How ecology can trap evolution under climate change

Madhav P. Thakur[1, *] & Catherine L. Peichel[1]

[1]*Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland*

*corresponding author (madhav.thakur@unibe.ch)

Abstract

Ecological responses to climate change, including plasticity, behaviour, demography, and interactions, can actively trap evolutionary trajectories, not simply facilitate or impede adaptation. Despite growing interest in eco-evolutionary dynamics under climate change, we lack a framework for predicting when ecological change reshapes evolutionary responses. Here, we propose three modes of eco-evolutionary traps: the Pause, where ecological buffering attenuates selection and accumulates hidden maladaptation; the Decoy, where disrupted cues steer trait evolution toward false optima or developmental dead ends; and the Surge, where rapid evolutionary tracking incurs genetic costs that erode future evolvability. We discuss these traps across evolutionary rescue, maladaptive evolution, genotype–phenotype relationships, and species interactions to predict how ecological responses shape, constrain, and redirect evolutionary trajectories under climate change.

1. Ecology sets the stage, and the traps

For decades, evolutionary ecology has focused on a central question: can populations evolve fast enough to track environmental change? **Evolutionary rescue** formalizes this as a race between a moving optimum and declining demography: if additive genetic variance is sufficient and populations persist long enough, selection can drive trait means toward a new fitness peak [1,2] (Figure 1A). Although we have a robust framework for diagnosing outcomes of this race, including **maladaptation** [3], explanations remain largely framed by quantitative constraints, such as insufficient genetic variance [4,5], demographic stochasticity [6,7], or physiological limits [8,9]. This framing often treats ecological dynamics, including species interactions, habitat selection, and **demographic storage**, as boundary conditions that set stressors and population limits rather than as processes that reshape selection gradients and targets. As a result, it can encourage the assumption that evolution is reliably beneficial [10]: if fast enough, it should restore viability by overcoming genetic and demographic constraints.

Under rapid climate change, however, ecological dynamics actively reshape the exposure, information, and interactions that define selection [11–16]. Organisms respond immediately through plasticity, habitat choice, dormancy, and shifting interactions [17,18], determining who experiences stress, when exposure occurs, and whether phenotypes are expressed in ways selection can target. Adaptive dynamics theory has long predicted that such eco-evolutionary feedbacks can generate nonlinear outcomes in which evolution leads not to rescue, but to evolutionary suicide or trapping equilibria [19]. Yet, we lack a diagnostic framework to identify when these feedbacks derail adaptation under environmental stress.

This motivates a shift in emphasis: instead of asking only whether evolution is fast enough, we must ask whether the evolutionary process itself is being disrupted. Schlaepfer et al. [20] provided the blueprint by showing how rapid environmental change can decouple cues from consequences, luring organisms into evolutionary traps of maladaptive behaviour. Here, we scale this logic from individual decisions to systemic failures of adaptive tracking under climate change. We define **eco-evolutionary traps** as situations in which ecological responses delay, misdirect, or destabilize adaptive trajectories. The paradox is that populations may look stable, or appear to track environmental change phenotypically, while hidden evolutionary risks accumulate.

We synthesize these dynamics into three trap modes that are mechanistically distinct but not mutually exclusive (Figure 1, Table 1). **Pause** reflects inertia: ecological buffers, such as

broad plasticity or demographic storage, attenuate selection, allowing maladaptation to accumulate as **evolutionary debt** [21,22]. **Decoy** reflects misdirection: environmental change uncouples cues from consequences, steering trait evolution toward false optima or **developmental dead ends** [20,23]. **Surge** reflects velocity costs: rapid evolutionary tracking incurs genomic costs, eroding genetic variance or accumulating mutation load, leaving populations vulnerable to future stress [24,25]. Together, Pause, Decoy, and Surge provide a diagnostic typology of eco-evolutionary failure modes, rate, direction, and cost, linking ecological responses to measurable signatures in phenotypes, selection gradients, genomes, and fitness outcomes (Table 1). This framework enables empirical tests of when "adaptation" restores persistence versus when it merely delays, misdirects, or destabilizes evolutionary trajectories.

2. Diagnostics of three types of eco-evolutionary traps

2.1 Pause

The pause arises when ecological buffering attenuates effective selection on heritable variation. Buffering can take the form of phenotypic plasticity, behavioural avoidance, microhabitat buffering, or demographic storage (e.g., seed banks, diapause). Because exposure to stress is often episodic (e.g., heat waves), phenotypes may appear to track environmental change while genetic change is weak relative to the phenotypic trend or to the pace of environmental change. Such buffering can buy time, but it can also accumulate a cryptic evolutionary debt when observed phenotypic responses are dominated by non-genetic components (Table 1). Demographically, pause populations may appear stable [3] – or even increasing – masking accumulating mismatch until buffering capacity is exceeded (Table1 , Box 1).

A key diagnostic signature of the pause trap is phenotypic change that is largely non-genetic. For instance, in common terns (*Sterna hirundo*), arrival dates advanced by 9.3 days over 27 years, yet estimated breeding values accounted for only ~5% of this shift [21]. This pattern implies that continued tracking could fail if environmental change pushes beyond the limits of plasticity or other non-genetic components. Plasticity is not the only buffer: temporal gene flow can deepen the pause trap even under strong selection. In annual plants, seed banks can reintroduce genotypes favoured under past conditions, slowing potential adaptation to future drought [22]. Similarly, in reptiles with temperature-dependent sex determination, behavioural buffering via maternal nest-site choice can modulate offspring

environments, potentially delaying genetic adjustment if warming outpaces the scope for behavioural compensation [26].

2.2 Decoy

This trap arises when climate change disrupts the **cue–fitness map**. Organisms rely on environmental cues (e.g., temperature thresholds, snow cover, hydrological triggers, photoperiod) to time their development, dispersal, and habitat choice; when those cues decouple from the conditions that actually determine fitness, plasticity and selection can steer phenotypes toward a **proxy optimum** that is locally attractive but maladaptive (Figure 1). Mechanistically, this reflects a liability of 'plasticity-led evolution', where the phenotypic variation exposed to selection is developmentally biased toward these false peaks, effectively steering lineages onto maladaptive trajectories [27]. It further extends the evolutionary trap logic of Schlaepfer et al. 2002 [20] from maladaptive behavioural decisions to any cue-mediated trait.

The diagnostic signature of the decoy trap is directional trait change that increases mismatch with the adaptive optimum or pushes individuals into a developmental dead end (Table 1). Simulated warming in an insect system (*Rhagoletis pomonella*) advanced life-history timing, yet one host-associated population (apple-associated) showed a large increase in maladaptive pre-winter emergence that would be fatal in nature, consistent with cue-mediated misdirection toward a decoy outcome [23]. Snowshoe hares (*Lepus americanus*) offer another decoy example: their seasonal coat-colour change follows a relatively fixed schedule, but warming has shifted when snow arrives and melts – decoupling molt timing from snow cover [28,29]. The resulting camouflage mismatch reduced survival by up to 7% per week of exposure [28], generating strong selection that could further reshape cue use or reaction norms under continued warming. Decoys can also arise through habitat choice when evolved preferences become uncoupled from realized fitness, producing persistent attraction to low-quality habitats [30]. At the community level, altered interactions can generate decoys by changing encounter rates and the reliability of heterospecific information, such that historically informative signals are no longer able to predict the fitness consequences of organismal responses to those cues [31,32].

2.3 Surge

The Surge occurs when ecological release, intense directional selection, or rapid range expansion accelerates evolutionary change, but the response incurs hidden costs that erode future **evolvability**. These costs can include depletion of standing variation under strong directional selection, accumulation of deleterious alleles through **expansion load** [33], or shifts toward fast life-history strategies that compromise tolerance to subsequent stress. This process highlights the erosion of **developmental variability** – the potential to generate novel phenotypes – which differs from the simple depletion of standing genetic variation [27].

The diagnostic signature of the surge trap is rapid phenotypic or genomic tracking of contemporary conditions coupled with reduced capacity to respond to further change. Critically, the surge populations may initially resemble successful evolutionary rescue – traits track the displaced optimum and demography may stabilize – making underlying erosion difficult to detect until additional stress exposes brittleness. In expanding or bottlenecked populations, serial founder events and allele surfing increase deleterious mutation frequency at range fronts (expansion load) [33]. **Genetic drift debt** compounds this: genomic erosion can lag behind population decline, masking future loss of adaptive capacity until subsequent stress exposes it [34,35].

Range expansion theory predicts that populations expanding into novel climates can suffer loss of genetic variation and accumulate mutation load, slowing later adaptation and increasing vulnerability [24]. Consistent with this, genomic time-series data from wild barley (*Hordeum vulgare* ssp. *spontaneum*) spanning 28 years of warming reveal climate-linked diversity loss and increased deleterious mutation burden, implying elevated genomic vulnerability under continued stress [25]. Surge dynamics can also arise through eco-evolutionary feedbacks in harvested systems: depending on whether feedbacks are synergistic or antagonistic, harvest selection can either drive rapid trait change or erode evolvability and impair persistence, even when short-term trait responses appear adaptive [36]. To identify surge diagnostics, such as variance depletion, load accumulation, or reduced performance under subsequent stress [12,14], it is helpful to define a “successful tracking” baseline. For example, experimental evolution in field mustard (*Brassica rapa*) under drought provides a useful benchmark for rapid adaptive tracking: strong, consistent selection produced largely parallel evolution of drought-escape traits within four generations, with increased fitness under drought [37].

3. Traps across eco-evolutionary processes

A better understanding of three trap modes can be achieved through their signatures in four fundamental eco-evolutionary processes: evolutionary rescue, maladaptive evolution, genotype–phenotype relationships, and ecological interactions. Across these processes, the traps represent three generic failure modes of adaptive tracking (Figure 1): rate failure (pause), direction failure (decoy), and cost failure (surge). The same empirical system can therefore be mapped simultaneously by (i) what process is at stake and (ii) which trap dominates (Box 2).

3.1 Evolutionary rescue

In rescue framing, traps specify why "sufficient variation + selection" need not translate into persistence. Pause-type failures occur when ecology relaxes or dilutes selection, so phenotypes track change while genetic response lags (Table 1). Temporally variable environments can generate this directly. Temporary environmental amelioration can impede rescue by lowering the fixation probability of beneficial mutations: favourable periods relax selection at the wrong time [38]. Similarly, temporal autocorrelation (runs of benign or stressful conditions) can inhibit tolerance evolution under growth–tolerance trade-offs, because the sequence and duration of stress, not only its long-term mean, shape which strategies are favoured [39]. Decoy-type failures arise when cue–fitness decoupling makes selection strong but mis-aimed; rapid response indicates rescue only if it reduces mismatch with the post-shift optimum (Figure 1, Table 1) [23,28]. Surge-type failures emerge in spatial or community contexts, where rapid tracking can incur hidden costs. In food webs, indirect evolutionary rescue can dominate direct rescue, and evolution in one species can reduce persistence of others, so successful rescue in one component can generate traps elsewhere [40]. Models of food-web responses to warming confirm that rapid evolution can leave persistent structural disruption even if warming reverses [41].

3.2 Maladaptive evolution

Traps clarify how maladaptation can be produced by evolution itself, not only by failure to evolve. Decoy is the most direct route: selection and plasticity follow misleading cues, producing trait change that increases mismatch or pushes individuals into dead ends (Figure 1, Table 1). Surge highlights how rapid adaptive change can become harmful when eco-evolutionary feedbacks propagate across species. In a harvested predator–prey system, prey adaptation can generate "evolutionary murder" of the predator, depending on fishing intensity and predator pressure, showing that evolution in one species can reverse persistence outcomes in another [42]. Such mismatches are likely under climate change, where interaction networks and selection targets can shift rapidly [1,12,43]. Pause can also contribute to maladaptation, but is harder to identify because buffering can be protective as

well as harmful. The key diagnostic is whether populations harbour hidden mismatch, testable via stress exposures that remove buffers and reveal whether fitness collapses. A meta-analysis in angiosperms found rapid trait shifts after environmental novelty followed by stasis, consistent with bounded responses constrained by standing variation and limited new adaptive variation [44]. Testing whether such stasis reflects stabilizing selection, Pause-, or Surge-driven mismatch requires genetic partitioning and stress tests that expose fitness consequences (Table 1).

3.3 Genotype–phenotype relationships

Which phenotypes are acted on by selection during climate change is determined by genotype–phenotype relationships, making them a primary pathway through which traps arise. Pause occurs when plasticity, behaviour, or the temporal structure of exposure weakens realized selection on heritable variation, allowing phenotypes to track change while genetic adaptation lags [45]. Decoy arises when reaction norms are triggered by cues that no longer predict fitness-relevant conditions, turning plasticity into maladaptive expression or steering populations toward proxy optima [20,23]. Surge is expected when rapid tracking erodes evolvability through variance depletion or hidden physiological costs – diagnosing it requires tracking adaptive genetic variance and costs over time, not trait means alone (Box 1). A recent meta-analysis illustrates such hidden costs: temperature variability did not affect the mean or variance of most traits, although it was associated with elevated stress-gene expression and reduced longevity [46].

3.4 Ecological interactions

Species interactions reshape demography, information flow, and selection targets, allowing traps to propagate through indirect effects and feedbacks. Pause can arise when competition or trophic suppression reduces effective population size or mutation supply, slowing adaptation even under strong environmental forcing [47–50]. Decoy can emerge when altered networks change encounter rates and the reliability of heterospecific information, such that historically informative cues no longer predict the fitness consequences of organismal responses [31], and mismatched phenological shifts can cascade across trophic levels [23]. Surge can emerge when rapid evolution in one species destabilizes others via indirect eco-evolutionary feedbacks [40], and via collapse–rescue dynamics with persistent restructuring even when evolution is allowed [41].

4. Outlook

The eco-evolutionary trap framework has implications for biodiversity forecasting and conservation. It reframes adaptive capacity as a property of trajectories, not simply standing

genetic variation [51,52], and suggests that the familiar dichotomy of climate-change "winners" and "losers" can obscure a third category: **apparent winners** that track change in the short term while accumulating hidden evolutionary risk.

Forecasting and ecological debt. Trap thinking clarifies why some ecological debts take decades to collect [14,53]. Pause systems can persist after conditions shift, paying their debt only when buffers fail. Decoy systems can appear responsive while moving toward cue-defined proxy optima that lower absolute fitness. Surge systems can track change yet lose the relevant genetic variation needed for future stress. Vulnerability assessments should therefore ask not only whether genetic variation exists, but whether selection is aligned with the fitness-relevant gradient and whether evolvability is being preserved. This logic helps explain abrupt biodiversity losses projected under climate change [54]: traps translate gradual forcing into nonlinear ecological and evolutionary tipping points.

Avoiding traps. Populations can escape traps through evolved cue use, bet-hedging, or plasticity that maintains viability without substituting for genetic tracking. Rapid evolution from standing variation can also drive demographic recovery, as recent work in *Mimulus cardinalis* demonstrates [55]. However, historically stressed populations in that study entered drought with depleted climate-associated variation, raising a key trap question: when does apparent rescue remain durable, and when does it become a Surge risk under the next stressor? Where intervention is feasible, trap-specific strategies follow from diagnostics: Pause calls for stress tests that reveal hidden mismatch before buffers fail; Decoy calls for restoring cue reliability or realigning reaction norms; Surge calls for protecting diversity-storing refugia, limiting bottlenecks, and monitoring relevant genetic variation rather than trait means alone.

Interaction networks as model arenas. Closely interacting systems, including host–parasitoid or host–pathogen pairs, obligate symbioses, and predator–prey interactions, provide powerful arenas for trap research because cue exchange, trophic mismatch, and eco-evolutionary feedbacks can be quantified on observable timescales [23,36,56]. Plant–soil microbial systems extend this agenda [57,58]: they link rapid microbial evolution to chemical signalling and host performance, and they are directly relevant to sustainable agriculture and nature-based climate solutions.

Under rapid climate change, particularly extreme climatic events, evolution is not only a question of being fast enough. Ecological responses can create inertia that delays genetic tracking, misdirection that steers trait change toward proxy optima, or rapid tracking that

erodes future evolvability. By distinguishing these as three trap modes, the framework shifts attention from adaptation rate to adaptation quality. Ecology is not passive context; it shapes the information, demography, and genetic architecture that determine evolutionary fate.

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Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work, the author(s) used ChatGPT, Gemini and Claude for re-iterative brainstorming on the topic. The author(s) reviewed and edited the output as needed and take full responsibility for the content of the published article.

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Table 1: Trap diagnostics across phenotypic, selection, and genomic metrics. Trap modes are indicated by characteristic deviations from ideal rescue (e.g., Figure 1A), in which phenotypic tracking is matched by genetic change, selection is aligned with the fitness-relevant optimum, and evolvability is maintained**.**

Diagnostic metric	**Pause**	**Decoy**	**Surge**
Phenotypic trajectory	Phenotypic tracking with weak genetic change; apparent stability until buffering limits are exceeded.	The phenotype shifts rapidly, but toward a cue-defined proxy optimum that increases mismatch with the post-shift survival optimum (e.g., the wrong timing).	The phenotype evolves rapidly and correctly tracks the optimum, often exceeding historical rates.
Selection gradient	Buffered or episodic selection; exposure reduced so selection differentials are weak despite environmental change.	Strong but misaligned selection because perceived cues no longer map to realized fitness.	Selection is extremely strong and directional, forcing a rapid shift in trait means.
Genomic signature	Cryptic or unexpressed variance maintained in storage stages or as standing variation; limited allele frequency change.	Erosion of diversity through specialization on the false peak or through demographic decline.	Diversity loss through sweeps or drift; mutation or expansion load; declining effective population size.
Fitness trajectory & population outcome	Fitness maintained under chronic stress; sharp decline under acute perturbations exceeding buffering capacity, risking abrupt collapse.	Fitness declining despite trait change; mismatch deepens as traits track unreliable cues rather than the true optimum.	Fitness initially recovers; brittleness emerges under novel or compounded stressors.
Key response variables (also see box 1)	Survival/fecundity under chronic vs. acute stress; performance gap when buffering is removed or exceeded.	Survival/fecundity over time; fitness at current trait values vs. at the optimum.	Survival/fecundity under new stressors; contemporary vs. ancestral performance; fitness variation across closely related species.

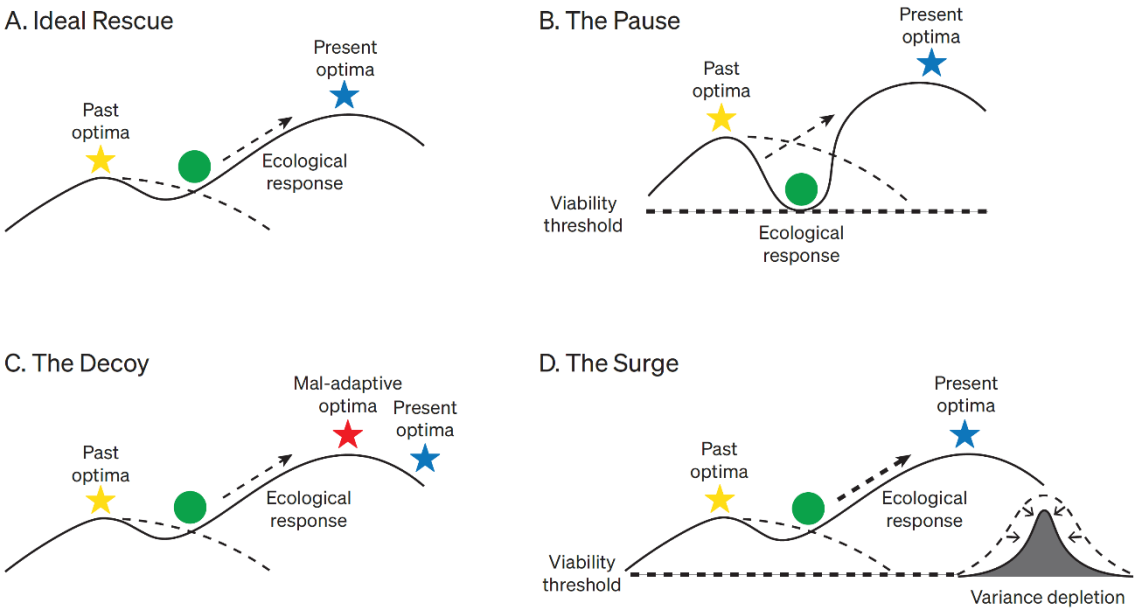

Figure 1. Adaptive landscape schematics of eco-evolutionary traps under climate change. Each panel shows a conceptual adaptive landscape (height representing fitness or a persistence-relevant performance proxy). The population mean phenotype is shown as a green ball. The dashed grey curve indicates the pre-shift landscape (shown as a truncated reference overlay, not a trajectory), and the solid dark curve indicates the post-shift landscape after climate-driven ecological change. Star colours encode optima: the yellow star marks the pre-shift optimum, the blue star marks the post-shift adaptive optimum, and the red star (panel C only) marks a cue-defined decoy optimum. The horizontal dashed black line (shown in panels B and D) denotes a **viability threshold** (a persistence boundary in absolute performance); crossing below it implies heightened extinction risk. Although shown separately for clarity, these modes can co-occur across traits or unfold sequentially through time as ecological conditions and feedbacks. **A. Ideal rescue.** After environmental change, the mean phenotype tracks the displaced optimum by moving uphill toward the post-shift optimum (blue star). **B. The Pause (inertia; rate failure).** Ecological buffering and demographic storage attenuate effective selection and slow genetic tracking. The low region occupied by the phenotype does not imply a new local optimum; it represents a zone where buffering and storage weaken the effective selection gradient, allowing mismatch to accumulate while remaining above the viability threshold. **C. The Decoy (misdirection; direction failure).** Cue–fitness decoupling draws trait change toward a decoy optimum (red star), diverting evolution away from the post-shift optimum (blue star). **D. The Surge (velocity costs; cost failure).** Tracking accelerates (thick trajectory), but rapid change erodes evolvability through **variance depletion** (inset distribution), increasing fragility to subsequent stress even when the post-shift optimum is reached and raising the likelihood of crossing the viability threshold under future perturbations.

Box 1. Experimental designs for diagnosing eco-evolutionary traps

The diagnostic signatures in Table 1 require separating phenotypic from genetic change, quantifying selection alignment, and detecting evolvability costs. Below are designs that can provide these signatures.

1. Long-term monitoring with genotype–phenotype–fitness data: Repeated annual or seasonal sampling of trait distributions, fitness components, environmental covariates, and genomic markers (e.g., allele frequencies, effective population size, genetic variance) can detect all three trap modes. Pause is indicated by trait shifts with weak or delayed genetic trends. Decoy is indicated when traits track a cue while fitness or demographic performance declines. Surge is indicated when rapid genetic tracking coincides with diversity loss, variance depletion, or increased mutational load.

2. Resurrection common gardens: Comparing ancestral and contemporary cohorts in common environments, including historical and contemporary cue or stress regimes, can separate genetic change from plasticity. These experiments reveal genetic shifts in trait means, changes in reaction norms, whether cue-following has become maladaptive (Decoy), and whether standing variation has eroded (Surge).

3. Press–pulse experiments: Experiments combining a sustained environmental press (e.g., warming or drying) with intermittent pulses (e.g., heatwaves, drought, rewetting) across multiple generations are especially useful for detecting trap transitions. They can reveal when buffering fails (Pause), when rapid tracking begins to incur costs (Surge), or when repeated pulses alter cue reliability (Decoy). They require repeated measurements of traits, fitness, and genomic change rather than only start–end comparisons.

4. Cue-manipulation experiments: These are particularly diagnostic for Decoy. Cues and fitness-determining environments should be manipulated orthogonally, for example by holding photoperiod constant while shifting thermal or resource regimes. A Decoy is supported when traits track the manipulated cue, but fitness is maximized under a different cue state or environmental regime.

5. Storage-manipulation experiments: These are particularly diagnostic for Pause. Manipulating demographic storage strength (e.g., seed-bank access, diapause rates, age structure) under a consistent stress regime can reveal whether storage maintains phenotypic persistence while slowing adaptation.

Minimal requirements for trap diagnosis: To diagnose a trap mode, studies need to link phenotypic change to fitness and genetic evidence. At minimum, this requires (i) trait distributions through time, (ii) at least one fitness currency, such as survival, fecundity, or population growth, and (iii) either estimates of genetic change (e.g., genomic time series) or

a design that distinguishes genetic change from plasticity (e.g., common gardens, reciprocal transplants, resurrection experiments).

Box 2. What makes a system trap-prone?

Trap modes emerge from the interaction between ecological context, traits, and **genetic architecture**. The same species can be pause-prone for one trait, decoy-prone for another, and surge-prone in various settings. Several conditions elevate trap risk and generate testable hypotheses.

Pause-prone systems: Strong buffering capacity (plasticity, behavior, dormancy); overlapping generations or seed banks; environmental autocorrelation that sustains buffer effectiveness. Long generation times and weak selection differentials increase the chance that genomes lag while phenotypes appear to track change.

Decoy-prone systems: Heavy reliance on climate-sensitive cues (temperature thresholds, snow cover, hydrological triggers) or climate-invariant cues misaligned with warming (photoperiod). Tight developmental windows, threshold traits, and strong cue integration increase vulnerability to developmental dead ends.

Surge-prone systems: Strong directional selection combined with small effective population size; spatial expansion with serial founder events; repeated bottlenecks. Range-front populations and fragmented landscapes are especially prone to drift and load accumulation.

Finally, trap transitions conditions are not mutually exclusive. A pause can transition to a surge when a buffer breaks and selection intensifies. A decoy can deepen if cue mismatch is reinforced by shifting interactions. Diagnosing trap mode therefore informs which mechanisms most threaten persistence—and which measurements provide early warning.

Glossary

Apparent winners: *A population showing seemingly favourable responses to climate change (e.g., stable abundance, range expansion, phenotypic tracking) that may be accumulating hidden evolutionary risk through eco-evolutionary traps.*

Cue–fitness map: *The relationship between environmental cues organisms use (e.g., photoperiod, temperature thresholds) and the fitness consequences of cue-mediated responses.*

Decoy trap: *A direction-failure mode where cue–fitness decoupling steers trait change toward a maladaptive target, increasing mismatch with the true optimum.*

Demographic storage: *The buffering of population persistence via life stages that survive unfavorable periods and contribute to future recruitment (e.g., seed banks, diapause, long-lived adults).*

Developmental dead end: *A cue-induced developmental pathway or life-history state that yields near-zero fitness under current conditions (e.g., breeding outside the viable seasonal window, failed diapause termination).*

Developmental variability: *phenotypic variation generated during development by stochastic processes, threshold effects, and cue-mediated plasticity. It is broader than phenotypic plasticity because it includes variation that can arise even under similar environmental conditions, without requiring immediate genetic change.*

Eco-evolutionary trap: *Ecological dynamics under rapid change that delay, misdirect, or destabilize evolutionary trajectories, producing hidden risk even when phenotypes appear responsive.*

Ecological debts: *Delayed costs resulting from biological buffering that maintains apparent stability under environmental change (usually extremes), while accumulating hidden vulnerability that becomes evident only after later disturbance.*

Evolutionary debts: *Delayed costs of environmental change that arise when ecological buffering or rapid tracking masks a growing mismatch or erodes evolvability, such that reduced adaptive capacity becomes apparent only after additional change or stress.*

Evolutionary rescue: *Adaptive evolutionary change that reverses negative population growth caused by environmental deterioration, restoring persistence.*

Evolvability: *The capacity of a population to respond to selection, typically tied to additive genetic variance, effective population size, genetic correlations, and mutation supply.*

Expansion load: *The accumulation and surfacing of deleterious mutations at expanding range fronts due to serial founder effects and allele surfing, which can reduce fitness and hinder future adaptation.*

Genetic architecture: *The genetic basis of a trait, including how many loci contribute, their individual effect sizes, and how they interact with each other and the environment to produce phenotypes.*

Genetic drift debt: *Delayed loss of genetic diversity after population decline due to genetic drift, such that genomic erosion remains hidden until later stress exposes reduced adaptive capacity.*

Maladaptation: *A state in which trait values reduce fitness under current conditions—either relative (lower performance than alternatives) or absolute (reproduction insufficient for persistence) fitness.*

Pause trap: *A rate-failure mode where ecological buffering attenuates effective selection, allowing phenotypic tracking while genetic adaptation lags and mismatch accumulates.*

Surge trap: *A cost-failure mode where rapid tracking incurs hidden costs (e.g., variance depletion, expansion load), eroding evolvability and increasing vulnerability to further change.*

Variance depletion: *A reduction in standing phenotypic and/or additive genetic variance caused by strong selection, selective sweeps, bottlenecks, or drift.*

Viability threshold: *A persistence boundary in absolute performance separating trajectories compatible with population persistence from those associated with decline and elevated extinction risk.*