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Abstract

The evolutionary origin of sexual dimorphism is classically explained by energetic trade-offs between gamete size and number interacting with fertilization ecology. These models, however, treat genome fidelity as a passive or metabolically subsumed property. Here we show that informational constraints alone - specifically the limited scalability of molecular machinery required for genome replication, repair, and chromatin maintenance are sufficient to destabilize symmetric reproductive strategies and generate stable reproductive dimorphism. We introduce the Molecular Fidelity-Encounter Competition (MF–EC) model, an Adaptive Dynamics framework in which reproductive strategies evolve along a heritable axis representing parental reproductive deployment. Encounter success increases concavely with deployment, whereas per-gamete molecular fidelity declines convexly due to dilution of finite parental fidelity budgets. Beyond a biologically realistic fidelity-dilution threshold, the unique evolutionary equilibrium becomes convergence-stable but invasion-unstable, enforcing disruptive evolutionary branching. Invasion fitness analysis and replicator dynamics demonstrate that the adaptive landscape supports exactly two mutually invasion-resistant strategies, while all intermediate strategies are eliminated. This framework provides a principled explanation for

the near-universality of binary sexual systems and identifies informational constraints as a fundamental, non-energetic driver of sexual dimorphism.

Keywords: Sexual dimorphism; anisogamy; adaptive dynamics; mutation load; genome fidelity; evolutionary branching.

Introduction

The origin and persistence of sexual dimorphism remain one of the most fundamental and enduring problems in evolutionary biology. Across the vast majority of eukaryotic lineages, sexual reproduction involves two discrete gamete strategies that differ profoundly in size, number, mobility, and investment, despite arising from ancestral systems in which gametes were morphologically similar or indistinguishable (isogamy). Explaining why such symmetry is evolutionarily unstable, and why divergence consistently resolves into a binary outcome rather than a continuum or multiple stable types, has motivated more than a century of theoretical and empirical research. Classical explanations for the evolution of anisogamy and sex differences are rooted in energetic and metabolic trade-offs. Early insights by Bateman demonstrated that reproductive success often scales more steeply with mating opportunities than with investment per gamete, particularly in males (Bateman 1948). Parker, Baker and Smith formalized this intuition by showing that disruptive selection emerges naturally from the size–number trade-off in gamete production when fertilization success depends on encounter rates (Parker, Baker & Smith 1972). These ideas were later synthesized and extended within the framework of evolutionary game theory and life-history evolution, establishing energetic asymmetry as a sufficient mechanism for the origin of anisogamy (Maynard Smith 1982; Charlesworth 1978; Bulmer & Parker 2002).

Subsequent theoretical work expanded these models to incorporate ecological context, gamete limitation, mating system structure, and feedbacks between reproductive strategies and population dynamics (Lehtonen & Kokko 2011; Lehtonen et al. 2016; Lehtonen & Parker 2014; Randerson & Hurst 2001). Together, these approaches form the dominant paradigm for understanding sex evolution: energetic constraints interacting with fertilization ecology generate disruptive selection, leading to divergence between many small gametes and fewer large ones.

However, reproduction is not only an energetic process; it is also fundamentally an informational one. Each reproductive event requires accurate genome replication, chromatin packaging, DNA repair, epigenetic maintenance, and error surveillance to ensure faithful transmission across generations. The molecular machinery responsible for these processes including DNA polymerases, mismatch-repair complexes, recombination factors, chromatin remodellers, histone chaperones, and epigenetic regulators are produced in finite quantities by the parent and must be partitioned among all gametes produced within a reproductive cycle (Eigen 1971; Eigen & Schuster 1979; Drake et al. 1998; Lynch 2010). Unlike metabolic resources, which can often be upregulated plastically, many components of fidelity machinery are constrained by expression limits, assembly complexity, and coordination costs.

Mutation-load theory has long emphasized that replication fidelity and mutation rates impose fundamental limits on evolutionary processes (Kimura 1967; Eigen 1971; Crow 1970; Lynch et al. 1993). In particular, the error-threshold concept predicts that systems producing more replicates accumulate disproportionately higher mutational burden unless fidelity mechanisms are strengthened correspondingly (Eigen & Schuster 1979). These ideas have been extensively explored in the context of population size, genome complexity, and the evolution of mutation rates, but they have rarely been integrated explicitly into models of reproductive strategy evolution. Empirical evidence across taxa indicates that such informational constraints are biologically consequential. In mammals, large-scale parent-offspring trio sequencing studies have demonstrated a strong, monotonic increase in offspring de novo mutation burden with paternal age, reflecting cumulative germline replication and gamete production intensity (Kong et al. 2012; Jónsson et al. 2017; Scally & Durbin 2012). Importantly, offspring mutation loads exhibit substantial inter-individual heterogeneity, even among siblings, indicating that fidelity allocation does not scale uniformly with reproductive output (Makova & Li 2002; Ellegren 2007; Lynch 2010). Comparable patterns of mutation-rate variability and fidelity limitation have been documented in birds, insects, plants, and unicellular eukaryotes, suggesting that fidelity partitioning constraints are a general feature of biological reproduction rather than a peculiarity of mammals (Baer et al. 2007; Sung et al. 2012; Sharp & Li 1989).

Despite this, most theoretical treatments of sex evolution either treat mutation as an exogenous parameter or subsume fidelity costs implicitly into energetic trade-offs. As a result, the evolutionary consequences of non-scalable molecular fidelity budgets remain underexplored. In particular, it remains unclear whether informational constraints alone can destabilize symmetric reproductive strategies and generate stable dimorphism, or whether energetic asymmetries are strictly required.

Here, we propose that a fundamental conflict between encounter competitiveness and molecular fidelity allocation constitutes an independent and sufficient mechanism for the evolution of sexual dimorphism. Gametes produced in greater numbers gain advantages in encounter rates and fertilization success, but these gains saturate due to ecological crowding, search inefficiency, and diminishing marginal returns (Bateman 1948; Parker et al. 1972; Levitan 1993; Lehtonen & Parker 2014). At the same time, increasing reproductive deployment imposes an accelerating fidelity cost as finite parental repair and chromatin-protection machinery is diluted across more gametes, elevating mutation risk and compromising genome integrity (Eigen 1971; Eigen & Schuster 1979; Lynch 2010; Waxman & Gavrilets 2005). To formalize this conflict, we introduce the MF–EC (Molecular Fidelity–Encounter Competition) Game, an Adaptive Dynamics framework in which reproductive strategies evolve along a single continuous axis representing a heritable parental reproductive allocation program. Crucially, this axis does not describe realized gamete number per se, but a genetically encoded reproductive strategy subject to mutation, invasion, and frequency-dependent selection (Eshel 1983; Dieckmann & Law 1996; Geritz et al. 1998). Within this framework, encounter benefits increase concavely with reproductive deployment, while molecular fidelity declines convexly due to finite informational resources.

This structure generates a distinct evolutionary regime, selection initially drives populations toward an intermediate reproductive strategy that balances encounter gains and fidelity losses. However, curvature analysis reveals that this equilibrium can become a fitness minimum once fidelity dilution pressure exceeds a biologically realistic threshold. Under these conditions, symmetric reproductive strategies are convergence-stable but invasion-unstable, forcing disruptive evolutionary branching (Wright 1932; Eshel 1983; Geritz et al. 1998; Rueffler et al. 2006; Ito & Dieckmann 2014). The resulting divergence produces exactly two mutually invasion-resistant strategies: one optimized for high fidelity through low reproductive deployment, and the other optimized for encounter competitiveness through high deployment. Crucially, because this conflict evolves along a one-dimensional fidelity copy number axis, the adaptive landscape supports only two stable peaks, rather than an unbounded proliferation of strategies. This sharply distinguishes the MF-EC mechanism from compatibility-driven mating-type systems in fungi, ciliates, and algae, where diversification occurs on multidimensional fusion-compatibility axes and can yield dozens or even hundreds of mating types (Nanney 1953; Kües 2000; Billiard et al. 2011; Hadjivasiliou et al. 2016).

In this study, we combine analytical Adaptive Dynamics with empirical germline mutation patterns to show that non-scalable molecular fidelity budgets are sufficient to destabilize isogamy and enforce stable reproductive dimorphism. By treating informational integrity as an explicit evolutionary currency, our framework complements classical energetic models and provides a general, biologically grounded route to the emergence and persistence of sex-specific reproductive roles across eukaryotes.

Methods

Overall modelling and analytical approach

We investigated the evolutionary dynamics of reproductive strategies using a theory-driven Adaptive Dynamics framework, designed to analyse the long-term evolution of continuous traits under frequency-dependent selection generated by rare mutations [Eshel 1983; Dieckmann & Law 1996; Geritz et al. 1998; Kisdi 2006]. This approach is appropriate for systems in which evolutionary change occurs through small mutational steps and ecological dynamics equilibrate on a faster timescale than evolution.

All analyses treat reproduction as an evolving heritable parental reproductive allocation program, rather than a realized gamete count. This distinction is essential for interpreting the Results and aligns with standard Adaptive Dynamics practice.

Empirical motivation and biological grounding

To motivate the biological plausibility of fidelity dilution constraints, we drew on published large-scale human parent–offspring trio sequencing studies reporting high-confidence coding de novo mutation (DNV) calls [Makova & Li 2002; Ellegren 2007; Kong et al. 2012; Jónsson et al. 2017].

These studies consistently demonstrate (i) substantial inter-offspring heterogeneity in mutation burden and (ii) a strong positive association between paternal age and offspring mutation load. In the present study, paternal age was treated conceptually as a monotonic proxy for cumulative germline replication and reproductive deployment intensity. No raw sequencing data were reanalysed, and no statistical inference or parameter fitting was performed. The empirical literature was used solely to assess directional and qualitative consistency with the model's core assumption that molecular fidelity cannot scale linearly with reproductive deployment.

Definition of the MF–EC payoff structure

Reproductive success was modelled as the outcome of two antagonistic biological processes: encounter–competition efficiency and molecular fidelity allocation. The payoff associated with a reproductive strategy n was defined as:

$$P(n;\theta,c) = \frac{(n\ln(1+n))}{}(1+\theta n) - \ cn^2$$

where n is a continuous heritable trait representing a parental reproductive allocation program.

Encounter–competition efficiency was modelled as:

$$EC(n) = \ln(1+n)$$

a concave increasing function capturing diminishing returns in fertilization success as gamete encounter rates saturate, consistent with classical fertilization and anisogamy theory [Bateman 1948; Parker et al. 1972; Lehtonen & Parker 2014].

Molecular fidelity allocation per gamete was modelled as:

$$MF(n) = \frac{1}{1+\theta n}$$

where θ>0 quantifies sensitivity to fidelity dilution. This formulation reflects mutation-load and error-threshold theory, which predicts accelerating loss of fidelity as replication intensity increases unless compensatory mechanisms evolve [Eigen 1971; Eigen & Schuster 1979; Lynch 2010].

The quadratic cost term cn^2 ensures bounded evolutionary dynamics and prevents runaway strategies, following standard practice in continuous-trait evolutionary models [Eshel 1983; Hofbauer & Sigmund 1998; Kisdi 2006].

Selection gradient analysis and identification of singular strategies

To identify evolutionary equilibria of the reproductive allocation trait n, we analysed the selection gradient, defined as the derivative of the reproductive payoff with respect to the trait value, dP / dn. The selection gradient quantifies the direction and strength of selection acting on small mutational changes in the reproductive strategy and is the central object used to locate evolutionary equilibria in Adaptive Dynamics frameworks [Eshel 1983; Dieckmann & Law 1996; Geritz et al. 1998].

Evolutionary equilibria, or singular strategies, correspond to trait values at which the selection gradient vanishes. At such points, small mutational deviations neither increase nor decrease reproductive payoff, indicating a balance between opposing selective forces. In the present model, setting $dP / dn = 0$ yields an implicit equilibrium condition determined by the antagonistic interaction between encounter–competition gains and fidelity dilution.

This equilibrium condition admits a unique positive solution for all biologically meaningful values of the fidelity dilution parameter $\theta > 0$, ensuring that the model predicts a single, well-defined singular strategy rather than multiple or degenerate equilibria. The uniqueness of this solution is important, as it guarantees that the evolutionary dynamics converge toward a single candidate equilibrium prior to any diversification.

The resulting singular strategy, denoted n^* can be expressed analytically using the Lambert W function, which naturally arises in transcendental equations of the form $xe^x = y$. The Lambert W function is widely used in evolutionary theory, population dynamics, and related fields to obtain closed-form solutions to such equations [Corless et al. 1996]. Expressing n^* in closed form allows the position of the evolutionary equilibrium to be characterized explicitly as a function of the fidelity dilution parameter, facilitating both analytical interpretation and numerical evaluation.

Convergence stability analysis

After identifying the singular reproductive strategy, we assessed whether evolutionary trajectories are expected to converge toward this equilibrium under gradual mutational change. Convergence stability addresses the question of directional evolution: whether small mutational deviations from the singular strategy are favoured or disfavoured by selection when the population is close to equilibrium.

Following standard Adaptive Dynamics theory, convergence stability was evaluated by analysing the local behaviour of invasion fitness in the neighbourhood of the singular strategy [Dieckmann & Law 1996; Geritz et al. 1998; Kisdi 2006]. Specifically, we examined the derivative of invasion fitness with respect to the mutant trait value, evaluated at the point where mutant and resident strategies coincide. A negative derivative indicates that selection acts to restore the population toward the singular strategy following small perturbations.

Under this criterion, the singular strategy identified in the MF–EC framework was classified as convergence-stable, meaning that evolutionary dynamics driven by small, rare mutations will reliably guide populations toward this equilibrium. This result ensures that the singular strategy is not merely a mathematical artifact but represents a dynamically reachable state under biologically realistic evolutionary processes.

Importantly, convergence stability does not imply long-term evolutionary stability. Rather, it establishes that the population will first approach the singular strategy before any potential diversification occurs, setting the stage for subsequent analyses of evolutionary stability and disruptive selection.

Curvature analysis and evolutionary stability

To determine whether the singular reproductive strategy corresponds to a fitness maximum or a fitness minimum, we analyzed the local curvature of the payoff landscape at the singular strategy n^*. Curvature analysis addresses evolutionary stability by asking whether selection acting on nearby trait values favors convergence toward the singular strategy or promotes divergence away from it.

Following standard Adaptive Dynamics theory, evolutionary stability was assessed by evaluating the second derivative of the payoff function with respect to the reproductive allocation trait at n^* [Eshel 1983; Geritz et al. 1998; Rueffler et al. 2006]. This second-order analysis captures the local shape of the fitness landscape and determines whether the singular strategy represents a local fitness peak or a local fitness valley.

To facilitate biological interpretation, curvature was decomposed into contributions arising from the two antagonistic components of the MF–EC framework. The encounter–competition component contributes a concave effect, reflecting diminishing returns in encounter success as reproductive deployment increases, whereas the molecular fidelity component contributes a convex effect, reflecting accelerating fidelity loss due to dilution of finite parental maintenance resources. The balance between these opposing curvature contributions determines the evolutionary nature of the singular strategy.

A negative curvature at n^* indicates that the singular strategy is a fitness maximum and therefore evolutionarily stable under small perturbations, leading to stabilizing selection. In contrast, a positive curvature indicates that the singular strategy is a fitness minimum. In this case, selection favors divergence away from the singular strategy, satisfying the necessary condition for evolutionary branching and the emergence of phenotypic diversification [Eshel 1983; Geritz et al. 1998; Rueffler et al. 2006].

Disruptive branching and invasion fitness

Once the singular reproductive strategy was identified as a fitness minimum, we analysed the resulting disruptive selection using invasion fitness criteria. Invasion fitness quantifies whether

a rare mutant strategy can increase in frequency when introduced into a population dominated by a resident strategy and is the appropriate measure for assessing evolutionary branching and evolutionary stability in Adaptive Dynamics [Dieckmann & Law 1996; Geritz et al. 1998].

Invasion fitness of a mutant strategy n_m in a resident population characterized by strategy n_r was defined as:

$$W_{\text{inv }(n_m,n_r)} = P(n_m) - P(n_r)$$

A positive value of W_{inv} indicates that the mutant can invade when rare, whereas a negative value indicates that the mutant is selectively disfavoured.

Following the onset of branching, two divergent strategy classes emerge on either side of the singular strategy. To determine whether these strategies constitute a protected dimorphic evolutionary stable strategy (ESS)**,** we evaluated mutual invasibility conditions. A dimorphic strategy pair is classified as protected when neither strategy can invade the other when rare, satisfying the classical ESS criteria for frequency-dependent selection [Maynard Smith 1982; Eshel 1983; Hofbauer & Sigmund 1998].

To assess whether more than two strategies could coexist on the same adaptive axis, we explicitly tested intermediate strategies for invasibility against both resident strategies. Intermediate strategies were found to be invasion-unstable in both directions, as they simultaneously incur encounter saturation and fidelity dilution. This analysis establishes the minimality of the two-cluster outcome, demonstrating that exactly two stable strategies can persist on a one-dimensional fidelity–deployment axis.

Replicator dynamics and frequency stability

Following evolutionary branching, we examined the population-level dynamics of strategy frequencies to determine whether the divergent reproductive strategies persist over evolutionary time. While invasion fitness analyses establish whether strategies can invade when rare, they do not describe how strategy frequencies change once multiple strategies coexist. To address this, we modelled post-branching dynamics using replicator equations, a standard framework for analysing frequency-dependent selection in evolutionary game theory [Maynard Smith 1982; Hofbauer & Sigmund 1998].

The temporal change in the frequency x_i of strategy iii was described by:

$$\frac{dx_i}{dt} = x_{i(P_i - \bar{P})}, \bar{P} = \sum_i x_i P_i,$$

where P_i denotes the payoff associated with strategy i, and $\bar{P}$ represents the mean payoff in the population. Under this formulation, strategies with payoffs exceeding the population mean increase in frequency, whereas strategies with lower-than-average payoffs decline.

Replicator dynamics were used to assess the long-term stability of the dimorphic outcome generated by evolutionary branching. Numerical evaluation of these dynamics confirmed that the two extreme strategies increase in frequency and are maintained over time, while intermediate strategies are progressively eliminated. This frequency-level analysis therefore complements the invasion fitness results by demonstrating that the dimorphic evolutionary stable strategy is not only invasion-resistant but also dynamically stable once established.

Comparative interpretation with multi-mating-type systems

To place the two-strategy outcome predicted by the MF–EC framework in a broader biological context, we conceptually contrasted our results with well-characterized multi-mating-type systems in fungi and ciliates. These systems are often cited as apparent counterexamples to binary reproductive dimorphism and therefore warrant explicit consideration.

In fungi and ciliates, diversification of mating types occurs along multidimensional compatibility axes, where reproductive success depends on molecular recognition and compatibility between mating partners rather than on parental allocation of reproductive deployment or molecular fidelity. In such systems, the emergence of additional mating types confers an immediate selective advantage by increasing the probability of finding a compatible partner, without necessarily incurring costs associated with genome replication fidelity or reproductive deployment [Nanney 1953; Kües 2000; Billiard et al. 2011].

By contrast, the MF–EC framework describes evolution along a single continuous adaptive axis defined by the antagonistic relationship between copy-dependent encounter success and non-scalable molecular fidelity allocation. On such a one-dimensional axis, evolutionary theory predicts that only a limited number of mutually protected strategies can coexist. The two-strategy outcome therefore reflects a constraint imposed by the dimensionality of the underlying evolutionary trade-off, rather than by taxonomic group or reproductive mode.

This conceptual distinction clarifies that multi-mating-type systems do not contradict the MF–EC prediction of stable reproductive dimorphism, but instead represent evolutionary solutions to fundamentally different selective constraints.

Software, numerical evaluation, and figure generation

All analytical derivations were carried out symbolically, and numerical evaluations were used where necessary to illustrate the qualitative behaviour of the model. Numerical analyses were employed to visualize payoff landscapes, identify singular strategies, examine curvature regimes, evaluate invasion conditions, and simulate post-branching replicator dynamics. These evaluations were used for illustrative and exploratory purposes only and did not involve

parameter fitting or statistical inference. Figures were generated using custom scripts developed for this study and subsequently refined to ensure clarity, consistency, and accessibility. No raw empirical datasets were reanalysed as part of this study. Empirical results cited in the manuscript are drawn exclusively from previously published literature and are used solely to motivate and contextualize the theoretical framework.

Reporting standards

All modelling assumptions are explicitly stated in the main text and Supplementary Information, and all parameters are biologically motivated rather than fitted to empirical data. Complete analytical derivations, invasion fitness analyses, and robustness checks are provided in the Supplementary Information to ensure transparency and reproducibility.

The study follows established best practices for theoretical and modelling research in evolutionary biology, including clear separation of assumptions, results, and interpretation; explicit identification of evolutionary equilibria and stability conditions; and careful distinction between analytical results and illustrative numerical evaluations [Eshel 1983; Dieckmann & Law 1996; Geritz et al. 1998; Kisdi 2006]. No new empirical data were generated, and previously published empirical studies are cited solely for biological context.

Results

Empirical motivation: germline mutation heterogeneity implies a non-scalable fidelity currency

A central assumption of the MF–EC framework is that molecular fidelity cannot scale linearly with reproductive deployment, because DNA repair, replication accuracy, and chromatin-protection machinery are synthesized in finite amounts by the parent and must be partitioned among all gametes. To establish the biological plausibility of such a constraint, we draw on high-confidence coding de novo mutation (DNV) data from large human parent–offspring trio sequencing studies (Kong et al. 2012; Jónsson et al. 2017).

Across offspring, mutation burden exhibits substantial inter-individual heterogeneity rather than collapsing around a narrow optimum, a robust feature of mammalian germlines documented across taxa and sequencing platforms (Makova & Li 2002; Ellegren 2007; Lynch 2010). Moreover, paternal age: an established proxy for cumulative germline replication and reproductive deployment intensity, shows a strong positive association with offspring mutation burden (Kong et al. 2012; Jónsson et al. 2017).

Although these data do not directly measure heritable reproductive strategies, they demonstrate two critical biological facts: (i) offspring genomes occupy distinct fidelity states, and (ii) increased reproductive deployment is systematically associated with increased mutation load. Together, these observations motivate treating molecular fidelity as an independent evolutionary currency subject to scalability limits, rather than subsuming it into metabolic or

energetic costs (Fig.1). Extended discussion of germline mutation heterogeneity and its interpretation within the MF–EC framework is provided in Supplementary Section S11.

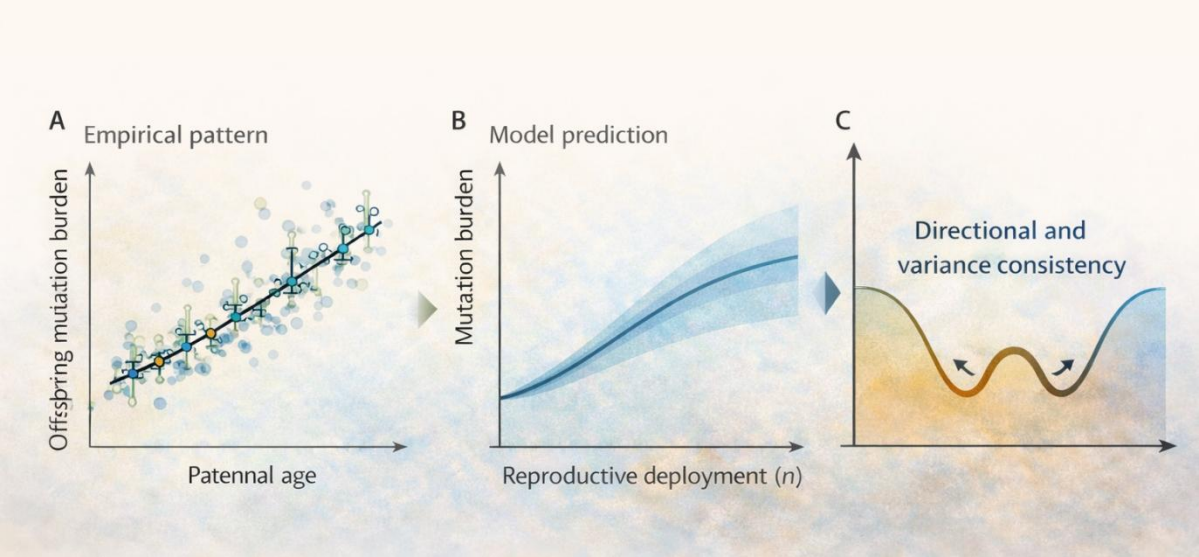


Figure 1 Empirical germline mutation scaling is consistent with MF–EC fidelity dilution. **(A)** Empirical relationship between paternal age and offspring de novo mutation burden reported in large-scale human parent–offspring trio sequencing studies, illustrating both a positive mean trend and substantial inter-individual variance. **(B)** Model-predicted increase in mutation burden with increasing reproductive deployment n under fidelity dilution, shown for illustrative parameter values. Shaded regions indicate variance arising from heterogeneous fidelity partitioning. **(C)** Conceptual comparison highlighting directional and variance-level consistency between empirical mutation scaling and MF–EC model predictions. Empirical data are shown for qualitative comparison only and are not used to parameterize or fit the model.

MF–EC payoff structure on a heritable reproductive program axis

We model reproduction as a heritable parental strategy specifying a gamete reproductive program, represented by a continuous trait n. Importantly, n denotes a genetically encoded reproductive allocation program, not a realized gamete count and evolves under mutation and frequency-dependent selection (Eshel 1983; Dieckmann & Law 1996).

The payoff associated with strategy n is defined as

$$P(n;\theta,c) = \frac{(n\ln(1+n))}{}(1+\theta n) - \ cn^2,$$

where the payoff arises from two antagonistic biological processes.

Encounter–competition efficiency increases with reproductive deployment according to

$$EC(n) = \ln(1+n),$$

a concave function capturing diminishing returns in fertilization success as encounter fields saturate (Bateman 1948; Parker et al. 1972; Lehtonen & Parker 2014). This term favors increasing n, but with decreasing marginal benefit.

In contrast, molecular fidelity per gamete declines due to finite parental allocation of replication and repair machinery, formalized as

$$MF(n) = \frac{1}{1 + \theta n},$$

where θ>0 quantifies fidelity dilution sensitivity. This convex decline reflects mutation-load theory predictions that fidelity loss accelerates as replication intensity increases (Eigen 1971; Eigen & Schuster 1979; Lynch 2010).

The quadratic cost term cn^2 ensures smooth evolutionary stability of continuous strategies without altering the qualitative conflict between encounter gains and fidelity dilution (Eshel 1983; Hofbauer & Sigmund 1998; Kisdi 2006). Together, this structure formalizes a non-metabolic conflict between encounter competitiveness and informational integrity. The MF–EC framework and its biological interpretation are illustrated in Fig. 2. Full derivations of encounter–competition efficiency, molecular fidelity dilution, and the combined payoff function are provided in Supplementary Sections S3–S5.

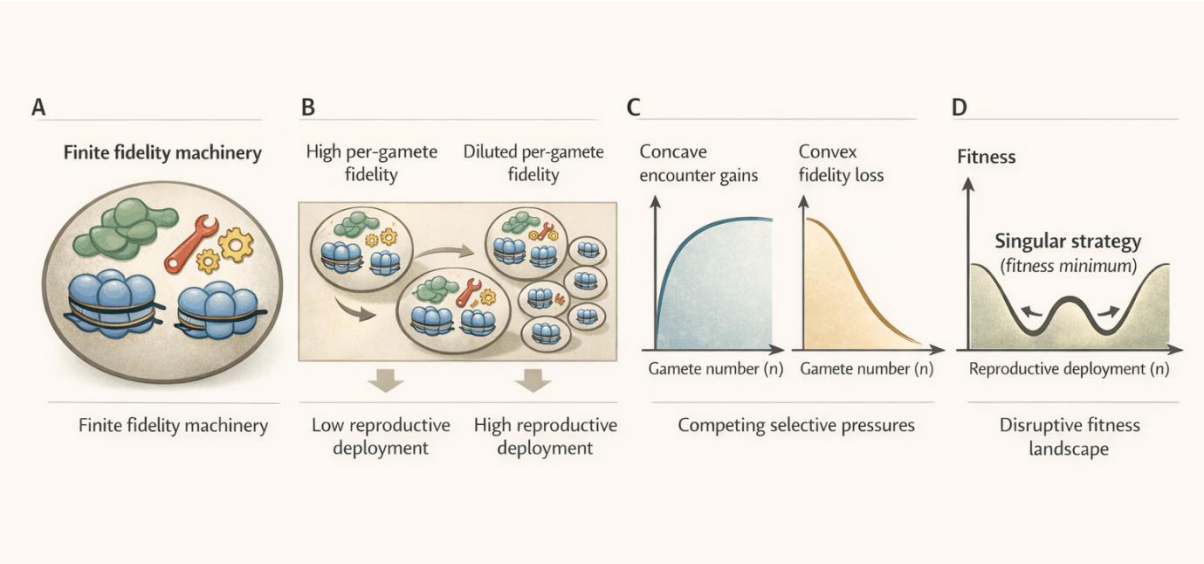


Figure 2 Fidelity–encounter conflict as an independent evolutionary currency. Conceptual illustration of the Molecular Fidelity–Encounter Competition (MF–EC) framework.
(A) Reproduction relies on finite molecular machinery for genome replication, repair, chromatin packaging, and epigenetic maintenance, imposing an upper limit on per-gamete fidelity.
(B) At low reproductive deployment, fidelity machinery can be concentrated across few gametes, resulting in high per-gamete fidelity; increasing deployment dilutes this machinery, reducing fidelity per gamete.

(C) The resulting selective pressures oppose each other: encounter–competition gains increase concavely with gamete number, whereas molecular fidelity declines convexly due to dilution of finite maintenance capacity.
(D) The interaction between these opposing forces generates a disruptive fitness landscape with a singular reproductive strategy that becomes evolutionarily unstable, promoting divergence into distinct reproductive strategies.

Existence and uniqueness of a singular evolutionary strategy

Adaptive Dynamics predicts evolutionary equilibria at points where the selection gradient vanishes. Solving $dP/dn = 0$ yields the implicit equilibrium condition

$$n^* e^{n^*} = \frac{1}{\theta},$$

which has a unique positive solution given exactly by the Lambert W function,

$$n^* = W\left(\frac{1}{\theta}\right),$$

where $W(x)e^{W(x)} = x$(Corless et al. 1996). The singular strategy n^* therefore emerges analytically from the antagonistic balance between encounter–competition gains and fidelity dilution, rather than being imposed a priori. Its position shifts predictably with the strength of fidelity dilution θ, linking the location of the evolutionary equilibrium directly to biological constraints on molecular fidelity (Fig. 3). The complete derivation of the selection gradient and the analytical solution using the Lambert W function is given in Supplementary Section S6 (see also Fig. S1).

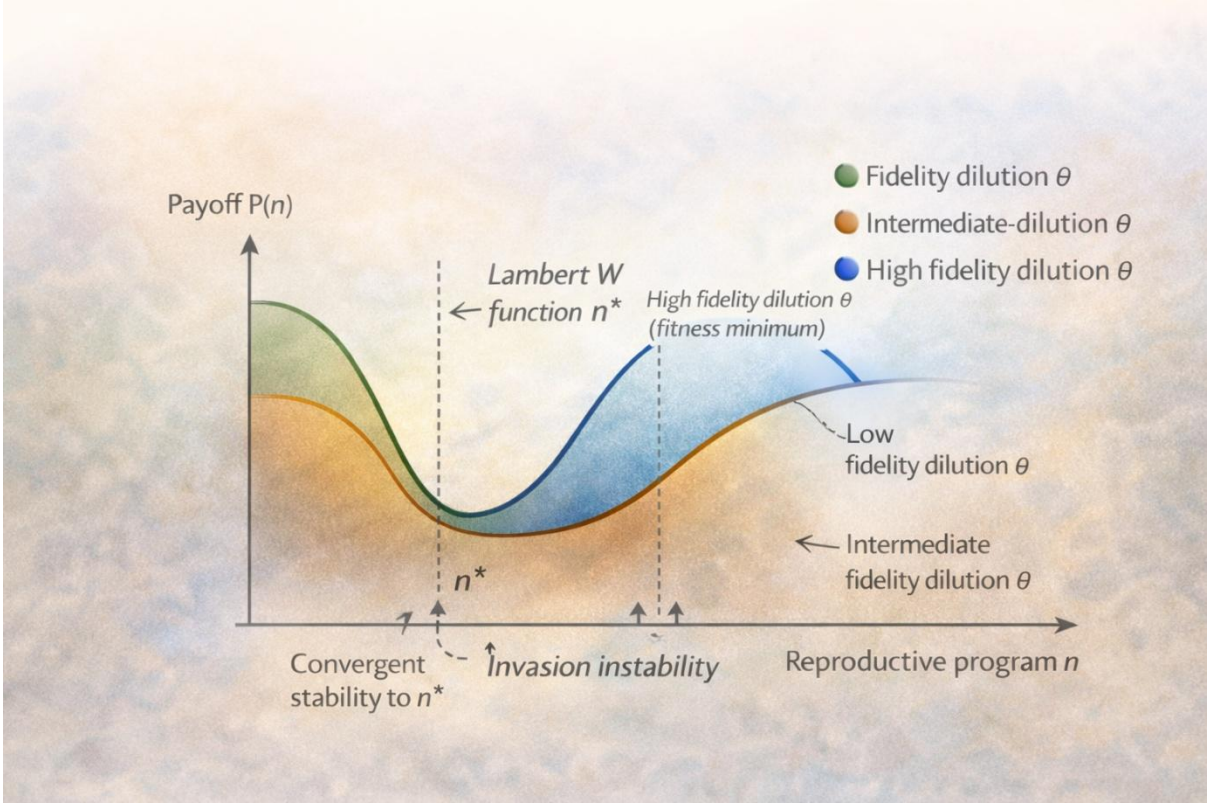


Figure 3 MF–EC payoff landscape and analytically derived singular strategy.
Reproductive payoff $P(n)$ as a function of the heritable reproductive program n under different regimes of fidelity dilution θ. The singular strategy n^* arises as the unique solution to the selection gradient condition and can be expressed analytically using the Lambert W function. Dashed vertical lines indicate the position of n^*.
For low fidelity dilution, the singular strategy corresponds to a fitness maximum and is evolutionarily stable. As fidelity dilution increases, curvature at n^* becomes positive, transforming the equilibrium into a fitness minimum. This regime is convergence-stable but invasion-unstable, satisfying the conditions for evolutionary branching.

Convergence stability of the singular strategy

Evaluation of invasion fitness gradients confirms that the singular strategy n^* is convergence-stable: small mutational deviations from n^* experience restoring selection that drives the population back toward the equilibrium (Dieckmann & Law 1996; Geritz et al. 1998; Kisdi 2006). Consequently, ancestral populations evolving under MF–EC trade-offs are expected to approach n^* gradually through successive mutational steps.

Convergence stability establishes n^* as an evolutionary attractor under directional selection, but by itself does not determine whether the singular strategy corresponds to a fitness maximum or a fitness minimum. This distinction is addressed by curvature analysis in the following section. Formal invasion-fitness gradients and stability conditions are provided in Supplementary Fig. S1. Formal convergence stability conditions and local invasion fitness derivatives are derived in Supplementary Section S7.

Curvature sign-flip reveals a fitness minimum at realistic fidelity dilution

To determine evolutionary stability, we examined the curvature of the payoff landscape at n^*. The second derivative combines opposing curvature contributions: encounter efficiency is concave $\frac{d^2EC}{dn^2} < 0$, whereas molecular fidelity declines convexly $\frac{d^2MF}{dn^2} > 0$.

As fidelity dilution pressure θ increases, the convex fidelity term steepens and eventually dominates the concave encounter term, producing a curvature sign-flip at n^*. At low θ, curvature is negative and the equilibrium is stabilizing. Above a threshold θ, curvature becomes positive and n^* is a fitness minimum (Fig. 4).

This transition occurs within biologically plausible ranges inferred from mammalian mutation-rate scalability (Makova & Li 2002; Ellegren 2007; Kong et al. 2012; Lynch 2010), indicating that disruptive selection is not a mathematical artifact but a realistic consequence of non-scalable fidelity budgets. The curvature analysis and identification of the critical fidelity dilution threshold θc are shown explicitly in Supplementary Section S8 and Fig. S2.

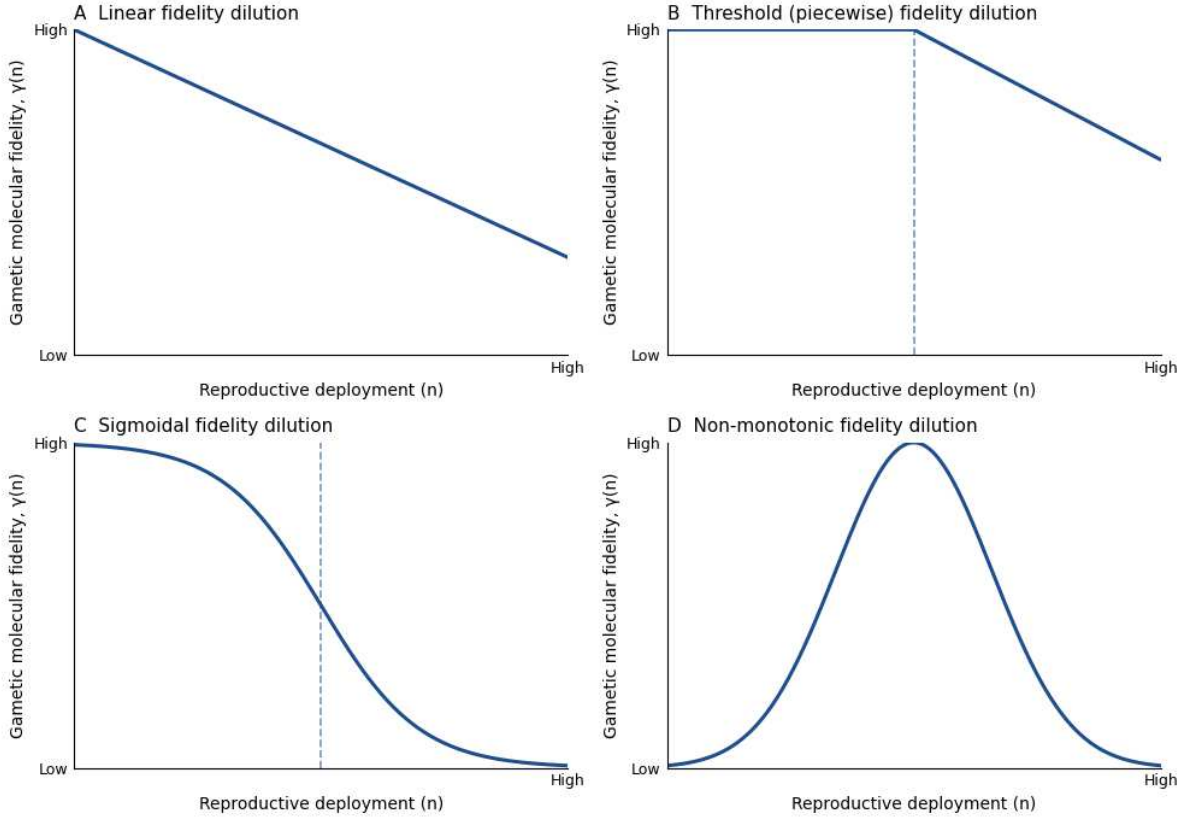


Figure 4 | Robustness of the MF–EC outcome across alternative fidelity–deployment relationships

Alternative functional forms describing how gametic molecular fidelity $\gamma(n)$ depends on reproductive deployment n.
(A) Linear fidelity dilution, in which per-gamete fidelity declines proportionally with increasing deployment.

(B) Threshold (piecewise) fidelity dilution, where fidelity is maintained up to a critical deployment level and then declines beyond a threshold.
(C) Sigmoidal fidelity dilution, representing gradual saturation of molecular maintenance capacity followed by accelerated fidelity loss.
(D) Non-monotonic fidelity dilution, capturing scenarios in which fidelity initially increases with deployment before declining due to overextension of molecular resources.

Across all functional forms, the qualitative MF–EC outcome—existence of a singular strategy and potential for disruptive selection when fidelity loss is sufficiently convex—is preserved, demonstrating that evolutionary branching does not depend on fine-tuned assumptions about the exact shape of fidelity regression.

Empirical consistency of the MF–EC model with germline mutation scaling

A key prediction of the MF–EC framework is that increased reproductive deployment should be associated with elevated mutation burden due to fidelity dilution, even in the absence of energetic trade-offs. Human trio sequencing studies provide an independent empirical pattern consistent with this prediction.

Offspring mutation burden increases monotonically with paternal age, a validated proxy for cumulative germline replication and reproductive deployment intensity (Kong et al. 2012; Jónsson et al. 2017). This increase is accompanied by substantial variance among offspring, indicating that fidelity allocation does not scale uniformly across reproductive events (Makova & Li 2002; Ellegren 2007; Lynch 2010).

When evaluated across biologically reasonable values of θ, the MF–EC model predicts a positive relationship between reproductive program intensity n and mutation burden, matching the direction and variance structure of the paternal-age effect. Although trio datasets do not directly measure heritable reproductive programs, this alignment demonstrates that the MF–EC trade-off can generate empirically observed mutation-scaling behaviour without invoking gamete-size or metabolic constraints. The data are therefore independently consistent with the model's core biological assumption. Additional discussion of empirical mutation scaling and its relationship to fidelity dilution is provided in Supplementary Section S11.

Disruptive branching and emergence of two strategy classes

Once curvature at the singular strategy n^* becomes positive, mutants arising on either side of the equilibrium can successfully invade the resident population. One class of mutants gains a selective advantage by reducing reproductive deployment and preserving per-gamete molecular fidelity, whereas the other gains by increasing deployment and enhancing encounter–competition success.

This regime satisfies the conditions for disruptive evolutionary branching (Wright 1932; Eshel 1983; Geritz et al. 1998; Rueffler et al. 2006; Ito & Dieckmann 2014), leading to divergence into two distinct reproductive strategies: a low-copy, high-fidelity strategy and a high-copy,

encounter-optimized strategy (Fig. 5). Formal branching conditions and invasion criteria are derived in Supplementary Section S8.

Mutual invasion resistance and minimality of the two-cluster outcome

Following divergence, mutual invasion analysis shows that neither extreme strategy can invade the other when rare. Both therefore satisfy the criteria for an evolutionarily stable strategy under frequency-dependent selection (Maynard Smith 1982; Eshel 1983; Hofbauer & Sigmund 1998; Kisdi 2006).

In contrast, any intermediate "generalist" strategy simultaneously incurs fidelity dilution and encounter saturation, yielding a lower payoff than either extreme. Such intermediates fail invasion tests against both resident strategies and are selectively eliminated. This establishes that the adaptive landscape on a one-dimensional fidelity–copy-number axis supports exactly two coexisting ESS clusters and no additional stable strategies. Pairwise invasibility plots confirming mutual invasion resistance and the exclusion of intermediates are shown in Supplementary Fig. S3. Extended invasion analyses and proof of minimality of the two-strategy outcome are provided in Supplementary Section S9.

Frequency separation under replicator dynamics

After branching, strategy frequencies evolve according to the canonical replicator equation,

$$\frac{dx_i}{dt} = x_{i(P_i - \bar{P})}, \bar{P} = \sum_i x_i P_i,$$

which amplifies payoff differences over time (Maynard Smith 1982; Hofbauer & Sigmund 1998). Numerical replicator dynamics supporting long-term frequency stability are shown in Fig. S4 and described in Supplementary Section S10. High-payoff clusters increase in frequency, while intermediate strategies decline, ensuring long-term maintenance of dimorphism (Fig. 5).

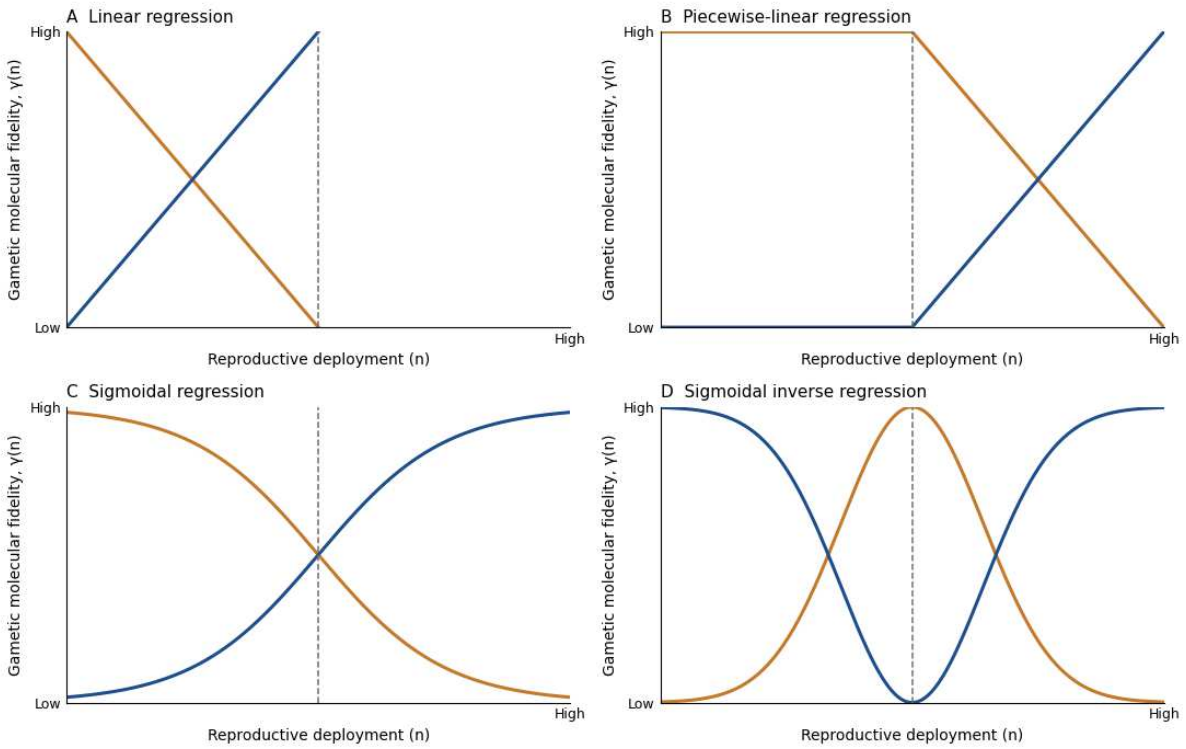


Figure 5 | Evolutionary trajectories under alternative encounter–fidelity regression structures

Illustration of how different functional relationships between reproductive deployment n and gametic molecular fidelity $\gamma(n)$ shape evolutionary trajectories in the MF–EC framework. Blue and orange curves represent opposing selective tendencies associated with encounter efficiency and fidelity maintenance, respectively. Dashed vertical lines indicate the location of the singular strategy predicted by selection gradient analysis.

(A) Linear regression, where fidelity declines linearly with increasing reproductive deployment, generating symmetric opposing selection pressures around the singular point.
(B) Piecewise-linear regression, in which fidelity is maintained up to a threshold deployment and declines thereafter, altering the local shape of selection near the singular strategy.
(C) Sigmoidal regression, representing gradual saturation of molecular maintenance capacity followed by accelerated fidelity loss, producing strong curvature near the equilibrium.
(D) Sigmoidal inverse regression, capturing non-monotonic fidelity responses in which fidelity initially increases and then decreases with deployment.

Distinction from multi-mating-type systems

The prediction of exactly two stable strategies does not contradict the existence of clades with multiple mating types, such as ciliates and fungi. In those systems, diversification occurs along multidimensional compatibility axes, where novel mating types gain immediate fusion advantages (Nanney 1953; Kües 2000; Billiard et al. 2011).

By contrast, the MF–EC Game evolves on a single axis defined by parental fidelity partitioning versus copy-dependent encounter competitiveness. Dimensionality, not taxonomic scope,

determines the number of stable peaks. On this one-dimensional conflict axis, only two mutually protected strategies can persist.

Together, these results show that when reproduction is constrained by a non-scalable molecular fidelity budget opposing concave encounter gains, isogamy is evolutionarily unstable. Adaptive Dynamics predicts convergence toward a unique singular strategy, but curvature analysis reveals this point to be a fitness minimum under realistic fidelity dilution pressures. The population therefore undergoes disruptive branching into exactly two mutually invasion-resistant strategies, while all intermediates are eliminated. This yields a stable dimorphic gamete ESS, driven by informational constraints rather than energetic trade-offs. A broader discussion of dimensionality constraints on diversification is provided in Supplementary Section S12.

Discussion

The evolution of sexual dimorphism has long been regarded as a paradigmatic example of how disruptive selection can arise from trade-offs inherent to reproduction. Classical theory has convincingly shown that energetic constraints, combined with fertilization ecology, are sufficient to destabilize isogamy and favour divergence into gametes specialized for either quantity or quality (Bateman 1948; Parker, Baker & Smith 1972; Maynard Smith 1982; Bulmer & Parker 2002; Lehtonen & Kokko 2011). However, these models implicitly treat the genome as a passive entity whose fidelity is either costless or subsumed into energetic budgets. Our results challenge this assumption by demonstrating that informational constraints alone specifically, non-scalable molecular fidelity budget can destabilize symmetric reproductive strategies and enforce stable dimorphism. A central contribution of the MF–EC framework is the explicit recognition that reproduction is not only a metabolic process but also an informational one. Genome replication, chromatin packaging, DNA repair, and epigenetic maintenance require complex, coordinated molecular machinery whose production and deployment are constrained by expression limits, assembly bottlenecks, and regulatory complexity (Eigen 1971; Eigen & Schuster 1979; Drake et al. 1998; Lynch 2010). Unlike many metabolic resources, these components cannot be arbitrarily upregulated without incurring substantial pleiotropic costs. As a result, increased reproductive deployment necessarily entails dilution of per-gamete fidelity, even under conditions of energetic abundance. By formalizing this constraint, the MF–EC model reveals a previously underappreciated evolutionary regime. Selection initially drives populations toward an intermediate reproductive allocation that balances encounter competitiveness against fidelity loss. Importantly, this equilibrium is not assumed, but arises analytically as a unique singular strategy of the payoff landscape, which can be expressed in closed form using the Lambert W function (see Fig. 3). This result establishes that the position of the evolutionary equilibrium is an emergent consequence of the fidelity–encounter antagonism, rather than a tuneable parameter.

However, once fidelity dilution pressure exceeds a biologically realistic threshold, curvature analysis shows that this singular strategy becomes a fitness minimum rather than a maximum. The population is therefore convergence-stable but invasion-unstable, satisfying the hallmark condition for evolutionary branching in Adaptive Dynamics (Wright 1932; Eshel 1983;

Dieckmann & Law 1996; Geritz et al. 1998; Rueffler et al. 2006). This curvature sign-flip is critical (Fig. 4): it explains how isogamy can appear locally stable while being fundamentally unstable over longer evolutionary timescales. Notably, this instability arises purely from informational scalability limits, without invoking energetic asymmetry or zygote provisioning differences. The MF-EC mechanism differs in important ways from classical anisogamy models. Size–number trade-off models rely on energetic investment per gamete and zygote provisioning to generate disruptive selection (Parker et al. 1972; Charlesworth 1978; Lehtonen & Parker 2014). In contrast, the MF-EC framework operates through concave encounter gains opposed by convex fidelity losses, a structure that is fundamentally informational rather than energetic. These two mechanisms are not mutually exclusive. Instead, they are likely to act synergistically in natural systems: energetic trade-offs may shape gamete size and provisioning, while fidelity dilution constrains viable reproductive deployment. Together, these forces reinforce the emergence and long-term stability of sex-specific reproductive roles.

One of the most robust predictions of the MF-EC framework is the emergence of exactly two stable reproductive strategies on a one-dimensional fidelity–deployment axis. This minimality is not imposed but follows directly from invasion analysis: intermediate strategies incur both encounter saturation and fidelity dilution simultaneously, rendering them invasion-unstable against both extremes. Mutual invasion resistance confirms that the two divergent strategies form a protected dimorphic ESS, while all intermediates are eliminated. This provides a principled theoretical explanation for a long-standing empirical observation—despite immense diversity in life histories and reproductive ecologies, eukaryotic sexual systems overwhelmingly resolve into a binary structure rather than a continuum. This perspective also clarifies why systems with multiple mating types do not contradict the generality of sexual dimorphism. In fungi, ciliates, and some algae, diversification occurs along multidimensional compatibility axes, where novel mating types gain immediate fusion advantages without incurring fidelity costs (Nanney 1953; Kües 2000; Billiard et al. 2011; Hadjivasiliou et al. 2016). By contrast, the MF–EC conflict operates along a single axis defined by parental fidelity allocation versus copy-dependent encounter success. Dimensionality, rather than taxonomic group or reproductive mode, therefore determines whether multiple stable strategies can coexist.

Although our study is theoretical, it is anchored in well-established empirical patterns. Large-scale parent–offspring trio sequencing studies show that offspring mutation burden increases monotonically with paternal age and exhibits substantial inter-individual variance (Makova & Li 2002; Ellegren 2007; Kong et al. 2012; Jónsson et al. 2017). These patterns are consistent with the prediction that increased reproductive deployment incurs fidelity costs due to finite germline maintenance capacity. We emphasize that such data do not directly test the MF–EC model, as heritable reproductive programs are not directly observable. Rather, they validate the biological realism of fidelity dilution as a constraint, supporting its inclusion as an explicit evolutionary currency. The MF–EC framework generates several testable predictions that could guide future empirical work. Lineages with greater genomic complexity such as larger genomes, higher transposable-element loads, or reduced repair efficiency should experience stronger fidelity dilution pressure and earlier divergence in reproductive strategies (Lynch & Conery 2003; Lynch 2010). Experimental evolution systems in which replication fidelity can

be manipulated independently of energetic input should show predictable shifts in branching behavior. Comparative analyses across taxa with distinct germline architectures may further reveal systematic associations between fidelity dilution sensitivity and the degree of reproductive dimorphism.

Several limitations of our approach warrant consideration. We model reproduction along a single continuous axis and assume smooth fitness landscapes, abstracting away from discrete developmental constraints, ecological feedbacks, and explicit genetic architectures. Fidelity dilution is represented phenomenologically rather than mechanistically. Nonetheless, robustness analyses demonstrate that the qualitative outcome convergence toward a singular strategy followed by disruptive branching into two protected strategies is preserved across a wide class of fidelity-dilution functions, indicating that the results do not depend on fine-tuned assumptions. Robustness analyses supporting these claims are provided in the Supplementary Information. More broadly, our results underscore the importance of considering informational scalability limits in evolutionary theory. Fidelity constraints are likely to shape not only sex evolution, but also life-history strategies, mutation-rate evolution, genome size dynamics, and the evolution of biological complexity (Kimura 1967; Crow 1970; Lynch et al. 1993; Lynch 2010). By explicitly integrating molecular fidelity into evolutionary games, the MF–EC framework provides a general lens through which the interplay between information and reproduction can be examined.

In conclusion, we show that non-scalable molecular fidelity budgets are sufficient to destabilize isogamy and enforce stable reproductive dimorphism. By deriving a unique singular strategy, demonstrating a curvature sign-flip that forces evolutionary branching, and proving the minimality of the resulting two-strategy outcome, this work provides a biologically grounded explanation for why sexual systems so consistently resolve into two distinct reproductive roles. More generally, it highlights how constraints on information processing and maintenance can shape major evolutionary transitions across the tree of life.

Statements and declarations

The Author declares that they have no conflict of interest.

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Data Availability Statement

No new empirical data were generated or analysed in this study. All empirical patterns discussed are drawn from previously published parent-offspring trio sequencing studies cited in the manuscript. Analytical derivations and numerical illustrations are fully described in the main text and Supplementary Information. Custom code used to generate figures and numerical evaluations is available from the corresponding author upon reasonable request.

Author contributions

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Raviraj V S: Software, Visualization, Writing—review & editing.

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