Eurasia Specialized Veterinary Publication

Entomological Research Letters

ISSN: 3108-639X

2021, Volume 1, Issue 1, Page No: 48-57
Copyright CC BY-NC-SA 4.0
Available online at: www.esvpub.com/

Resource Allocation Across Metamorphosis Determines Which Larval Effects Persist, Disappear, or Re-Emerge in Adult Insects

Sofía Martínez[1]*, Carlos Gómez[1], Lucia Navarro[2]

[1]Department of Metamorphosis and Resource Allocation, Faculty of Biosciences, Polytechnic University of Madrid, Madrid, Spain.
[2]Department of Carry-Over Effects and Adult Performance, Faculty of Biology, University of Barcelona, Barcelona, Spain.

***E-mail** ✉ sofia.martinez@upm.es

ABSTRACT

Metamorphosis is often treated as a developmental boundary that either transmits larval effects into adulthood or eliminates them. That binary interpretation obscures a more mechanistic problem: larval environments can alter resources, structures, physiological states, and regulatory processes that differ greatly in their probability of surviving tissue remodeling, being compensated, becoming masked by adult acquisition, or remaining latent until adult demand. This perspective develops a resource-allocation interpretation of cross-stage effects in insects while explicitly separating resource-mediated persistence from immune, endocrine, symbiotic, and other forms of developmental continuity. Evidence from holometabolous insects shows that larval nutritional history can influence adult size, stored reserves, metabolism, stress resistance, reproduction, and physiological scaling, but effects are strongly trait-, sex-, species-, and environment-dependent. Conversely, adult conditions can override some larval effects without demonstrating complete biological erasure. We therefore distinguish persistence, disappearance, and proposed demand-dependent re-emergence as mechanistically different outcomes rather than interchangeable observations. The resulting synthesis treats metamorphosis as a selective reorganization boundary through which different components of larval history have different fates. This framing generates experimentally discriminating predictions about resource retention, compensation, adult replacement, and latent physiological constraints.

Keywords: Developmental carry-over, Holometaboly, Larval nutrition, Metamorphic remodeling, Resource allocation, Transstadial effects

Received: 31 March 2021
Revised: 07 May 2021
Accepted: 12 May 2021

How to Cite This Article: Martínez S, Gómez C, Navarro L. Resource Allocation Across Metamorphosis Determines Which Larval Effects Persist, Disappear, or Re-Emerge in Adult Insects. Entomol Res Lett. 2021;1(1):48-57.
https://doi.org/10.51847/JkspdcAqRV

Introduction

Environmental effects acquired during larval development can influence later phenotypes, yet the existence of a cross-stage association does not identify why it persists. Carry-over effects may be direct, latent, or indirect, and their evolutionary interpretation depends on how developmental stages are coupled rather than simply on whether an early environment predicts a later trait [1]. In insects with complete metamorphosis, this problem is especially acute because larval and adult bodies are separated by extensive tissue remodeling, while empirical responses can nevertheless remain partly coupled across that boundary [2, 3]. Thus, metamorphosis creates neither guaranteed continuity nor guaranteed independence.

The resulting adult phenotype is also not reducible to a single larval-condition proxy. In the Glanville fritillary, short larval food stress produced sex-dependent adult consequences under semi-natural conditions; pupal mass

© 2021 Entomological Research Letters

explained some but not all later performance differences [4]. Such results caution against treating adult body size as a sufficient summary of developmental history.

This perspective addresses a narrower mechanistic question: which components of larval history are positioned to survive metamorphosis, which are likely to be remodeled or compensated, and which may become consequential only when adult demand exposes a previously non-limiting constraint? We use resource allocation as an organizing lens because larval acquisition can be partitioned among growth, storage, maintenance, developmental commitment, and tissue reconstruction. However, resource allocation is not assumed to be the universal cause of carry-over. Immune state, endocrine regulation, symbiotic continuity, and persistent molecular regulation can cross developmental boundaries through partially distinct routes. The central contribution is therefore a proposed resource-allocation model of carry-over that explicitly preserves those competing mechanisms and treats persistence, disappearance, and re-emergence as outcomes requiring different evidence.

Metamorphosis as reorganization rather than complete reset

Complete metamorphosis reorganizes the insect rather than producing an organism without developmental history. Endocrine control of metamorphosis integrates juvenile hormone, ecdysteroid signaling, developmental primordia, and stage-specific tissue programs, creating continuity in developmental regulation even when larval morphology is profoundly replaced [5]. At the tissue level, programmed cell death through apoptotic and autophagic processes contributes to elimination or remodeling of larval structures, but these processes are organ- and taxon-dependent [6]. It is therefore inappropriate to infer either that all larval material is retained or that all larval states are erased.

Cross-stage continuity can occur even when the original larval phenotype or challenge no longer exists. In *Tribolium castaneum*, larval parasite exposure altered immune-gene expression into pupal and adult stages despite clearance associated with metamorphosis, with covariance differing among tissues and stages [7]. Holometabolous symbioses show similarly heterogeneous outcomes: some microorganisms persist or relocate through metamorphosis, whereas others are lost, replaced, or reacquired [8]. These examples demonstrate that persistence of biological state is broader than persistence of energetic stores.

Metamorphic signaling can itself link physiological systems that would be misleadingly classified as simple resource transfer. In *Drosophila melanogaster*, ecdysone-related signaling through Broad regulates immune effectors during metamorphosis, demonstrating mechanistic interaction between endocrine and immune functions [9]. Such evidence creates an essential boundary for the present synthesis: an adult consequence of larval history should be called resource-mediated only when the relevant resource state, allocation process, or downstream resource-dependent mechanism is actually measured or experimentally implicated.

Accordingly, metamorphosis is best treated here as a selective reorganization boundary. Components of larval history may be destroyed with larval tissues, incorporated into adult structures, retained as stores, transformed metabolically, propagated through regulatory states, or replaced by later acquisition. These alternatives predict different patterns of apparent persistence and disappearance and cannot be inferred from adult phenotype alone.

Resource acquisition during larval development

Larval acquisition is temporally structured. In *D. melanogaster*, food intake and macronutrient choice change around critical weight, indicating that nutritional priorities differ before and after a developmental commitment point [10]. Nutrient sensing can also act directly on metamorphic timing: nutrient-dependent TOR activity and endocycling in the prothoracic gland regulate steroidogenic capacity and the transition toward metamorphosis [11]. Thus, equal amounts of food obtained at different larval times need not have equivalent consequences.

Resource quality is also distinct from quantity. In *Bactrocera tryoni*, larval carbohydrate identity altered developmental and adult traits, including adult lipid reserves, while developmental performance did not map uniformly onto later storage state [12]. In male *Aedes aegypti*, larval diet interacted with rearing temperature to influence teneral energetic reserves, longevity, and thermal tolerance [13]. Developmental acquisition should therefore be represented by at least three separable dimensions: amount acquired, biochemical composition, and environmental context affecting utilization.

Adult body size remains useful but cannot serve as a universal surrogate for these dimensions. In male *A. aegypti*, larval food affected size and several adult-performance measures, yet survival, swarming, and copulation outcomes did not collapse onto a single body-size relationship [14]. Size records structural outcome; it does not directly reveal the residual stores, metabolic state, or regulatory history carried into adulthood.

For the proposed resource-allocation account, the biologically relevant larval state is therefore not "good" versus "poor" condition. It is the set of resources and developmental commitments available at metamorphic entry, together with the environmental conditions under which those resources were acquired and processed.

Allocation to growth, storage, and tissue remodeling

Acquired larval resources can enter adult life through different channels. Developmental nutrition in honeybees altered survival to adulthood, adult body traits, and the allometric scaling of resting metabolic rate, while body size itself did not explain the metabolic pattern [15]. Structural growth and physiological allocation must therefore remain analytically separate even when both arise from the same larval diet.

Adult reserve physiology also retains developmental information in some systems. Larval nutrition can alter adult fat stores and starvation resistance in *Drosophila*, while nutritional deprivation in *Aedes albopictus* can be partly compensated by prolonged larval development yet still leave altered adult metabolic and reserve phenotypes. Larval predator exposure likewise produces persistent adult metabolic or oxidative effects that vary between mosquito species and sexes [16–18]. These studies support the shared conclusion that developmental conditions can modify adult energetic physiology, but they do not support a single direction or common molecular mechanism.

A useful counterexample comes from the hemimetabolous damselfly *Lestes macrostigma*. Larval salinity reduced adult net energy budget while adult muscle mass, flight performance, and immune investment did not show corresponding carry-over effects [19]. Because this taxon lacks holometabolous pupation, it cannot establish resource transfer through a pupal boundary. It does, however, show why physiological carry-over cannot be inferred solely from conspicuous adult performance traits.

The distinction needed here is therefore between structural commitment, retained storage, metabolic-state persistence, and remodeling expenditure. These categories are analytical rather than claims that a fixed fraction of larval resources enters each destination. Their value is that they specify what must be measured before an adult outcome can be assigned to resource allocation rather than to another developmental process.

Because the same adult phenotype can arise from different allocation histories, the interpretive boundaries are more efficiently separated in a mechanism–boundary matrix than in a sequence of trait examples.

Table 1. Distinguishing larval allocation outcomes that can produce similar adult phenotypes

Allocation distinction	Associated dimensions	Allocation distinction	Associated dimensions
Structural commitment		**Retained storage**	
Evidence · Interpretation for adult carry-over	Adult mass, dimensions, tissue investment Larval acquisition becomes incorporated into adult structure	**Evidence · Interpretation for adult carry-over**	Biochemical reserve assays near emergence Larval resources remain available to adult physiology
Limits and uncertainty · Test implication	Structure does not reveal residual energetic state Measure structure separately from reserves and metabolism	**Limits and uncertainty · Test implication**	Reserve abundance does not establish later utilization Track reserve identity and depletion through adult time
Biological setting · Evidential standing	Adult size, morphology, tissue quantity Evidence-supported distinction	**Biological setting · Evidential standing**	Lipid, carbohydrate, protein or other accessible reserves Evidence-supported distinction
Metabolic-state persistence		**Developmental compensation**	
Evidence · Interpretation for adult carry-over	Metabolic rate, metabolite pools, ATP or stress physiology Larval history alters how adult resources are processed	**Evidence · Interpretation for adult carry-over**	Development time, size recovery, emergence success Apparent recovery may coexist with hidden physiological difference
Limits and uncertainty · Test implication	May reflect regulatory programming rather than retained material Pair resource assays with pathway or flux measurements	**Limits and uncertainty · Test implication**	Normal morphology is not evidence of physiological reset Test adult function after normalization of size or timing
Biological setting · Evidential standing	Adult energetic processing differs after larval treatment Evidence-supported distinction	**Biological setting · Evidential standing**	Growth or timing normalizes despite larval stress Evidence-supported distinction

Remodeling expenditure		Trait-level decoupling	
Evidence · Interpretation for adult carry-over	Tissue-specific remodeling and energetic measurements Metamorphosis may alter which larval resources remain accessible	**Evidence · Interpretation for adult carry-over**	Parallel structural, energetic and performance measures Carry-over may be restricted to one biological level
Limits and uncertainty · Test implication	Direct quantitative transfer is seldom measured Measure pre-pupal stores and post-emergence fate within individuals or matched cohorts	**Limits and uncertainty · Test implication**	Null performance does not prove absence of physiological carry-over Sample multiple levels rather than one proxy
Biological setting · Evidential standing	Resources are consumed or redirected during metamorphosis Proposed analytical category	**Biological setting · Evidential standing**	One adult trait changes while another remains stable Proposed interpretive rule

Note: "Proposed" identifies classifications introduced here to organize evidence, not empirically validated allocation states. No numerical allocation fractions or universal directions are implied.

Mechanisms of persistence across metamorphosis

Persistence can reflect transformation of developmental resources rather than simple conservation of larval stores. In *D. melanogaster*, developmental diet can alter an adult lipid-metabolic pathway that influences lifespan through production of lipid-derived toxic compounds, providing a mechanistic example in which larval nutrition changes later metabolic rules rather than merely adult body mass [20]. The pathway is species- and context-specific and should not be generalized as a universal insect mechanism.

Other persistent states are clearly not reducible to energetic carry-over. In *Anopheles gambiae*, larval immune activation increased several adult antibacterial measures yet was accompanied by increased susceptibility to malaria infection, showing that persistent physiological activation can have opposing consequences rather than a single adaptive benefit [21]. In *Galleria mellonella*, larval diet and immune challenge interacted in sex-dependent ways, and low nutrition did not uniformly suppress later immune capacity [22]. These observations caution against classifying all cross-stage immune variation as a resource shortage or surplus.

Early stress can also survive complete metamorphosis without an identified resource mediator. Egg-stage heat stress in *Bicyclus anynana* reduced later growth, survival, and body mass, while adult acute heat survival itself was not altered by egg temperature [23]. Conversely, in a tephritid fruit fly, adult feeding did not simply compensate larval-diet effects on stress resistance, and richer larval nutrition was not uniformly associated with superior adult resistance [24]. Persistence is therefore trait-specific and may remain mechanistically ambiguous even when the cross-stage effect itself is robust.

These findings support a multilevel reconciliation rather than a single carry-over pathway. Evidence-supported routes include structural incorporation, adult reserve differences, altered metabolic processing, persistent immune state, endocrine coupling, and symbiotic continuity. The article's proposed synthesis adds an explicit inference boundary: resource-mediated persistence should be claimed only when a resource pool, resource-dependent structure, or resource-processing mechanism links larval history to the adult state; otherwise persistence should remain mechanistically unassigned or assigned to the directly demonstrated non-resource process.

The required distinctions are condensed in **Figure 1**, which places the metamorphic boundary between larval history and adult phenotype while keeping resource-mediated, regulatory, immune, and symbiotic continuity analytically separate.

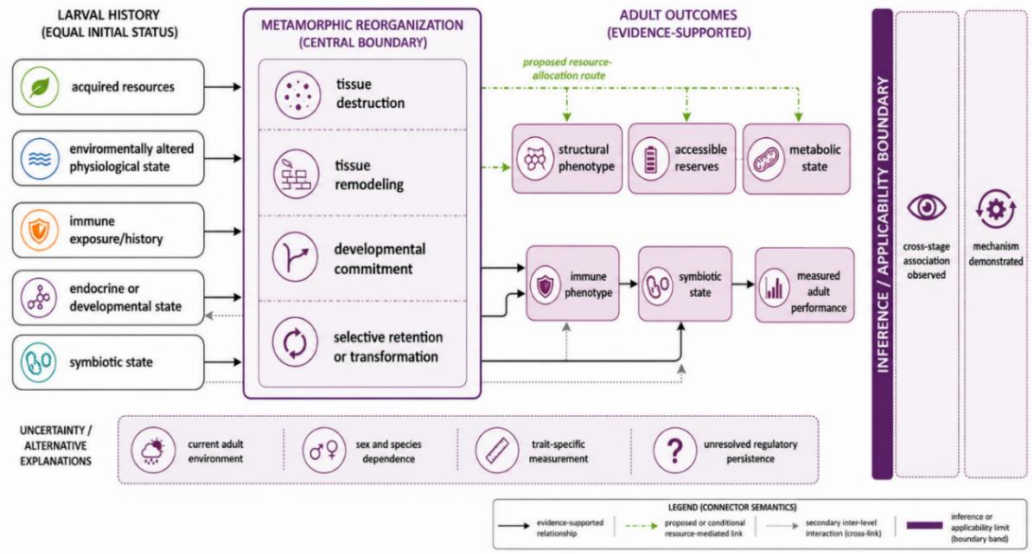


Figure 1. Metamorphic persistence is produced by multiple continuity routes that do not support the same causal inference

Conditions producing disappearance of larval effects

Failure to detect a larval effect in adults can result from several biologically different processes. Adult conditions may become the dominant determinant of a measured trait while developmental molecular signatures persist. In *D. melanogaster*, developmental diet left transcriptomic effects into later adulthood, yet adult diet exerted stronger influence on several phenotypic outcomes and persistent expression differences did not map straightforwardly onto lifespan. Likewise, developmental and adult diets can contribute differently to survival and reproduction, with effects depending on sex, trait, and adult age [25–27]. These findings support adult override for particular outcomes, not complete erasure of developmental history.

Disappearance can also be active compensation rather than replacement by adult resources. In the winter moth, photoperiodic information contributed to compensation for earlier phenological shifts, demonstrating that later developmental cues can buffer a prior environmental effect [28]. This mechanism is not primarily nutritional, but it establishes a broader inference problem: a normalized later phenotype may result from compensatory regulation rather than absence of prior developmental influence.

For resource-mediated effects, at least four disappearance routes should therefore be distinguished. Remodeling loss occurs when the relevant larval structure or state is dismantled during metamorphosis. Developmental compensation occurs when growth, timing, or physiology adjusts before adulthood. Adult replacement or override occurs when newly acquired adult resources dominate the measured adult trait. Phenotypic masking occurs when larval history persists at a molecular or physiological level but is not expressed in the selected adult endpoint. Only the first route approximates biological elimination; the others can produce the same observational result while leaving different latent states.

A critical methodological consequence follows: a nonsignificant adult treatment contrast is insufficient evidence that the larval effect has disappeared biologically. Demonstrating disappearance requires measurements capable of distinguishing loss, compensation, replacement, and masking. **Table 2** separates those inference states across biological scales.

Table 2. When an absent adult phenotype does and does not imply loss of larval history

Disappearance state	Article-specific dimension	Scientific content
Remodeling loss	**Biological scale or context · Observable pattern**	Tissue or organ reorganized during metamorphosis Larval structure/state absent after remodeling
	Interpretation · Key uncertainty	Relevant substrate may genuinely be eliminated Equivalent function may be rebuilt by another tissue
	Discriminating test · Status · Evidential standing	Follow the specific tissue, molecule, or stored pool across metamorphosis Evidence-supported mechanism class

Developmental compensation	**Biological scale or context · Observable pattern**	Growth, timing or physiology adjusts before adulthood Adult trait approaches control despite earlier perturbation
	Interpretation · Key uncertainty	Later regulation offsets earlier effect Compensation may be incomplete at unmeasured levels
	Discriminating test · Status · Evidential standing	Measure hidden physiological states after apparent normalization Evidence-supported mechanism class
Adult resource override	**Biological scale or context · Observable pattern**	Adult feeding strongly controls later phenotype Early larval effect weakens as adulthood proceeds
	Interpretation · Key uncertainty	Current acquisition outweighs developmental contribution Larval state may persist but cease to be limiting
	Discriminating test · Status · Evidential standing	Cross larval and adult diets with repeated adult measurements Evidence-supported mechanism class
Phenotypic masking	**Biological scale or context · Observable pattern**	Molecular or physiological difference persists without corresponding focal phenotype Adult endpoint converges while another level remains divergent
	Interpretation · Key uncertainty	Apparent disappearance is measurement-dependent Persistent signal may be causally irrelevant
	Discriminating test · Status · Evidential standing	Measure multiple biological levels and test mediation Evidence-supported inference state
Trait-specific decoupling	**Biological scale or context · Observable pattern**	Some adult traits retain history and others do not Mixed persistence among performance, reserve, metabolic or reproductive measures
	Interpretation · Key uncertainty	Carry-over is trait-specific rather than organism-wide Different traits may have different causal routes
	Discriminating test · Status · Evidential standing	Assay several outcomes within the same developmental treatment Evidence-supported inference state
Demand-dependent latency	**Biological scale or context · Observable pattern**	Adult phenotype appears normalized until later challenge No difference under low demand; predicted divergence under stress or reproduction
	Interpretation · Key uncertainty	Larval history may remain as a non-limiting constraint Direct vanish-then-reappear evidence remains sparse
	Discriminating test · Status · Evidential standing	Predefine adult demand and compare states before and after challenge Proposed state

Note: The final row is a proposed synthesis requiring prospective experimental discrimination. “Disappearance” elsewhere in the table refers to the observed adult phenotype, not necessarily elimination of all developmental information.

Latent effects that re-emerge during adult demand

A larval effect need not remain continuously visible to matter later. In female *Aedes aegypti*, larval nutrition influenced adult size, adult nutrition more strongly affected survival, and both stages contributed to fecundity [29]. Stage-specific resource dependence therefore permits a developmental constraint to be inconspicuous while adult resources are sufficient but limiting when reproduction, starvation, thermal stress, or another demand increases.

Direct evidence for literal disappearance followed by re-emergence is sparse, so re-emergence is treated here as a proposed state. Developmental compensation in *Aedes albopictus* can coexist with altered adult metabolism [17], while larval environments can alter adult energy budgets without parallel changes in conspicuous performance [19]. Adult feeding also need not erase larval-history effects on stress resistance [24]. These studies justify demand-unmasking tests but do not establish a universal latent-to-re-emergent sequence.

Resource-allocation model of carry-over

The proposed model treats metamorphosis as a selective allocation boundary. Larval-acquired resources or their consequences may be committed to adult structure, retained as stores, transformed into persistent metabolic states, consumed during remodeling, compensated, or overridden by adult acquisition. Developmental diet can alter later metabolic processing rather than merely resource quantity [20], and the contribution of larval nutrition to an adult trait can decline as current diet becomes dominant [26].

Three observational states follow. Persistence is a detectable adult difference linked to developmental history. Disappearance is convergence of the measured adult phenotype through possible destruction, compensation,

replacement, or masking. Re-emergence is proposed as demand-dependent divergence after earlier apparent convergence. None identifies mechanism by itself. Immune, endocrine, symbiotic, and regulatory continuity must remain in a parallel non-resource pathway.

Table 3 separates adult observations from the interpretations and tests needed before they can be assigned to larval resource history.

Table 3. Conditional states and failure modes in assigning adult outcomes to larval resource history

Competing explanation	Proposed resource interpretation · Failure mode	Evidence needed · Test implication
	Persistent difference	
Non-resource continuity	Retained store, structural commitment, or metabolic persistence Calling association resource transfer	Direct mediator linkage Measure candidate mediator
	Adult convergence	
Low power or insensitive endpoint	Remodeling loss, compensation, or adult replacement Treating a null contrast as erasure	Locate when divergence disappears Track multiple levels through metamorphosis
	Hidden physiological divergence	
Molecular signal without functional relevance	Phenotypic masking Equating persistence with causation	Physiological difference linked to later function Test mediation
	Divergence only under demand	
Adult challenge creates a new effect	Latent resource constraint Claiming re-emergence without baseline	Pre-demand similarity plus larval-history-linked post-demand divergence Prespecify challenge and repeated measures
	Adult environment dominates	
Independent adult plasticity	Resource replacement or override Declaring developmental history irrelevant	Crossed larval/adult treatments Quantify stage contributions
	Mixed trait response	
Separate causal pathways	Trait-specific allocation Whole-organism generalization from one trait	Parallel structural, metabolic, and performance measures Preserve trait-level inference

Note: Resource interpretations are proposed unless their mediator is directly demonstrated. The matrix is not a scoring system.

Figure 2 represents the same logic spatially: adult convergence is an inference problem rather than evidence of one specific developmental fate.

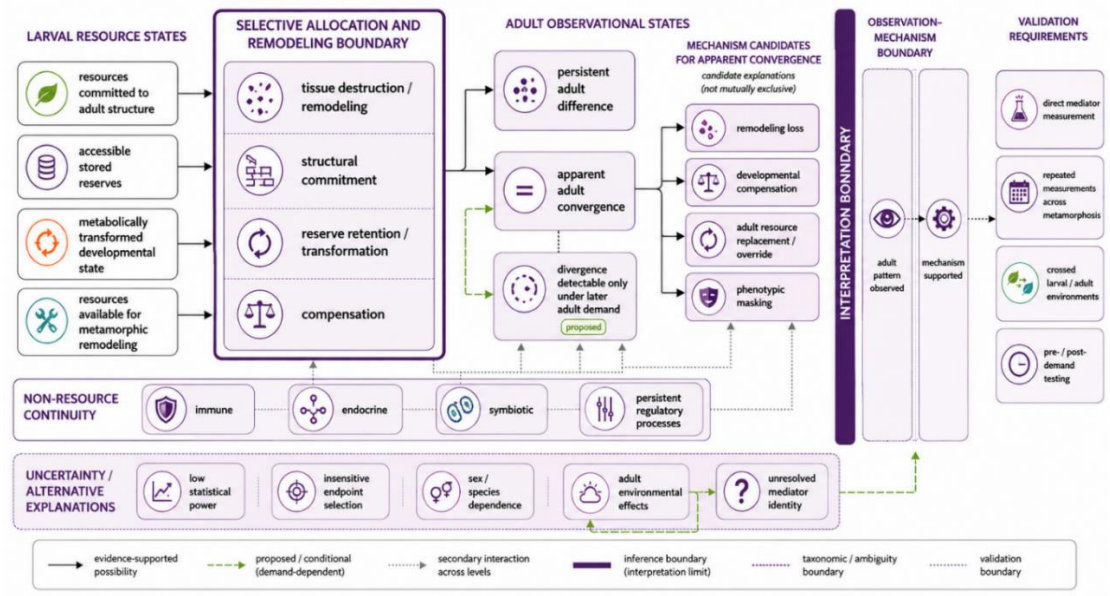


Figure 2. Adult convergence cannot distinguish erasure, compensation, masking, and resource replacement

Mechanistic predictions

A resource-mediated persistent effect should remain associated with a measured store, resource-dependent structure, or metabolic process after coarse proxies such as body size are considered; developmental nutrition and adult metabolic scaling show why size alone is insufficient [15]. Disappearance should be demonstrated by locating loss, compensation, or replacement rather than by a nonsignificant adult contrast; persistent transcriptomic differences despite adult-diet dominance illustrate this distinction [25].

A latent effect requires adults to be measured before and after a prespecified demand. Re-emergence would be supported only if post-demand divergence remains linked to manipulated larval history rather than being created solely by the adult challenge. The appropriate starvation, reproductive, thermal, or immune challenge must match the proposed mechanism.

Trait-specific prediction is equally important. If metamorphosis reallocates or replaces only some components of larval state, structural, metabolic, reproductive, and performance traits should not be expected to change in parallel. The mixed pre- and post-metamorphic temperature responses in *Arctia plantaginis* provide an empirical precedent for this decoupling [3]. A convincing test should therefore define in advance which biological level is expected to retain the larval signal and which alternative result would falsify that expectation.

Results and Discussion

The evidence supports partial developmental coupling rather than total continuity or total reset. Metamorphosis can remove larval tissues while other states persist or are transformed. Semi-natural butterfly evidence further shows that adult consequences of larval food stress need not be reducible to pupal mass [4]. Laboratory mechanisms therefore require cautious transfer to natural fitness.

Resource allocation is best treated as one layer of a broader architecture. Transstadial immune activation can produce opposing adult consequences [21], metamorphic endocrine signaling can regulate immune processes [9], and persistent molecular differences need not mediate the focal adult phenotype [25]. These mechanisms define the model's boundaries rather than exceptions to be absorbed into it.

Generalization is constrained by strong representation of Diptera and Lepidoptera, fewer other orders, uneven sex coverage, and predominantly laboratory designs. The hemimetabolous damselfly comparison reinforces a further boundary: delayed energetic consequences can occur without a holometabolous pupal transition [19]. Such evidence supports the general importance of life-stage resource history but cannot establish the same remodeling mechanisms. The strongest version of the model should therefore be tested within holometabolous orders before its architecture is generalized to insects with different developmental transitions.

Validation should combine repeated measurements across metamorphosis with direct resource assays, tissue-specific mechanisms, crossed adult environments, and explicit competing hypotheses. Strong tests should distinguish stored quantity from metabolic processing, structural commitment from remaining reserves, phenotypic convergence from biological erasure, and challenge-induced new effects from genuine unmasking of developmental history.

Conclusion

Metamorphosis gives larval effects multiple possible fates. Developmental history can persist through resources, structure, metabolism, or non-resource continuity; disappear through remodeling, compensation, replacement, or masking; and, as proposed here, become consequential when adult demand exposes a hidden constraint. Adult phenotype alone cannot distinguish these processes. Progress requires tracing relevant states across metamorphosis and testing latent effects longitudinally rather than inferring mechanism from endpoint differences.

Acknowledgments: None

Conflict of Interest: None

Financial Support: None

Ethics Statement: None

References

1. Moore MP, Martin RA. On the evolution of carry-over effects. J Anim Ecol. 2019;88(12):1832-44. doi:10.1111/1365-2656.13081
2. Rolff J, Johnston PR, Reynolds S. Complete metamorphosis of insects. Philos Trans R Soc Lond B Biol Sci. 2019;374(1783):20190063. doi:10.1098/rstb.2019.0063
3. Galarza JA, Dhaygude K, Ghaedi B, Suisto K, Valkonen J, Mappes J. Evaluating responses to temperature during pre-metamorphosis and carry-over effects at post-metamorphosis in the wood tiger moth (Arctia plantaginis). Philos Trans R Soc Lond B Biol Sci. 2019;374(1783):20190295. doi:10.1098/rstb.2019.0295
4. Rosa E, Saastamoinen M. Sex-dependent effects of larval food stress on adult performance under semi-natural conditions: Only a matter of size? Oecologia. 2017;184(3):633-42. doi:10.1007/s00442-017-3903-7
5. Truman JW, Riddiford LM. The evolution of insect metamorphosis: A developmental and endocrine view. Philos Trans R Soc Lond B Biol Sci. 2019;374(1783):20190070. doi:10.1098/rstb.2019.0070
6. Tettamanti G, Casartelli M. Cell death during complete metamorphosis. Philos Trans R Soc Lond B Biol Sci. 2019;374(1783):20190065. doi:10.1098/rstb.2019.0065
7. Critchlow JT, Norris A, Tate AT. The legacy of larval infection on immunological dynamics over metamorphosis. Philos Trans R Soc Lond B Biol Sci. 2019;374(1783):20190066. doi:10.1098/rstb.2019.0066
8. Hammer TJ, Moran NA. Links between metamorphosis and symbiosis in holometabolous insects. Philos Trans R Soc Lond B Biol Sci. 2019;374(1783):20190068. doi:10.1098/rstb.2019.0068
9. Nunes C, Koyama T, Sucena É. Co-option of immune effectors by the hormonal signalling system triggering metamorphosis in Drosophila melanogaster. PLoS Genet. 2021;17(11):e1009916. doi:10.1371/journal.pgen.1009916
10. Almeida de Carvalho MJ, Mirth CK. Food intake and food choice are altered by the developmental transition at critical weight in Drosophila melanogaster. Anim Behav. 2017;126:195-208. doi:10.1016/j.anbehav.2017.02.005
11. Ohhara Y, Kobayashi S, Yamanaka N. Nutrient-dependent endocycling in steroidogenic tissue dictates timing of metamorphosis in Drosophila melanogaster. PLoS Genet. 2017;13(1):e1006583. doi:10.1371/journal.pgen.1006583
12. Morimoto J, Nguyen B, Lundbäck I, Than TA, Tabrizi ST, Ponton F, et al. Effects of carbohydrate types on larval development and adult traits in a polyphagous fruit fly. J Insect Physiol. 2020;120:103969. doi:10.1016/j.jinsphys.2019.103969
13. Sasmita HI, Tu WC, Bong LJ, Neoh KB. Effects of larval diets and temperature regimes on life history traits, energy reserves and temperature tolerance of male Aedes aegypti (Diptera: Culicidae): Optimizing rearing techniques for the sterile insect programmes. Parasit Vectors. 2019;12(1):578. doi:10.1186/s13071-019-3830-z
14. Lang BJ, Idugboe S, McManus K, Drury F, Qureshi A, Cator LJ. The effect of larval diet on adult survival, swarming activity and copulation success in male Aedes aegypti (Diptera: Culicidae). J Med Entomol. 2018;55(1):29-35. doi:10.1093/jme/tjx187
15. Nicholls E, Rossi M, Niven JE. Larval nutrition impacts survival to adulthood, body size and the allometric scaling of metabolic rate in adult honeybees. J Exp Biol. 2021;224(14):jeb242393. doi:10.1242/jeb.242393
16. Rehman N, Varghese J. Larval nutrition influences adult fat stores and starvation resistance in Drosophila. PLoS One. 2021;16(2):e0247175. doi:10.1371/journal.pone.0247175
17. Dittmer J, Gabrieli P. Transstadial metabolic priming mediated by larval nutrition in female Aedes albopictus mosquitoes. J Insect Physiol. 2020;123:104053. doi:10.1016/j.jinsphys.2020.104053
18. Roux O, Renault D, Mouline K, Diabaté A, Simard F. Living with predators at the larval stage has differential long-lasting effects on adult life history and physiological traits in two anopheline mosquito species. J Insect Physiol. 2021;131:104234. doi:10.1016/j.jinsphys.2021.104234
19. Lambret P, Janssens L, Stoks R. The impact of salinity on a saline water insect: Contrasting survival and energy budget. J Insect Physiol. 2021;131:104224. doi:10.1016/j.jinsphys.2021.104224
20. Stefana MI, Driscoll PC, Obata F, Pengelly AR, Newell CL, MacRae JI, et al. Developmental diet regulates Drosophila lifespan via lipid autotoxins. Nat Commun. 2017;8(1):1384. doi:10.1038/s41467-017-01740-9

21. Brown LD, Shapiro LLM, Thompson GA, Estévez-Lao TY, Hillyer JF. Transstadial immune activation in a mosquito: Adults that emerge from infected larvae have stronger antibacterial activity in their hemocoel yet increased susceptibility to malaria infection. Ecol Evol. 2019;9(10):6082-95. doi:10.1002/ece3.5192
22. Kangassalo K, Valtonen TM, Sorvari J, Kecko S, Pölkki M, Krams I, et al. Independent and interactive effects of immune activation and larval diet on adult immune function, growth and development in the greater wax moth (Galleria mellonella). J Evol Biol. 2018;31(10):1485-97. doi:10.1111/jeb.13345
23. Klockmann M, Kleinschmidt F, Fischer K. Carried over: Heat stress in the egg stage reduces subsequent performance in a butterfly. PLoS One. 2017;12(7):e0180968. doi:10.1371/journal.pone.0180968
24. Weldon CW, Mnguni S, Démares F, du Rand EE, Malod K, Manrakhan A, et al. Adult diet does not compensate for impact of a poor larval diet on stress resistance in a tephritid fruit fly. J Exp Biol. 2019;222(6):jeb192534. doi:10.1242/jeb.192534
25. May CM, Zwaan BJ. Relating past and present diet to phenotypic and transcriptomic variation in the fruit fly. BMC Genomics. 2017;18(1):640. doi:10.1186/s12864-017-3968-z
26. Min KW, Jang T, Lee KP. Thermal and nutritional environments during development exert different effects on adult reproductive success in Drosophila melanogaster. Ecol Evol. 2021;11(1):443-57. doi:10.1002/ece3.7064
27. Duxbury EML, Chapman T. Sex-specific responses of life span and fitness to variation in developmental versus adult diets in Drosophila melanogaster. J Gerontol A Biol Sci Med Sci. 2020;75(8):1431-8. doi:10.1093/gerona/glz175
28. Salis L, van den Hoorn E, Beersma DGM, Hut RA, Visser ME. Photoperiodic cues regulate phenological carry-over effects in an herbivorous insect. Funct Ecol. 2018;32(1):171-80. doi:10.1111/1365-2435.12953
29. Yan J, Kibech R, Stone CM. Differential effects of larval and adult nutrition on female survival, fecundity, and size of the yellow fever mosquito, Aedes aegypti. Front Zool. 2021;18(1):10. doi:10.1186/s12983-021-00395-z