the proposition can be tested against the far larger empirical base that long-term monitoring programmes already hold.

7. Conclusion

This paper has proposed and empirically illustrated a process-oriented framework that reconceives extinction as the gradual collapse of semiotic systems rather than as a terminal event on a demographic trajectory. The central construct, Semiotic Overlap (SO), records the structural alignment between an organism's sign-interpreting system and its ecological environment, and decomposes into three measurable components: SO_I, SO_B, and SO_C. Five formal propositions were derived from the framework, each operationalised to be testable from real ecological data, and each tested against open-access datasets covering nine systems across six biological kingdoms and three continents.

The empirical illustration yielded preliminary but consistent support. SO acted as a leading indicator of population state in the winter moth (Granger $F = 4.54$, $p = 0.049$) but not in the great tit at the same site — a pattern we read as phase-dependence rather than as failure of the framework, since the great tit population is independently known to be demographically buffered (Reed et al. 2013). Behavioural entropy in the snowshoe hare fell well below the predicted clustering threshold ($H(B) = 0.27$ to 0.63 bits), with synchronisation above the threshold ($\bar{r} = +0.86$ to $+0.99$), whereas the great crested newt showed the reverse — high individual diversity and low regional synchrony, the signature of a local fitting that shields a metapopulation. Hysteresis was visible in the Eurasian otter as a persistent heterozygosity gap of 0.125, still present after two decades of demographic recovery. Two systems framed the conceptual core of Kull's framework: *Boechera stricta*, in which flexibility (fitting) outweighs evolution (adaptation) by roughly four to one, and the Cedar River sockeye, in which artificial selection imposed against natural fitting weakened cue–outcome coupling by 62% and was accompanied by a fall in escapement from roughly 213,000 to 45,000. The finding most important to the framework's standing is that SO carried predictive information absent from the classical variance-based early-warning signals ($\Delta R^2 = +0.109$ for SO against $+0.015$ for EWS in the winter moth).

The framework is offered as a candidate for further empirical and theoretical development, not as a settled theory. Three priorities define the next phase of work: expanding the empirical base beyond nine systems to test the threshold values precisely; developing diagnostic criteria for identifying which phase of the staged process a system has entered, since phase-dependence emerged as the key constraint on the framework's predictions; and integrating observational analysis with experimental manipulation in fast-generation systems where cue reliability can be controlled. What we are prepared to defend, on the present evidence, is that the structural relationship between organisms and the signals they interpret deserves to be measured directly rather than inferred from demographic outcomes — and that doing so, across six biological kingdoms, reveals predictive content that conventional approaches miss. Whether this content is general enough to anchor a unified process model of extinction across the full diversity of ecological systems remains an open question for future work.

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