

Adaptive Validation Loops in Eco-Evolutionary Dynamics: A Formal Framework for Niche Construction

Abstract

Eco-evolutionary feedback loops represent a fundamental challenge in evolutionary biology: species evolve in response to environments they simultaneously modify. Despite growing recognition of these dynamics, we lack a unified formal framework explaining *why* such loops emerge and *how* they operate across scales. Here, we propose that adaptive systems operate through generation-validation cycles: organisms generate phenotypic variants (incomplete fitness specification), environments validate these variants through selection (partial fitness resolution), and validation itself modifies environmental conditions, creating new generation problems. This framework unifies niche construction, coevolution, and evolutionary transitions under a single mathematical structure. We derive testable predictions regarding the relationship between environmental modification rates and evolutionary rates, conservation patterns in multi-level validation hierarchies, and the re-emergence of latent phenotypes following validation removal. Our approach provides formal grounding for Baldwin effects, genetic assimilation, and ecosystem engineering, while offering novel insights into evolvability and macroevolutionary transitions.

Keywords: eco-evolutionary dynamics, niche construction, generation-validation cycles, adaptive feedback, evolutionary transitions, formal theory

1. Introduction

1.1 The Eco-Evolutionary Feedback Problem

A central challenge in evolutionary biology is understanding how organisms and environments reciprocally shape each other over time (Lewontin, 1983; Laland et al., 2011). Traditional evolutionary theory treats the environment as an external selective force acting upon organismal variation. However, organisms actively modify their selective environments through niche construction, creating feedback loops where evolution shapes ecology, and ecology shapes evolution (Odling-Smee et al., 2003).

These eco-evolutionary dynamics operate at timescales once thought to be incompatible: ecological processes occurring within generations can drive evolutionary change, while evolutionary adaptation can alter ecological dynamics (Hendry, 2017; Govaert et al., 2019). Classic examples include:

- Darwin's finches, where beak morphology evolution affects seed availability, which in turn affects selection on beak morphology (Grant & Grant, 2006)
- Guppies, where predation-driven evolution of life history traits alters nutrient cycling in stream ecosystems (Bassar et al., 2010)
- Antibiotic resistance, where bacterial evolution modifies the chemical environment for other species (Day & Gandon, 2007)

Despite extensive empirical documentation, we lack a fundamental theoretical principle explaining *why* eco-evolutionary feedback loops are ubiquitous and *how* they operate across biological scales—from molecular systems to ecosystems.

1.2 Limitations of Current Models

Existing approaches to eco-evolutionary dynamics fall into two categories:

Coupled differential equations model population dynamics and evolutionary change as simultaneous processes (Hairston et al., 2005; Schoener, 2011):

$$\begin{aligned} dN/dt &= f(N, E, \theta) \text{ [ecological dynamics]} \\ d\theta/dt &= g(N, E, \theta) \text{ [evolutionary dynamics]} \\ dE/dt &= h(N, E, \theta) \text{ [environmental feedback]} \end{aligned}$$

While mathematically tractable, these models lack a unifying principle for *why* coupling occurs or *what* determines feedback strength.

Niche construction theory emphasizes that organisms modify selective environments (Laland et al., 2016). However, it remains largely conceptual, without formal mathematical foundations specifying the mechanisms of feedback.

What's missing: A fundamental framework that:

1. Explains why feedback loops emerge as a general principle
2. Operates consistently across scales (molecular to ecosystem)
3. Generates testable predictions about feedback structure
4. Unifies disparate phenomena under a common formalism

1.3 Our Approach

We propose that adaptive biological systems operate through **generation-validation cycles**: a two-phase process where (1) organisms generate phenotypic variants representing incomplete fitness specifications, and (2) environments validate these variants through selection, partially resolving fitness values. Crucially, validation modifies the environment itself, creating new generation problems in subsequent cycles.

This framework:

- Provides a fundamental principle for eco-evolutionary feedback
- Operates across scales from molecules to ecosystems
- Unifies niche construction, coevolution, and evolutionary transitions
- Generates novel, testable predictions

The remainder of this paper develops the formal framework (Section 2), applies it to key phenomena (Section 3), derives predictions (Section 4), and discusses implications (Section 5).

2. Theoretical Framework

2.1 Generation-Validation Cycles

We formalize biological adaptation as a two-phase cyclical process:

Generation Phase (G)

Organisms produce phenotypic or behavioral variants through:

- Genetic mutation and recombination
- Developmental plasticity
- Behavioral exploration and learning
- Epigenetic variation

Formally: The generation phase represents an *incomplete specification* of fitness. At time t , an organism (or population) exists in state $O(t)$, embedded in environment $E(t)$. The fitness landscape $W(O, E)$ is not fully determined—multiple phenotypic states O' are possible, each with uncertain fitness.

The generation phase produces a distribution of variants:

$$O(t) \rightarrow \{O'_1, O'_2, \dots, O'_n\}$$

This distribution represents the organism's "phenotypic exploration" of possible states.

Validation Phase (V)

The environment selects among generated variants through:

- Differential survival
- Reproductive success
- Resource acquisition
- Biotic and abiotic interactions

Formally: Validation is a *partial resolution* of fitness values. The environment $E(t)$ imposes selection on the variant distribution, yielding:

$$V: (\{O'_i\}, E(t)) \rightarrow O(t+1)$$

Where $O(t+1)$ represents the post-selection state (which variants persist/proliferate).

Environmental Feedback

Critically, the validation process *modifies the environment*:

$$E(t+1) = E(t) + \Delta E[O(t+1)]$$

This is niche construction: the post-selection organismal state changes environmental conditions, which in turn alter future validation criteria.

The complete cycle:

$G: O(t) \rightarrow \{O'_i\}$	[generation: produce variants]
$V: (\{O'_i\}, E(t)) \rightarrow O(t+1)$	[validation: selection]
$F: O(t+1) \rightarrow \Delta E$	[feedback: environment modification]
$E(t+1) = E(t) + \Delta E$	[updated environment]

The system then iterates: $O(t+1)$ in environment $E(t+1)$ enters a new generation phase.

2.2 Why Loops Are Inevitable

A key insight: **Validation can never be complete.**

Even after selection, the organism faces:

1. **New environmental states** (created by niche construction)
2. **New biotic interactions** (other species have also evolved)
3. **New scales of organization** (ecosystem-level effects)

Thus, validation necessarily produces residual incompleteness—new fitness uncertainties that drive the next generation phase. *This is why eco-evolutionary feedback is ubiquitous*: it's not a special case, but a necessary consequence of incomplete validation.

2.3 Hierarchical Validation

Validation occurs at multiple, nested scales:

Molecular: Protein folding validated by cellular environment

Cellular: Cell viability validated by tissue/organism

Organismal: Phenotype validated by population/ecosystem

Population: Allele frequencies validated by long-term environmental trends

Ecosystem: Community composition validated by biogeochemical cycles

Critical property: Each level's validation creates *new generation problems* at the next higher level.

Example:

- A protein's amino acid sequence (molecular) is validated by whether it folds correctly (cellular environment)
- But the cellular environment itself is shaped by organismal-level selection
- Organismal phenotypes are validated by population dynamics
- And populations modify ecosystems (niche construction)

This creates a *cascade* of generation-validation cycles across scales.

Formal representation:

$$G_1 \rightarrow V_1 \rightarrow G_2 \rightarrow V_2 \rightarrow G_3 \rightarrow V_3 \rightarrow \dots$$

Where:

V_i operates at scale i

V_i 's output becomes G_{i+1} 's input (different scale $i+1$)

2.4 Evolvability as Validation Structure

Our framework suggests that **evolvability**—the capacity to generate adaptive variation—depends on validation structure:

High evolvability requires:

1. **Generative capacity:** Ability to produce diverse variants (large G)
2. **Effective validation:** Selection that distinguishes variants (informative V)
3. **Feedback efficiency:** Validation modifies environment sufficiently to create new problems (strong F)

Conversely, evolutionary stasis occurs when:

- Generation is constrained (developmental canalization, genetic limits)
- Validation is weak (flat fitness landscapes, environmental stability)
- Feedback is minimal (organisms don't modify environment)

This explains **why some lineages are highly evolvable** (e.g., Darwin's finches) **while others are "living fossils"** (e.g., horseshoe crabs): differences in G-V-F cycle structure.

3. Applications

3.1 Niche Construction

Classic example: Beaver dams (Naiman et al., 1988)

Generation phase: Beavers exhibit dam-building behavior (phenotypic trait). Within a population, there is variation in:

- Dam construction skill
- Dam placement preferences
- Dam maintenance behaviors

Validation phase: Environment selects among these behavioral variants:

- Well-placed, well-maintained dams → increased survival and reproduction
- Poor dams → increased predation risk, reduced foraging access

Environmental feedback: Successful dams create wetlands, modifying:

- Hydrology (water table, flow patterns)
- Vegetation (shift to wetland plants)
- Community composition (aquatic insects, fish, waterfowl)
- Nutrient cycling (sediment deposition, organic matter accumulation)

New generation problem: The wetland environment created by successful dam-building *changes* the validation criteria for future generations:

- Selection now favors beavers adapted to wetland foraging
- Predator-prey dynamics shift
- Competition with other wetland species emerges

Result: An ongoing G-V-F cycle where beavers and their environment co-evolve.

Formal representation:

Let $B(t)$ = beaver phenotype distribution (dam-building capability)

Let $E(t)$ = environmental state (hydrology, vegetation)

G: $B(t) \rightarrow \{B'_i\}$ [behavioral variation in dam construction]
 V: $(\{B'_i\}, E(t)) \rightarrow B(t+1)$ [selection for effective dam builders]
 F: $B(t+1) \rightarrow \Delta E$ [wetland creation]
 $E(t+1) = E(t) + \Delta E(B)$ [modified environment]

Prediction: Beaver populations with stronger niche construction (larger ΔE) should exhibit faster behavioral evolution, as they more rapidly create new selective pressures. This is testable by comparing beaver populations across habitats with different hydrology.

3.2 Coevolution

Example: Predator-prey toxin-resistance (Brodie & Brodie, 1999)

Consider garter snakes (*Thamnophis sirtalis*) and toxic newts (*Taricha granulosa*):

Prey generation: Newts produce varying levels of tetrodotoxin (TTX) due to:

- Genetic variation in toxin synthesis pathways
- Developmental plasticity in response to predation pressure

Prey validation: Predation by snakes validates toxicity levels:

- High TTX → survival (snake deterrence or death)
- Low TTX → predation

Predator generation: Snakes produce varying TTX resistance due to:

- Mutations in sodium channel genes ($Na_v1.4$)
- Variation in liver detoxification capacity

Predator validation: Ability to consume newts validates resistance:

- High resistance → access to calorie-rich prey → reproductive success
- Low resistance → starvation or toxicity

Mutual feedback:

- Increased newt toxicity (ΔE_{prey}) changes validation for snake resistance
- Increased snake resistance ($\Delta E_{\text{predator}}$) changes validation for newt toxicity

Result: Arms race escalation—a positive feedback loop in G-V-F cycles.

Formal representation:

Let $N(t)$ = newt toxicity level

Let $S(t)$ = snake resistance level

Prey cycle:

$G_N: N(t) \rightarrow \{N'_i\}$ [toxicity variants]

$V_N: (\{N'_i\}, S(t)) \rightarrow N(t+1)$ [survival under predation]

$F_N: N(t+1) \rightarrow \Delta S_{\text{pressure}}$ [selection pressure on snakes]

Predator cycle:

$G_S: S(t) \rightarrow \{S'_i\}$ [resistance variants]

$V_S: (\{S'_i\}, N(t)) \rightarrow S(t+1)$ [feeding success]

$F_S: S(t+1) \rightarrow \Delta N_{\text{pressure}}$ [selection pressure on newts]

These cycles are **mutually coupled**: each species' validation becomes the other's environmental feedback.

Prediction: Geographic variation in toxicity and resistance should correlate (already confirmed empirically, but our framework explains *why*). Furthermore, the *rate* of coevolutionary change should correlate with the strength of coupling (testable via time-series data).

3.3 Evolutionary Transitions

Example: Unicellular → Multicellular transition

One of the major evolutionary transitions (Maynard Smith & Szathmáry, 1995) can be understood as a *shift in validation hierarchy*.

Unicellular phase:

$G: \text{Cell}(t) \rightarrow \{\text{Cell}'_i\}$ [mutations affecting cell traits]

$V: (\{\text{Cell}'_i\}, E_{\text{external}}(t)) \rightarrow \text{Cell}(t+1)$ [selection by external environment]

Validation is direct: cell phenotype is validated by external environment (nutrients, temperature, competitors).

Transition to multicellularity:

Cells begin aggregating (e.g., Dictyostelium, volvocine algae, early animal lineages). Now:

$G_{\text{cell}}: \text{Cell}(t) \rightarrow \{\text{Cell}'_i\}$ [as before]

$V_{\text{organism}}: (\{\text{Cell}'_i\}, \text{Organism_context}) \rightarrow \text{Cell}(t+1)$ [NEW: cells validated by organism]

$G_{\text{organism}}: \text{Organism}(t) \rightarrow \{\text{Organism}'_i\}$ [organism-level variants]

$V_{\text{external}}: (\{\text{Organism}'_i\}, E_{\text{external}}) \rightarrow \text{Organism}(t+1)$ [organism validated by environment]

Key change: A new validation layer is inserted. Cells are no longer validated directly by the external environment, but by *their organismal context* (e.g., do they contribute to collective function?). The organism as a whole is then validated by the external environment.

Consequence: This creates new generation problems:

- Cell-level: How to cooperate, differentiate, suppress cheaters?
- Organism-level: How to coordinate multicellular development, physiology, reproduction?

Formal representation of hierarchy:

Level 1: Cell \rightarrow {Cell'} \rightarrow Selected_Cell

Level 2: Organism(Selected_Cells) \rightarrow {Organism'} \rightarrow Selected_Organism

Level 3: Population(Selected_Organisms) \rightarrow Evolution

Each level's validation output becomes the next level's generation input.

Prediction: Transitions involving hierarchical validation shifts should exhibit:

1. Increased conservation at lower levels (cells become "locked in" to organismal context)
2. New sources of variation at higher levels (organism-level traits)
3. Trade-offs between levels (e.g., cell proliferation vs. organism fitness)

These predictions align with observations (e.g., tumor suppressor genes as mechanisms enforcing Level 2 validation).

3.4 Ecosystem Engineering

Extension to community ecology:

Ecosystem engineers (Jones et al., 1994) are species whose niche construction has disproportionate effects on community structure.

Our framework predicts:

Strong ecosystem engineers should generate **cascading G-V-F cycles** affecting multiple species:

Example: Coral reefs

- Coral generation: Colony morphology, symbiont associations
- Coral validation: Survival, growth (affected by water quality, temperature, herbivory)
- Coral feedback: Reef structure creation \rightarrow modifies hydrodynamics, light, substrate
- Community response: Hundreds of species now validated by reef environment
 - Fish: Shelter availability affects survival
 - Algae: Light environment affects growth
 - Invertebrates: Substrate type affects settlement

Result: Coral G-V-F cycle creates *downstream* G-V-F cycles for entire communities.

Prediction: Loss of ecosystem engineers should disrupt not just community composition, but the *rate and direction* of evolutionary change in other species. This is testable via long-term studies in degraded vs. intact ecosystems.

4. Testable Predictions

Our framework generates several novel, quantifiable predictions:

4.1 Environmental Modification Rate Correlates with Evolutionary Rate

Prediction: Species with stronger niche construction (larger ΔE per generation) should exhibit faster phenotypic evolution, as they more rapidly create new selective pressures.

Test: Compare evolutionary rates (e.g., morphological disparity, molecular evolution) across taxa with varying niche construction intensity:

- Strong constructors: beavers, earthworms, reef-building corals
- Weak constructors: many parasites, pelagic marine species

Expected result: Positive correlation between niche construction strength and evolutionary rate, controlling for generation time.

Quantification:

$$\text{Evolutionary_rate} \propto \|\Delta E\| \times \text{Generational_turnover}$$

Where $\|\Delta E\|$ is the magnitude of environmental modification.

4.2 Multi-Level Validation Predicts Conservation Patterns

Prediction: Traits validated at multiple hierarchical levels should exhibit greater evolutionary conservation than traits validated at a single level.

Rationale: Multi-level validation creates stronger constraints—changing the trait requires simultaneous changes at multiple scales.

Examples:

- HOX genes: Validated at molecular (protein function), cellular (gene regulation), organismal (body plan), and population levels → highly conserved
- Neutral intergenic regions: Validated only at molecular level → rapidly evolving

Test: Comparative genomics across phylogenies, categorizing genes by validation level count.

Expected result: Conservation (sequence identity, purifying selection) increases with number of validation levels.

4.3 Validation Removal Allows Latent Phenotype Re-emergence

Prediction: When environmental validation is experimentally removed, previously suppressed phenotypic variants should re-emerge ("evolutionary reversal" or "atavism").

Rationale: Validation suppresses certain variants but doesn't eliminate generative capacity. Remove validation → variants reappear.

Examples:

- Cave fish (*Astyanax mexicanus*): Loss of light validation → eye loss, but developmental machinery retained → eyes can re-evolve
- Bacterial antibiotic resistance: Removal of antibiotics → resistance plasmids may be retained even if costly

Test: Experimental evolution in bacteria or rapidly reproducing organisms:

1. Impose strong selection (e.g., antibiotic)
2. Population adapts (resistance evolves)
3. Remove selection (no antibiotic)
4. Measure re-emergence of ancestral phenotypes

Expected result: Traits suppressed by validation should reappear faster than predicted by neutral evolution alone, as generative capacity is retained.

4.4 Niche Construction Intensity Predicts Evolvability

Prediction: Lineages with sustained niche construction should exhibit higher evolvability (capacity to respond to novel selection pressures) than lineages in stable environments.

Rationale: Ongoing G-V-F cycles maintain generative capacity and prevent canalization.

Test: Comparative analysis across clades:

- High niche construction: Darwin's finches, anoles, cichlids

- Low niche construction: horseshoe crabs, tuataras, coelacanths

Measure evolvability via:

- Phenotypic disparity
- Response to artificial selection experiments
- Morphological integration patterns

Expected result: Niche constructors exhibit higher evolvability metrics.

5. Discussion

5.1 Relation to Existing Theory

Niche construction theory (Odling-Smee et al., 2003; Laland et al., 2016):

Our framework provides formal mathematical grounding for niche construction, specifying the mechanisms of feedback (validation → generation cycles) and explaining *why* niche construction is evolutionarily significant (it modifies validation criteria).

Baldwin effect and genetic assimilation (West-Eberhard, 2003):

These phenomena emerge naturally from our framework: phenotypic plasticity (generation phase) allows organisms to explore novel niches, which then validates certain variants, eventually leading to genetic accommodation. The G-V-F cycle formalizes this process.

Developmental systems theory (Oyama, 1985):

Our hierarchical validation structure aligns with DST's emphasis on developmental context. Development itself is a G-V cycle, where cellular states are validated by tissue/organism context.

Extended evolutionary synthesis (Laland et al., 2015):

Our framework contributes to EES by formalizing reciprocal causation between organisms and environments, providing mathematical structure for "developmental bias" and "niche construction."

5.2 Implications for Evolutionary Biology

1. Evolvability is structural, not incidental

High evolvability results from specific G-V-F cycle architectures (strong generation, informative validation, effective feedback). This suggests evolvability itself is subject to selection—lineages can evolve *increased capacity to evolve*.

2. Stasis is active, not passive

Evolutionary stasis (e.g., living fossils) reflects weak G-V-F cycles: constrained generation, stable validation, minimal feedback. Stasis is not absence of evolution, but a particular evolutionary dynamic.

3. Macroevolution involves validation hierarchy shifts

Major transitions (unicellular → multicellular, asexual → sexual, solitary → eusocial) involve restructuring of validation hierarchies, not just gradual trait change.

4. Predictability and contingency

Our framework suggests evolution is *neither* fully deterministic *nor* fully contingent. The G-V-F structure constrains possible trajectories (predictability), but specific outcomes depend on history and environmental fluctuations (contingency).

5.3 Broader Applicability

While developed for evolutionary ecology, this framework appears generalizable to other adaptive systems:

Immune systems: Antibody generation (somatic hypermutation) → validation (antigen binding) → feedback (clonal selection modifying immune repertoire)

Neural systems: Synaptic variation (structural plasticity) → validation (correlation-based learning rules) → feedback (neural circuit rewiring)

Cultural evolution: Idea generation (creativity, innovation) → validation (social acceptance, functionality) → feedback (modified cultural environment)

For extended theoretical foundations across multiple domains, see [Author] (2025), available at [zenodo.org/\[DOI\]](https://zenodo.org/[DOI]).

5.4 Limitations and Future Directions

Empirical challenges:

- Quantifying $\|\Delta E\|$ (environmental modification magnitude) across systems
- Measuring validation strength in natural populations
- Disentangling G, V, and F components in real-time eco-evolutionary dynamics

Theoretical extensions:

- Incorporating spatial structure (G-V-F cycles in metapopulations)
- Multiple timescale dynamics (fast ecological, slow evolutionary)
- Stochastic formulations (demographic and environmental noise)
- Game-theoretic analysis (frequency-dependent validation)

Experimental priorities:

1. Test Prediction 4.1 (niche construction intensity vs. evolutionary rate)
 2. Resurrect ancestral phenotypes to test Prediction 4.3
 3. Comparative genomics to test Prediction 4.2
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6. Conclusion

We have proposed that eco-evolutionary dynamics operate through generation-validation cycles: organisms generate phenotypic variants (incomplete fitness specification), environments validate variants through selection (partial resolution), and validation modifies environments (creating new generation problems). This framework:

1. **Explains** why eco-evolutionary feedback is ubiquitous (validation is never complete)
2. **Unifies** niche construction, coevolution, and evolutionary transitions
3. **Predicts** relationships between niche construction intensity and evolutionary rate, multi-level validation and conservation, and validation removal and phenotypic re-emergence
4. **Generalizes** beyond ecology to other adaptive systems

By formalizing the reciprocal dynamics between organisms and environments, this approach contributes to the Extended Evolutionary Synthesis and provides a foundation for understanding adaptation as an inherently feedback-driven process. Future work integrating this framework with population genetics, quantitative genetics, and ecosystem ecology promises deeper insights into the creative dynamics of evolution.

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References

Bassar, R. D., et al. (2010). Local adaptation in Trinidadian guppies alters ecosystem processes.

Brodie, E. D., & Brodie, E. D., Jr. (1999). Costs of exploiting poisonous prey: evolutionary trade-offs in a predator-prey arms race. *Evolution*, 53(2), 626-631.

Day, T., & Gandon, S. (2007). Applying population-genetic models in theoretical evolutionary epidemiology. *Ecology Letters*, 10(10), 876-888.

Govaert, L., et al. (2019). Eco-evolutionary feedbacks—Theoretical models and perspectives. *Functional Ecology*, 33(1), 13-30.

Grant, P. R., & Grant, B. R. (2006). Evolution of character displacement in Darwin's finches. *Science*, 313(5784), 224-226.

H Hairston, N. G., et al. (2005). Rapid evolution and the convergence of ecological and evolutionary time. *Ecology Letters*, 8(10), 1114-1127.

Hendry, A. P. (2017). *Eco-evolutionary dynamics*. Princeton University Press.

Jones, C. G., Lawton, J. H., & Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos*, 69(3), 373-386.

Laland, K., et al. (2011). Cause and effect in biology revisited: Is Mayr's proximate-ultimate dichotomy still useful? *Science*, 334(6062), 1512-1516.

Laland, K. N., et al. (2015). The extended evolutionary synthesis: its structure, assumptions and predictions. *Proceedings of the Royal Society B*, 282(1813), 20151019.

Laland, K. N., et al. (2016). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B*, 282(1813), 20151019.

Lewontin, R. C. (1983). Gene, organism and environment. In D. S. Bendall (Ed.), *Evolution from molecules to men* (pp. 273-285). Cambridge University Press.

Maynard Smith, J., & Szathmáry, E. (1995). *The major transitions in evolution*. Oxford University Press.

Naiman, R. J., Johnston, C. A., & Kelley, J. C. (1988). Alteration of North American streams by beaver. *BioScience*, 38(11), 753-762.

Odling-Smee, F. J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton University Press.

Oyama, S. (1985). *The ontogeny of information*. Cambridge University Press.

Schoener, T. W. (2011). The newest synthesis: Understanding the interplay of evolutionary and ecological dynamics. *Science*, 331(6016), 426-429.

West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

Supplementary Materials

Appendix S1: Mathematical formalization of generation-validation cycles

Appendix S2: Derivation of predictions from formal model

Appendix S3: Worked examples with parameter values

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