The Principle of Natural Selection and its Laws of Reproduction and Speciation: A Formal Framework for Reproductive Architecture and Ancestry

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Abstract

This paper presents a formal framework for reproductive architecture and ancestry across reproductive modes and speciation. Natural selection is defined as the generational propagation of heritable characteristics through varying inclusions and exclusions; characteristics that are not heritable do not propagate. A single general expression states one generational cycle: an inherited ancestry field is acted upon by epigenesis and carried forward by reproductive contribution, producing the ancestry field the next generation acts on. Setting the parameters of that expression yields five laws — of asexual replication, facultative sexual reproduction, obligate sexual reproduction, hemiclonal reproduction, and speciation — resolving to five ancestry forms: full continuity, reduced continuity, integration, hemiclonal continuity, and divergence. The framework operates upstream of population-genetic models, specifying the reproductive and ancestral structures those models presuppose rather than tracking allele frequencies within them. The five laws culminate in the Principle of Natural Selection, which states that where heritable characteristics vary in inclusion and exclusion through any reproductive process, each completed generation resolves to one ancestry form. Repeated across generations, that cycle is evolution.

Keywords: Evolutionary laws · Natural selection · Parthenogenesis · Hybridogenesis · Asexual reproduction · Epigenesis

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The Framework in Brief

Organisms do not meet their conditions of life equally: some persist, some reproduce, and some do not. The generational propagation of heritable characteristics through varying inclusions and exclusions is natural selection.

The figure below and the expression that follows it are the same single generational cycle — the one drawn, the other written. Each law is that expression with its parameters set.

The Expression

$$\left[\, E_n(Q_n)\,;\, T_n \,\right] \;\longrightarrow\; Q_{n+1}$$

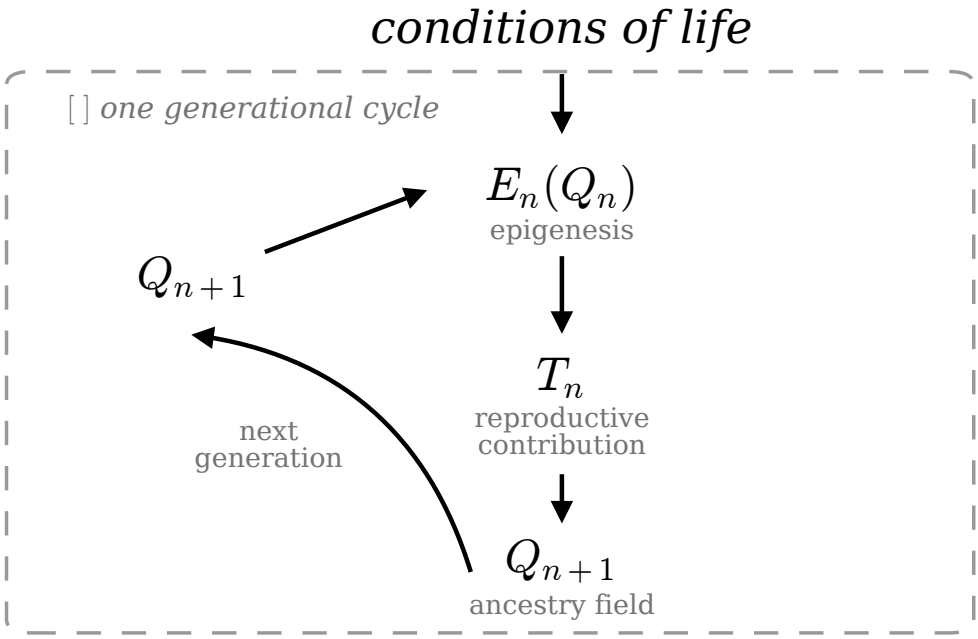

Figure 1: One generational cycle of natural selection. Conditions of life enter through $E_n(Q_n)$; E operates within the generation, while T delivers the reproductive contribution to Q_{n+1}, which the next cycle acts on as its Q_n.

Natural selection fits in three elements and an arrow.

Q is the ancestry field — the inherited generational lineage structure carried into each cycle and carried forward from it. Only reproduction carries it forward.

E is epigenesis — the organism's developmental and functional interaction with its conditions of life. Each interaction carries two roles: the organism's own activity, and what it receives. Both run at every scale, from molecular chemistry to behavior. Resources, predation, climate, mates, rivals: each reaches reproductive outcome through E, sensed or unsensed. Where sensory systems exist, sensing and feedback are among E's mechanisms.

T is reproductive contribution — the parental lineage pathways delivered at a single generational event. The reproductive operation belongs to T whole: segregation, recombination, transmission, errors arising within those operations, and exclusions produced within reproduction itself. The reproductive process is identified by T_a, T_m, T_s, or T_h: asexual replication, self-recombination, sexual reproduction, or hemiclonal reproduction.

Mutation, drift, and gene flow keep their names and lose their separate element. Mutation is a class of heritable sequence changes, not one operation. Damage received from conditions and imprecise internal activity arise within E. Errors of the reproductive operation arise within T. Stochastic events occur within E and T. Drift names their accumulated consequence across successive ancestry fields Q — a population-level trajectory, not an operator. Gene flow is realized through both generators: en-

counter and incorporation through E, and heritable joining or transmission through T. Stochasticity is a mode of both generators, not an element.

$[E_n(Q_n)\ ;\ T_n]$ is one generational cycle. The square brackets hold the cycle: the two generators interacting with what Q_n carries. The bracketed construction is read whole — one cycle, not a multiplication. The semicolon marks T's distinct role: E operates within the generation; T is the contribution delivered to the next. Whatever E does reaches the next generation only within T.

And then the arrow — which delivers **Q_{n+1}**, the ancestry field the cycle produces, in one of the ancestry forms defined below.

Q_{n+1} is carried into the cycle that follows, where the generational expression repeats. That recurrence is where the work gets done. The expression is stated for one generation and run again on what the last one left. Repeated across generations, this generational process constitutes evolution. Each completed generation updates the evolutionary history, recording either change or continuity from the preceding generation.

I. Introduction

Evolutionary biology has historically been described as a theoretical framework rather than as a system governed by formally stated laws. As a result, evolutionary explanations are usually told as narrative or tallied as statistics. Natural selection is the process at their center. In this paper, we write the structure itself down.

Our purpose is organizational and analytical. This framework is built on reproductive architecture, ancestry, and generational repetition. We are asking a prior question: what are the minimum structural conditions under which continuity, variation, integration, and divergence can occur at all?

In this framework, natural selection is the generational propagation of heritable characteristics through varying inclusions and exclusions. Characteristics that are not heritable do not propagate. The boundary is drawn at that propagation rather than at the portion of it attributable to fitness or adaptation.

E and T can each determine inclusion and exclusion through different operations, and the expression gives those operations their addresses. Some of those operations are stochastic and some are not. Both kinds vary inclusion and exclusion, and drift names the trajectory the stochastic ones accumulate across successive ancestry fields. Population-level statistics describe aggregate outcomes of events emanating from constituent organisms, cells, gametes, and reproductive interactions.

I.1 Relationship to Existing Frameworks

The present framework operates at a different level of description than standard population-genetic models. The Price equation (Price 1970) provides a general statistical identity describing selection and transmission across generations. The replicator equation models frequency-dependent selection in populations (Taylor & Jonker

1978). These are quantitative tools for tracking allele frequencies, fitness distributions, and trait changes within populations.

We do not compete with these tools. We operate upstream of them, asking: what reproductive and ancestral structures must be in place for any such quantitative dynamics to occur? Lewontin's (1970) conditions for evolution by natural selection — phenotypic variation, differential fitness, heritable fitness — are structural rather than quantitative. Godfrey-Smith (2009) develops those conditions into his characterization of "Darwinian populations": the structural conditions that make a population capable of undergoing evolution in the sense Darwin (1859) originally described. The present framework belongs with that tradition rather than with models that track evolutionary change within a given population. Lewontin's three conditions are the antecedent of every law stated here, parameterized by reproductive process; what the framework adds is the consequent — which ancestry form a generation resolves to.

Prior formalization programs operate at a different level again. Grafen's Formal Darwinism project (Grafen 2007, 2014) formally links population-genetic dynamics to fitness optimization. Rice (2004) develops the mathematical and conceptual foundations of evolutionary theory across its standard models. Those programs formalize dynamics and optimization. This framework formalizes reproductive architecture and ancestry across reproductive modes — the structures those dynamics presuppose.

Existing classifications of reproductive mode sit on different axes again. Cytological classifications name what occurs at the reproductive event — apomixis, automixis, gynogenesis, hybridogenesis and the rest (Schön, Martens, & van Dijk 2009). Organismal-relational classifications name how reproductive characters interact, through fertilization mode and parent–offspring provisioning (Cortés-García, Etxeberria, & Nuño de la Rosa 2024). This framework replaces neither. Each mode enters as a setting of Q and T and resolves to one of the ancestry forms the laws produce; a mode resolves within the formalism unless it requires both a reproductive contribution the framework does not carry and an ancestry form the laws do not produce.

A word on *law*. Whether biology has laws has been contested since Smart (1959), most forcefully in Beatty's (1995) evolutionary contingency thesis. We use the term in the constraint sense developed by Duguid (2025). A law in that sense limits and structures the other regularities of its domain. A law here states how a generative process resolves under defined structural conditions, rather than an exceptionless generalization. That literature argues whether biology has laws; this paper states five laws and the general principle that unites them.

I.2 Contribution

Our organizational contribution is to unify asexual, facultative sexual, obligate sexual, and hemiclonal reproduction — and speciation across all of them — under a single notation. The notation makes explicit the structural parameters that distinguish these modes. Existing frameworks typically address one reproductive mode at a time or treat reproductive mode as an exogenous parameter (see, e.g., Maynard Smith & Szathmáry 1995; Schön, Martens, & van Dijk 2009; Simon, Rispe, & Sunnucks 2002,

on the evolution of sex and parthenogenesis). Here, reproductive architecture lives inside the formalism itself.

Concretely, we make visible two relationships that existing models leave implicit, each demonstrated in the laws that follow. First, convergence topology — the pattern by which ancestral lineages meet at a reproductive event — is one structural constraint on the lineage input available there (Section II.1). That constraint shapes the combinatorial opportunity from which divergence can build. Second, the transition from integration to speciation requires no change in the generative process — only persistent separation, whether it accumulates over generations or arrives in a single one.

II. Formal Structural Laws of Reproduction and Speciation

II.1 Quaternary Ancestral Structure and Reproductive Synthesis

Sexual reproduction produces offspring as a synthesis of two parental contributions. Each parent carries a two-branch ancestral structure: one maternal lineage pathway and one paternal. At the moment of reproduction, the two structures converge, resolving into a quaternary architecture — four grandparental lineage pathways combining through two parents into one offspring.

$$M_1 + F_1 \;\rightarrow\; C_0$$

$$\{\, M_{2a},\; F_{2a},\; M_{2b},\; F_{2b} \,\} \;\rightarrow\; C_0$$

Here M_1 and F_1 denote the two parents of C_0; M_2a/F_2a and M_2b/F_2b denote the maternal and paternal ancestors of those two parental branches at depth two. The first display gives the width of a reproductive event; the second gives its depth.

Q is ordered, not amorphous: ancestry occupies generation-indexed positions — parents, grandparents, and so on. Reproductive architecture sets the number of positions; history determines their occupants.

The parental tier has two ancestral positions, the grandparental tier four. Those four quaternary positions are the depth-two tier: 2^2 of the 2^d positions biparental reproduction generates at depth d. It is the nearest tier that exposes the ancestral structure of both parental contributions.

Across successive generations, repeated reproductive events extend those immediate ancestral positions into the broader ancestry field Q. Quaternary structure describes immediate recombination; Q encompasses the extended generational field, including dispersed autosomal contributions beyond the immediate parental lines. In humans, the seventh generation back holds up to 128 ancestral positions, absent pedigree collapse. The number of those ancestors represented by surviving autosomal segments is smaller, and increasingly stochastic with depth, because recombination progressively breaks and redistributes inherited material. Beyond roughly this range, ge-

nealogical ancestry increasingly exceeds identifiable autosomal ancestry (Donnelly 1983; Ralph & Coop 2013; Agranat-Tamir et al. 2024).

Q records ancestral positions and their occupants across generational depth. T is the parental lineage contribution delivered from those ancestry fields at the reproductive event. T therefore carries a contribution from Q, not the ancestry field itself.

An organism carries a local realization of Q. Across a reproductively connected population, overlapping individual ancestry fields form the broader ancestry field through which reproductive exchange proceeds, accumulating through repeated reproductive joining of local fields, each joining delivered by T.

Ancestral redundancy is horizon-relative. Every ancestry in a finite population eventually loops back on itself, but ancestors shared beyond the detection horizon have been recombined below identifiability, and pathways drawing on them carry no redundancy at the only resolution the framework measures. Ancestors shared within the window are real redundancy. Where that redundancy reaches the four quaternary positions, the quaternary arithmetic prices it directly; where the shared ancestors lie deeper, as in a cousin mating, the redundancy belongs to the broader ancestry field.

Inbreeding forms a gradient of ancestral redundancy, from partial pedigree overlap to complete reuse of the same ancestry field. Self-fertilization sits at that extreme: sexual reproduction still joins two gametic contributions, but both originate within the same individual ancestry field. It requires no new reproductive law: both contributions trace to one ancestry field, and the outcome is RC_{n+1}.

Uniparentally inherited markers are the control case that shows the horizon belongs to recombination. Mitochondrial DNA follows the maternal line; most of the Y chromosome follows the paternal line. Both undergo little or no recombination, so their lineage signals remain identifiable substantially longer than recombining autosomal ancestry. Where recombination does not reshuffle, the horizon does not fall.

Clarification on scope: The quaternary concept describes the convergence topology of reproduction, not ploidy, chromosome number, or Mendelian segregation. Structural diversity is the width and depth of ancestry represented in Q, not genomic diversity or heterozygosity. The four-position quaternary tier is the immediate depth-two part of that structure, and it supplies the comparison used in II.4's facultative example.

II.2 Inclusion and Exclusion

Inclusion and exclusion name differences in what is carried forward and how strongly it is represented. Both have causes; neither implies a selecting agent.

An organism's own activity can affect what it contributes, and so can consequences it receives from conditions or from other organisms. Both are roles within E. So can the reproductive operation within T. Natural selection is the propagation carried through these varying inclusions and exclusions.

The peppered moth illustrates both sides of interaction: birds hunted, and moths

received the consequence. Camouflage that worked against pale bark worked less well once soot darkened it. No bird chose a morph frequency. Clean-air laws lightened the bark and the differential reversed, the trait unchanged (Cook & Saccheri 2013).

Adaptive is not a property a trait owns; it is a relation between trait and prevailing conditions, indexed to place and time.

II.3 The Law of Asexual Replication (Continuity)

Where heritable characteristics vary in inclusion and exclusion through asexual replication, the outcome is full continuity of the lineage.

$$\left[\, E_n(Q_{a,n})\,;\, T_a \,\right] \;\longrightarrow\; FC_{n+1}$$

Legend:

- $Q_{a,n}$ — Asexual ancestry field at cycle n: one reproductive ancestral branch at each generational depth
- T_a — Single organism contribution: one lineage pathway replicated whole. $T_a \rightarrow T_a + T_a$ (two descendant copies from one lineage)
- FC_{n+1} — Full continuity

Replication copies one lineage pathway whole. The ancestry field gains no new lineage input and carries forward with one ancestral branch at each generational depth. Differential representation therefore remains bound to each line of descent: against the same soil, one lineage persists and another fails.

Heritable variation still arises through events of interaction and replication, but the absence of recombination between reproductive ancestry fields keeps combinatorial opportunity narrow.

Horizontal gene transfer (conjugation, transformation, transduction), as observed in bacteria and archaea, introduces genetic variation outside of sexual reproduction. The encounter is E's — the organism meets a phage, another bacterium, free DNA. The acquired sequence is incorporated through the organism's own molecular activity, entering Q and delivered forward through T_a in subsequent replications. Horizontal gene transfer therefore operates through the existing elements without requiring a separate operator or changing how the lineage reproduces.

II.4 The Law of Facultative Sexual Reproduction (Alternating Continuity and Recombination)

Where heritable characteristics vary in inclusion and exclusion through facultative reproduction, the outcome is full continuity, reduced continuity, or integration.

Apomictic generation:

$$[\, E_n(Q_n)\,;\, T_a\,] \;\longrightarrow\; FC_{n+1}$$

Self-recombination (automixis):

$$[\, E_n(Q_{m,n})\,;\, T_m\,] \;\longrightarrow\; RC_{n+1}$$

Sexual reproduction, first generation following self-recombination:

$$[\, E_n(Q_{m,n})\,;\, T_s\,] \;\longrightarrow\; RC_{n+1}$$

Sexual reproduction, full ancestry field:

$$[\, E_n(Q_n)\,;\, T_s\,] \;\longrightarrow\; In_{n+1}$$

Legend:

- $Q_{m,n}$ — Ancestry at cycle n carrying self-recombination history at the relevant tier.
- Q_n — Ancestry field at cycle n; here, the full-ancestry case.
- T_a — Apomictic replication.
- T_m — Self-recombination.
- T_s — Sexual reproduction.
- FC_{n+1} — Full continuity
- RC_{n+1} — Reduced continuity
- In_{n+1} — Integration

Recombination occurs without a full biparental field. The ancestry field persists with reduced lineage input — fewer than four distinct positions at the quaternary tier.

The second expression is the first qualifying sexual generation following self-recombination, and its represented ancestry remains reduced at .75: the full-ancestry parent supplies .50 of the offspring's distinct quaternary lineage input, while the parent produced by self-recombination supplies .25 at that tier. The third is sexual reproduction with a full ancestry field at the relevant tier, and it produces In_{n+1}.

Some organisms alternate between uniparental reproduction and sexual recombination depending on environmental or demographic conditions. Which mode is the baseline and which the exception varies by species. Cyclical parthenogens run continuity as the norm, with periodic sexual passes. Facultative parthenogens such as the Komodo dragon run sexual recombination as the norm, with self-recombination as the fallback under isolation. The law covers both configurations, because the defining feature is the switch itself — not which side of it a species lives on. Asexual replication marks the zero-recombination boundary of the system. Obligate sexual reproduction marks the continuous-recombination boundary. Facultative systems occupy the intermediate cases, alternating between the two modes.

A uniparental generation may be apomictic or automictic. Apomixis replicates the maternal field whole, and the outcome is FC_{n+1}. Automixis employs meiotic machinery without a second parent, and the outcome is RC_{n+1}.

Full sexual recombination is the four-to-one topology set out in II.1. In self-recombination (parthenogenetic automixis), the mother's diploid material undergoes meiotic reduction and diploidy is restored from her meiotic products. The offspring is diploid in chromosome count but carries uniparental lineage input from at most two of four quaternary sources. That represents at most 50% of the ancestral structure available at the quaternary tier.

The outcome is neither fully sexual nor fully asexual, and the framework gives it its own arithmetic, distinct from both T_a and full sexual recombination.

Mode resolution:

Each generation resolves to exactly one mode. The switch is a mode-switching condition within E — mate availability in the Komodo dragon; photoperiod, season, or crowding in cyclical parthenogens. Each is an environmental condition, and therefore already an input to epigenesis (E).

Across generations, the lineage's trajectory is a sequence over $\{FC_{n+1}, RC_{n+1}, In_{n+1}\}$, and that alternation — not any single outcome — is what distinguishes facultative reproduction from Laws II.3 and II.5.

II.4.1 Worked Example: Facultative Reproduction in the Komodo Dragon
Facultative parthenogenesis has been documented in captive Komodo dragons (Watts et al. 2006) and in wild vertebrate populations more broadly (Booth et al. 2012; Booth & Schuett 2016).

Notation for this example:

- Qa, Qb, Qc, Qd — The four positions of the full biparental quaternary reference: Qa and Qb from the maternal ancestry field; Qc and Qd from the paternal ancestry field.
- .25 — One of the four ancestry positions at the quaternary tier. An absent position contributes 0, and redundantly present material supplies no additional position.
- Tcb — The resulting male offspring; c denotes offspring and b denotes male.
- ′ (prime) — Redundant input. A primed symbol marks maternal material already represented by Qa or Qb. It fills a structural position but supplies no additional lineage input.

When females are isolated from males, they can produce offspring through self-recombination, generating viable male offspring (Tcb) that are diploid in chromosome count (Qa .25 + Qb .25 + Qa′ .25 + Qb′ .25 = 1.0) but represent at most two distinct ancestral positions at the quaternary tier rather than four (Qa .25 + Qb .25 + Qc 0 + Qd 0 = 0.50), with the outcome RC_{n+1}. In Komodo dragons, documented viable parthenogenetic offspring are ZZ males (Watts et al. 2006).

$$[\, E_n(Q_{m,n})\,;\, T_m \,] \;\longrightarrow\; RC_{n+1}$$

When mature males become available — including those produced parthenogenetically — sexual recombination resumes.

The parthenogenetic son (Tcb):

The mother carries two lineage pathways: Qa (her mother) and Qb (her father). In full sexual reproduction, a father would contribute Qc and Qd; in parthenogenesis, those two positions have no paternal lineage input. The son is constructed entirely from those two pathways — structurally maternal, but not a copy.

The same arithmetic covers the unfertilized eggs of haplodiploid species: uniparental lineage input at the quaternary tier, and the outcome RC_{n+1}. Reduced continuity is a structural result, not a property of facultative reproduction.

II.5 The Law of Obligate Sexual Reproduction (Recombination Within an Open Population)

Where heritable characteristics vary in inclusion and exclusion through biparental recombination under unrestricted reproductive exchange, the outcome is integration.

$$\left[\, E_n(Q_n)\,;\, T_s \,\right] \;\longrightarrow\; In_{n+1}$$

Legend:

- Q_n — Ancestry field at cycle n
- T_s — Sexual reproduction
- In_{n+1} — Integration

Two full parental ancestry fields recombine and merge under unrestricted reproductive exchange, with all four quaternary positions carrying distinct lineage input where there is no ancestral overlap. Genomic configurations are transient, continually redistributed rather than preserved.

A cousin mating inside an open population creates ancestral redundancy without closing reproductive exchange — within-horizon overlap in the broader ancestry field described in II.1.

A reproductively restricted subset mating within itself, generation over generation, narrows the ancestry field through which exchange occurs; the field closes toward the confinement of II.7.

II.6 The Law of Hemiclonal Reproduction (Hybridogenesis)

Where heritable characteristics vary in inclusion and exclusion through hemiclonal reproduction, the outcome is biparental ancestry with asymmetric transmission.

$$[\, E_n(Q_{h,n})\,;\, T_h\,] \;\longrightarrow\; HC_{n+1}$$

Legend:

- $Q_{h,n}$ — Ancestry at cycle n carrying hemiclonal history: one parental lineage persists through the hybrid lineage while the complementary lineage is reacquired each reproductive cycle.
- T_h — Hemiclonal reproduction.
- HC_{n+1} — Hemiclonal continuity
- A — The parental lineage that persists clonally through the hemiclonal lineage.
- B — The complementary parental lineage, supplied anew each cycle by the sexually reproducing host lineage.

Two parental genomes combine in the offspring while only one is transmitted onward. The ancestry field is biparental within the generation and asymmetric across generations: A persists, B is replaced.

The host lineage reproduces sexually and independently, producing both female and male offspring:

B female + B male ⟶ B female or B male

Males from that host lineage supply the complementary contribution to the hemiclonal lineage:

A egg + B sperm ⟶ AB daughter

The AB daughter carries both A and B ancestry. During formation of her reproductive contribution, B is excluded and A is retained:

AB daughter ⟶ A egg

A new B contribution is then acquired from the sexually reproducing host lineage:

A egg + new B sperm ⟶ new AB daughter

Thus the offspring remains biparental in ancestry, while transmission is asymmetric across generations: A persists through the hemiclonal lineage; successive B contributions enter through sexual reproduction and terminate within each hybrid generation (Doležálková et al. 2016).

Hemiclonal reproduction is the only configuration here that cannot run alone: the hemiclonal lineage persists only while a sexually reproducing host lineage persists beside it. The other four require nothing outside the lineage they describe. Hybridogenesis is given a law of its own because it requires its own reproductive contribution, T_h, and resolves to an ancestry form no other process here produces.

II.7 The Law of Speciation (Persistent Separation)

Where heritable characteristics vary in inclusion and exclusion through persistent separation, the outcome is divergence of the separated ancestry fields.

$$[\, E_n(Q_n)\,;\, T_n \,] \;\longrightarrow\; D_{n+1}$$

Legend:

- Q_n — Ancestry field at cycle n, in any reproductive architecture
- T_n — Reproductive contribution, in any of the framework's reproductive processes
- D_{n+1} — Divergence

Recombination continues within the lineage and ceases between it and other lineages, including the ancestral population. The separated ancestry fields diverge.

Factors such as geography, ecology, behavior, and chromosomal change can separate lineages and maintain that separation across generations.

Where separation persists, differential representation proceeds independently on either side, and each side can accumulate a different series of mutations even under similar conditions (Schluter 2009). Ecological divergence can accelerate the process, but is not required.

Where reproduction is sexual, the framework uses reproductive incompatibility — the biological species concept — as the criterion of speciation, because reproductive exchange is what the framework tracks; alternative concepts (morphological, ecological, phylogenetic) index other properties.

Whole-genome duplication, documented at its origin in plants (*Tragopogon*, Ownbey 1950; *Spartina*, Ainouche et al. 2009), can produce reproductive incompatibility with the ancestral population in a single generation. Where the new lineage remains reproductively viable, speciation therefore does not require gradual accumulation across generations.

Persistent separation can originate through E, T, or their interaction without requiring an additional generative element. Integration and divergence result from the same generative processes under different conditions. Speciation therefore requires no mechanism of its own.

Strictly asexual lineages are the limiting case. Under sexual reproduction, an ancestry field is a web: separate parental branches converge at every mating. There is therefore reproductive exchange for confinement to cut, and cutting it is one route to D_{n+1}.

Under asexual replication, the ancestry field is a tree: $T_a \rightarrow T_a + T_a$ branches it at every replication, and its branches never re-merge through reproduction. Horizontal gene transfer can move material laterally between branches, through the interactions II.3 defines. But moving material is not merging ancestry: the reproductive genealogy stays a tree.

There is nothing to cut, because nothing re-mixes. But branching is not separation: replication alone yields FC_{n+1}, generation after generation. Where clonal lineages become persistently separated, differences can accumulate through E, T, or their interaction, producing D_{n+1}. What taxonomy does with such lineages is classification, and classification lies outside this framework's operational definition of speciation.

The specific ancestry form follows from Q and T; where these are shared, whether separation persists distinguishes the outcome:

Ancestry field	Reproductive process	Ancestry form	Law
$Q_{a,n}$	$T_a \rightarrow T_a + T_a$	FC_{n+1} (full continuity)	Asexual Replication (II.3)
Q_n	T_a	FC_{n+1} (full continuity)	Facultative, apomictic generation (II.4)
$Q_{m,n}$	T_m	RC_{n+1} (reduced continuity)	Facultative, self-recombination (II.4)
$Q_{m,n}$	T_s	RC_{n+1} (reduced continuity)	Facultative, first sexual generation following self-recombination (II.4)
Q_n	T_s	In_{n+1} (integration)	Facultative, full ancestry field (II.4)
Q_n	T_s	In_{n+1} (integration)	Obligate Sexual — unrestricted reproductive exchange (II.5)
$Q_{h,n}$	T_h	HC_{n+1} (hemiclonal continuity)	Hemiclonal Reproduction (II.6)
Q_n	T_n	D_{n+1} (divergence)	Speciation — persistent separation, in any reproductive architecture (II.7)

Each configuration in the table, under the condition stated beside it, resolves to exactly one ancestry form. Two rows share a configuration: in its sexual generation a facultative lineage is architecturally identical to an obligate sexual one, and only the alternation across generations (II.4) distinguishes them.

Configuration transitions. Each law binds while the configuration that satisfies its antecedent persists. A lineage can therefore move between rows without violating a law when its reproductive architecture or the conditions governing persistence change.

Reproductive architecture is itself inherited structure and can change. What holds across all such configurations is stated in the Principle of Natural Selection that follows.

III. The Principle of Natural Selection

Where heritable characteristics vary in inclusion and exclusion through any reproductive process, each completed generation resolves to one ancestry form.

$$[\, E_n(Q_n)\,;\, T_n\,] \;\longrightarrow\; Q_{n+1}$$

where Q_{n+1} is the ancestry field the cycle produces, and its form is what the generation resolved to. The laws above establish five such forms:

$$FC_{n+1} \qquad RC_{n+1} \qquad In_{n+1} \qquad HC_{n+1} \qquad D_{n+1}$$

IV. Conclusion

This framework organizes established biological processes and structures as five laws and the Principle of Natural Selection. E and T, operating in interaction with inherited Q, propagate heritable characteristics through varying inclusions and exclusions. That generational propagation is natural selection.

Where heritable characteristics vary in inclusion and exclusion through any reproductive process, each completed generation resolves to one ancestry form.

The cycle, repeated, is evolution.

Statements and Declarations

Competing interests. The author declares no competing interests.

Funding. No funding was received for this work.

Data availability. This is a theoretical study. No datasets were generated or analysed.

Author contributions. A.M. is the sole author of this work.

Use of AI tools. Portions of this manuscript were refined with the assistance of AI tools, used under the author's direction for language clarification, drafting support, source verification, and structural alignment. Conceptual synthesis, definitions, and formulations remain the sole work of the author.

References

Agranat-Tamir, L., Mooney, J. A., & Rosenberg, N. A. (2024). Counting the genetic ancestors from source populations in members of an admixed population. *Genetics*, 226(4), iyae011. https://doi.org/10.1093/genetics/iyae011

Ainouche, M. L., Fortune, P. M., Salmon, A., Parisod, C., Grandbastien, M.-A., Fukunaga, K., Ricou, M., & Misset, M.-T. (2009). Hybridization, polyploidy and invasion: lessons from *Spartina* (Poaceae). *Biological Invasions*, 11(5), 1159–1173. https://doi.org/10.1007/s10530-008-9383-2

Beatty, J. (1995). The evolutionary contingency thesis. In G. Wolters & J. G. Lennox (Eds.), *Concepts, Theories, and Rationality in the Biological Sciences* (pp. 45–81). Pittsburgh, PA: University of Pittsburgh Press.

Booth, W., & Schuett, G. W. (2016). The emerging phylogenetic pattern of parthenogenesis in snakes. *Biol J Linn Soc*, 118(2), 172–186. https://doi.org/10.1111/bij.12744

Booth, W., Smith, C. F., Eskridge, P. H., Hoss, S. K., Mendelson, J. R. III, & Schuett, G. W. (2012). Facultative parthenogenesis discovered in wild vertebrates. *Biol Lett*, 8(6), 983–985. https://doi.org/10.1098/rsbl.2012.0666

Cook, L. M., & Saccheri, I. J. (2013). The peppered moth and industrial melanism: evolution of a natural selection case study. *Heredity*, 110(3), 207–212. https://doi.org/10.1038/hdy.2012.92

Cortés-García, D., Etxeberria, A., & Nuño de la Rosa, L. (2024). The evolution of reproductive characters: an organismal-relational approach. *Biol Philos*, 39(5), 26. https://doi.org/10.1007/s10539-024-09961-1

Darwin, C. (1859). *On the Origin of Species by Means of Natural Selection*. London: John Murray.

Doležálková, M., Sember, A., Marec, F., Ráb, P., Plötner, J., & Choleva, L. (2016). Is premeiotic genome elimination an exclusive mechanism for hemiclonal reproduction in hybrid males of the genus *Pelophylax*? *BMC Genetics*, 17, 100. https://doi.org/10.1186/s12863-016-0408-z

Donnelly, K. P. (1983). The probability that related individuals share some section of genome identical by descent. *Theor Popul Biol*, 23(1), 34–63. https://doi.org/10.1016/0040-5809(83)90004-7

Duguid, C. (2025). Developing the structure of laws in biology. *Biol Philos*, 40, 7. https://doi.org/10.1007/s10539-025-09979-z

Godfrey-Smith, P. (2009). *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.

Grafen, A. (2007). The formal Darwinism project: a mid-term report. *J Evol Biol*, 20(4), 1243–1254. https://doi.org/10.1111/j.1420-9101.2007.01321.x

Grafen, A. (2014). The formal darwinism project in outline. *Biol Philos*, 29(2), 155–174. https://doi.org/10.1007/s10539-013-9414-y

Lewontin, R. C. (1970). The units of selection. *Annu Rev Ecol Syst*, 1, 1–18. https://doi.org/10.1146/annurev.es.01.110170.000245

Maynard Smith, J., & Szathmáry, E. (1995). *The Major Transitions in Evolution*. Oxford: W.H. Freeman.

Ownbey, M. (1950). Natural hybridization and amphiploidy in the genus *Tragopogon*. *American Journal of Botany*, 37, 487–499. https://doi.org/10.1002/j.1537-2197.1950.tb11033.x

Price, G. R. (1970). Selection and covariance. *Nature*, 227, 520–521. https://doi.org/10.1038/22752

Ralph, P., & Coop, G. (2013). The geography of recent genetic ancestry across Europe. *PLoS Biol*, 11(5), e1001555. https://doi.org/10.1371/journal.pbio.1001555

Rice, S. H. (2004). *Evolutionary Theory: Mathematical and Conceptual Foundations*. Sunderland, MA: Sinauer Associates.

Schluter, D. (2009). Evidence for ecological speciation and its alternative. *Science*, 323(5915), 737–741. https://doi.org/10.1126/science.1160006

Schön, I., Martens, K., & van Dijk, P. (Eds.). (2009). *Lost Sex: The Evolutionary Biology of Parthenogenesis*. Dordrecht: Springer.

Simon, J.-C., Rispe, C., & Sunnucks, P. (2002). Ecology and evolution of sex in aphids. *Trends Ecol Evol*, 17(1), 34–39. https://doi.org/10.1016/S0169-5347(01)02331-X

Smart, J. J. C. (1959). Can biology be an exact science? *Synthese*, 11(4), 359–368. https://doi.org/10.1007/BF00486197

Taylor, P. D., & Jonker, L. B. (1978). Evolutionary stable strategies and game dynamics. *Mathematical Biosciences*, 40, 145–156. https://doi.org/10.1016/0025-5564(78)90077-9

Watts, P. C., Buley, K. R., Sanderson, S., Boardman, W., Ciofi, C., & Gibson, R. (2006). Parthenogenesis in Komodo dragons. *Nature*, 444, 1021–1022. https://doi.org/10.1038/4441021a