The multi-type bisexual Galton-Watson process

Nicolás Zalduendo, INRAE Montpellier

Work in collaboration with Coralie Fritsch (Inria Nancy) and Denis Villemonais (U. de Strasbourg)

Besançon Meeting on Probability, Ecology & Evolution - December, 2024

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We consider the extension of the previous model to dimension p.

Define the process $(Z_n)_{n\in\mathbb{N}} \subseteq \mathbb{N}^p$ given by

$$Z_{n+1,j} = \sum_{i=1}^{p} \sum_{k=1}^{Z_{n,i}} V_{i,j}^{(k,n)},$$

where for every $1 \leq i \leq p$, $(V_{i,\cdot}^{(k,n)})_{k,n\in\mathbb{N}}$ are i.i.d. random vectors.

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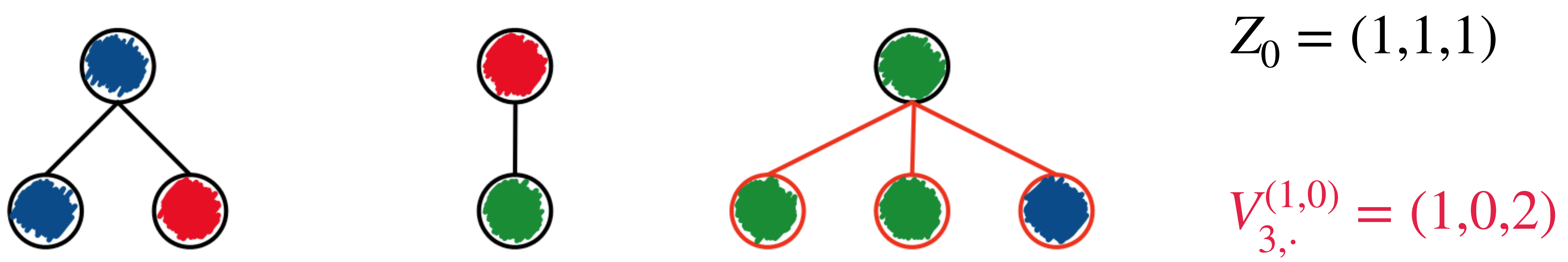

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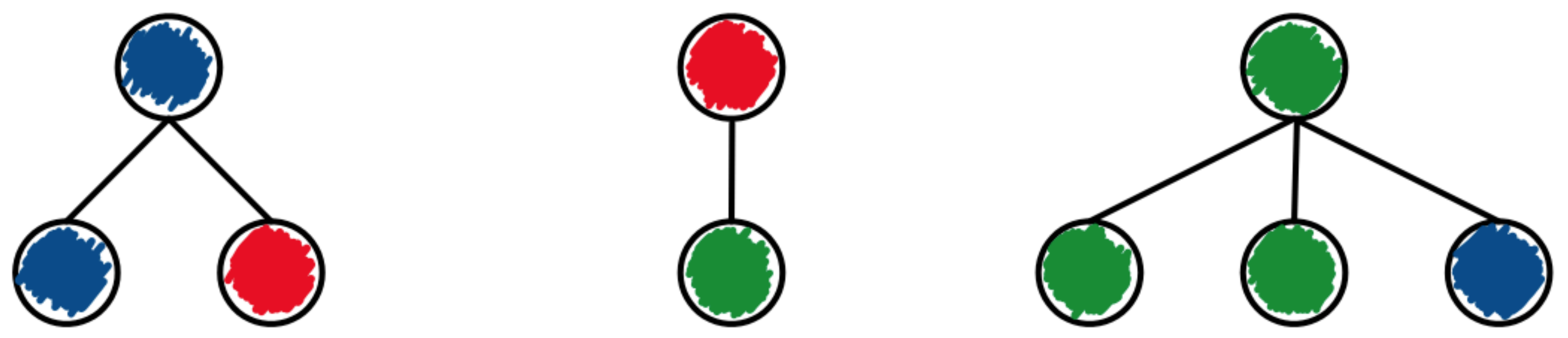

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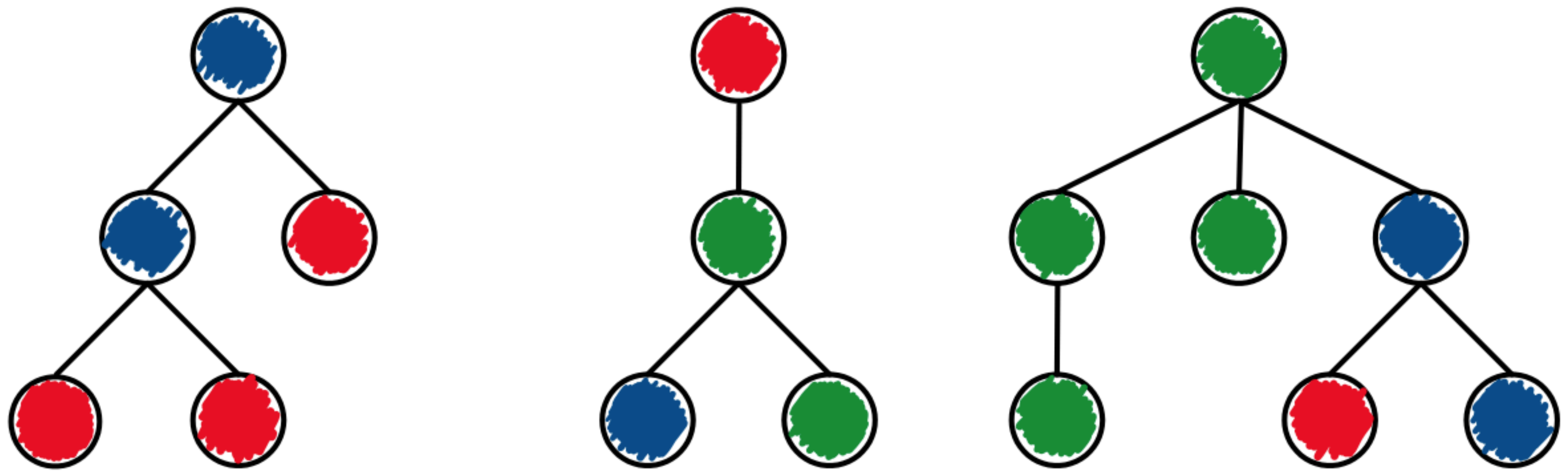

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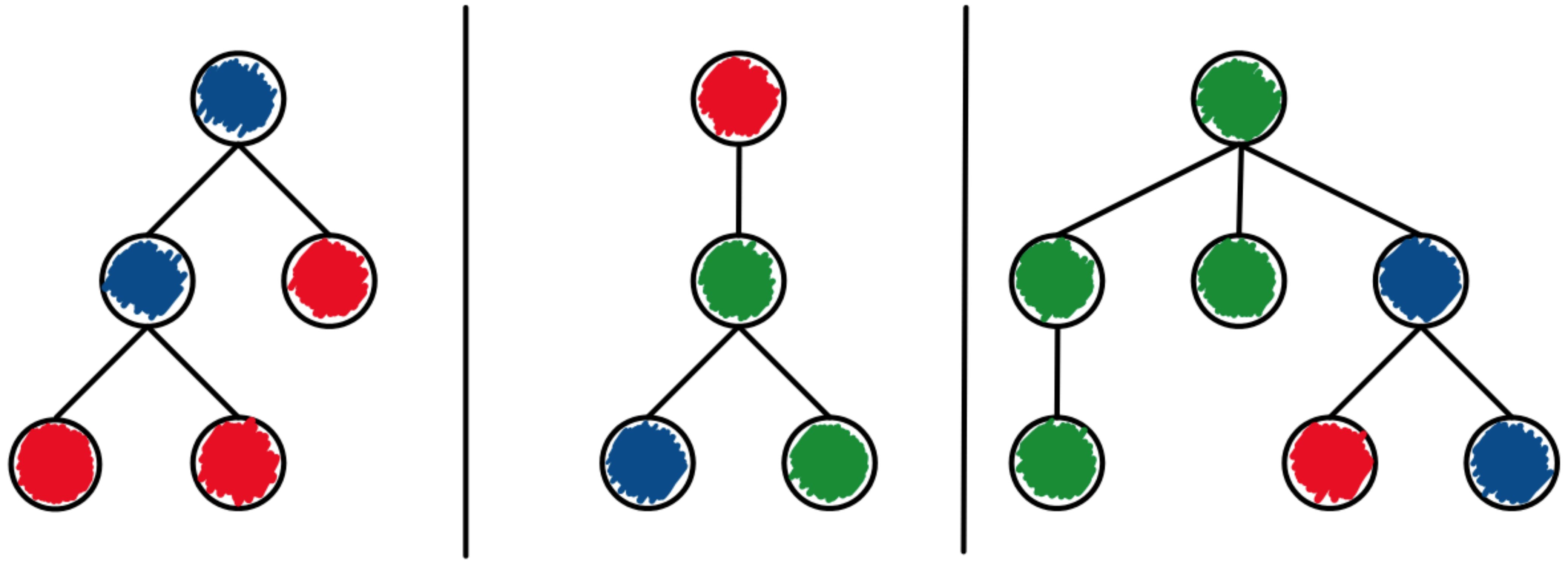

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Branching Property

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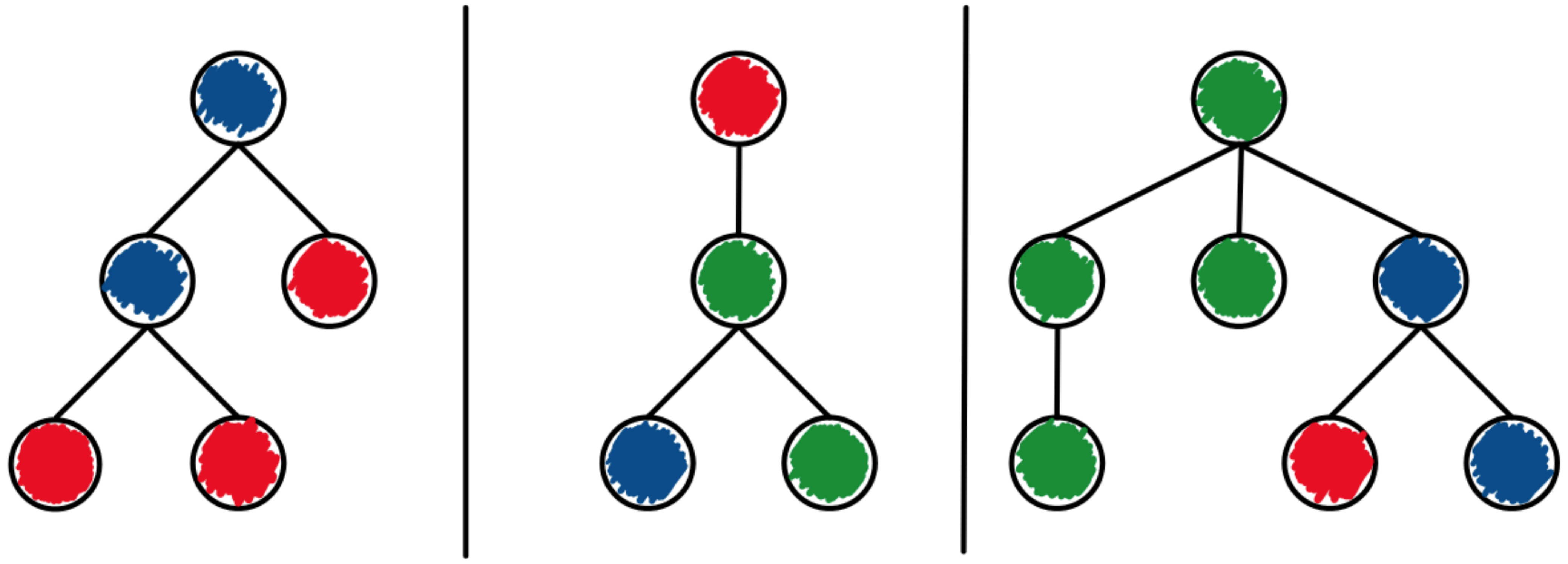
Setting the matrix $A_{i,j} := \mathbb{E}(V_{i,j}) < +\infty$, we have that

$$Z_n \xrightarrow[\text{a.s.}]{n\to+\infty} 0 \iff \lambda^* \leq 1,$$

where λ^* is the largest eigenvalue of A.



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Branching Property

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The (single-type) bisexual Galton-Watson process

Given Z_n couples,

$$F_{n+1} = \sum_{k=1}^{Z_n} X^{(k,n)} \quad \text{and } M_{n+1} = \sum_{k=1}^{Z_n} Y^{(k,n)}$$

where $((X^{(k,n)}, Y^{(k,n)}))_{k,n\in\mathbb{N}}$ are i.i.d. random vectors.

We then set

$$Z_{n+1} = \xi(F_{n+1}, M_{n+1}),$$

where ξ is the mating function

$Z_0 = 2$

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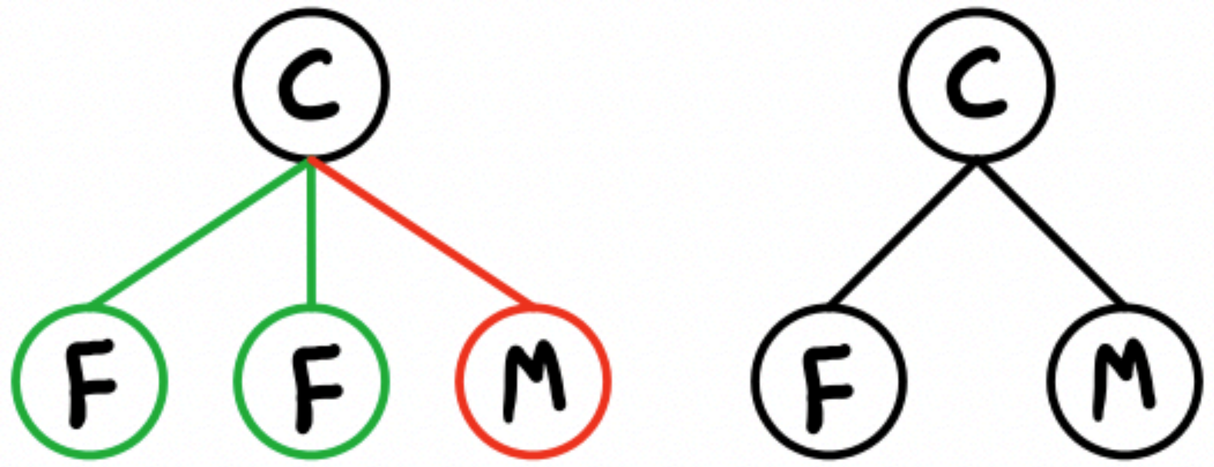

$Z_0 = 2$

$X^{(1,0)} = 2$, $Y^{(1,0)} = 1$

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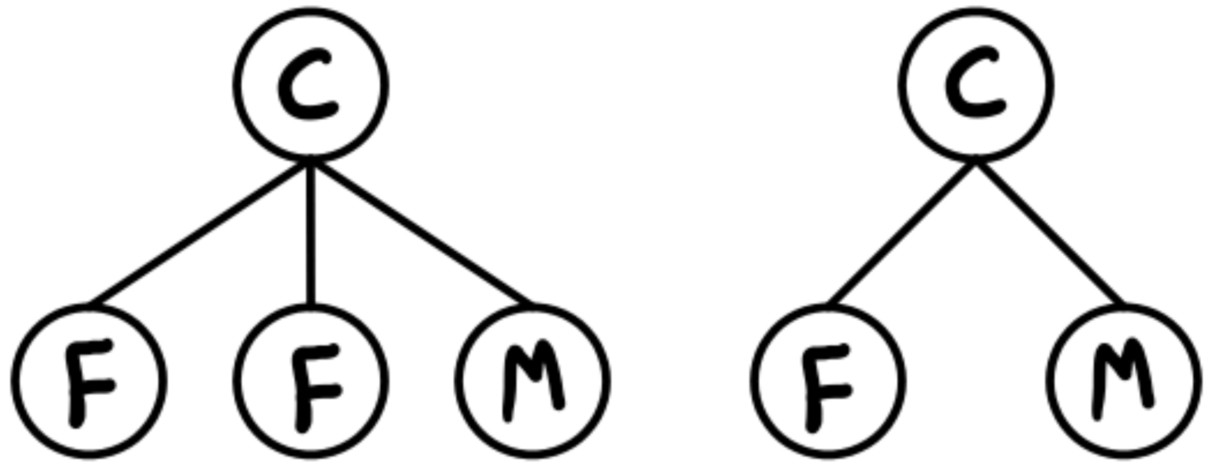

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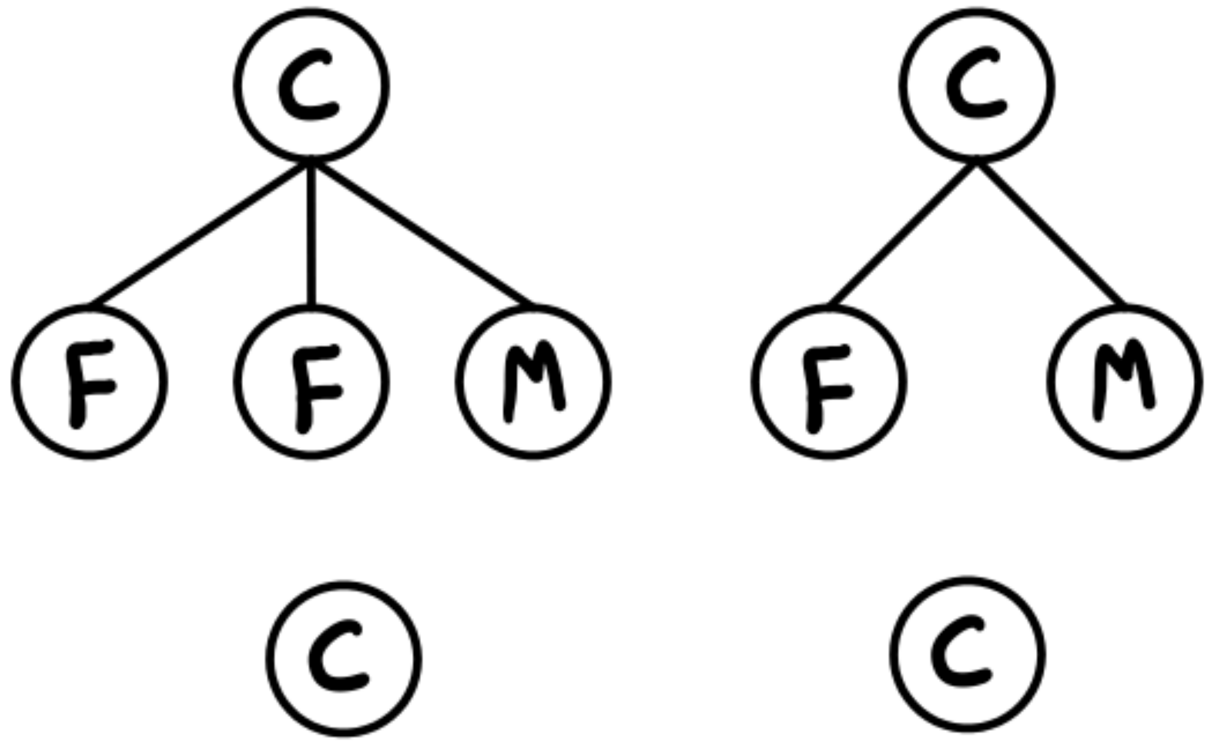

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$Z_1 = \xi(3{,}2) = 2$

Perfect fidelity mating $\xi(x, y) = \min\{x, y\}$.

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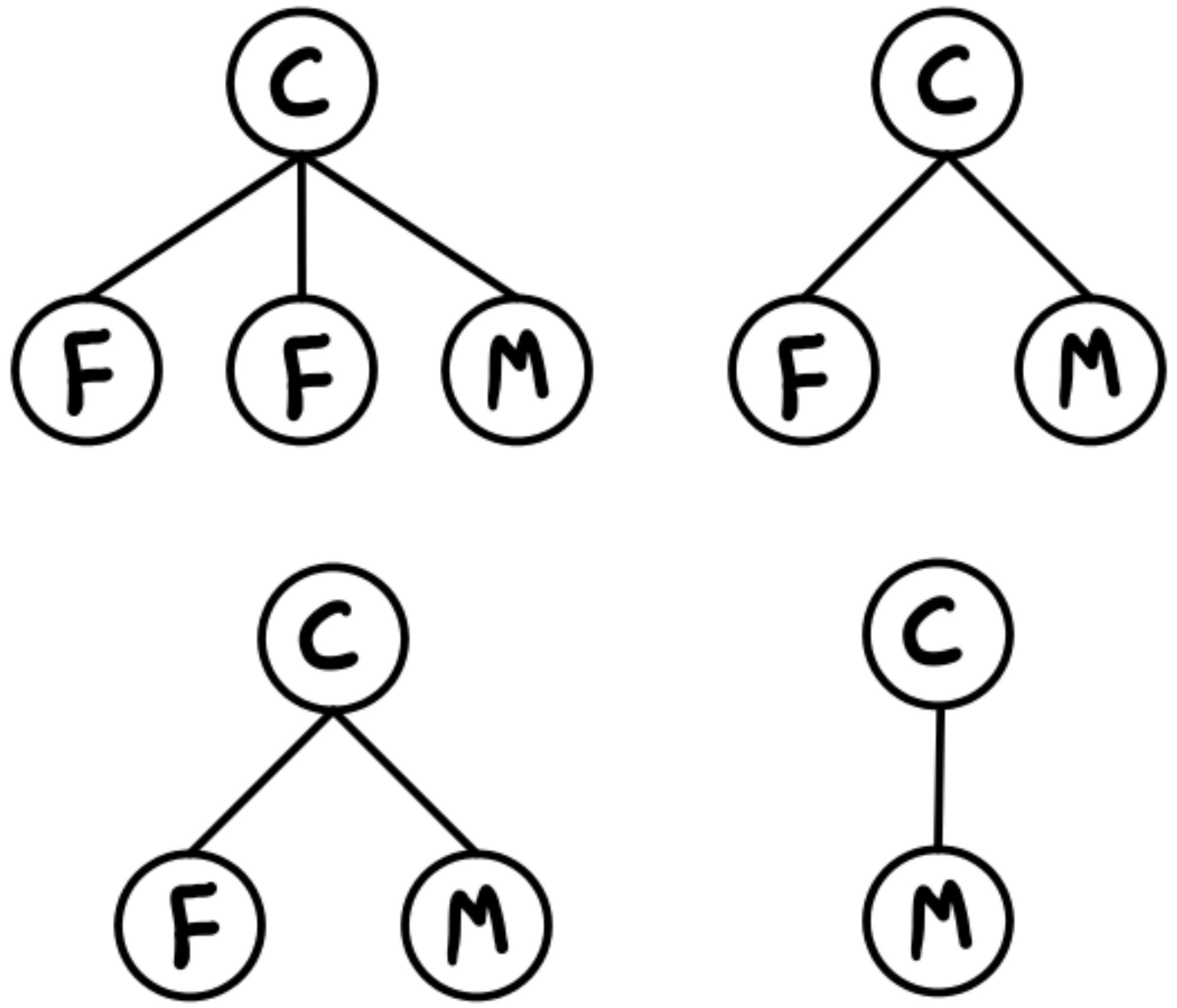

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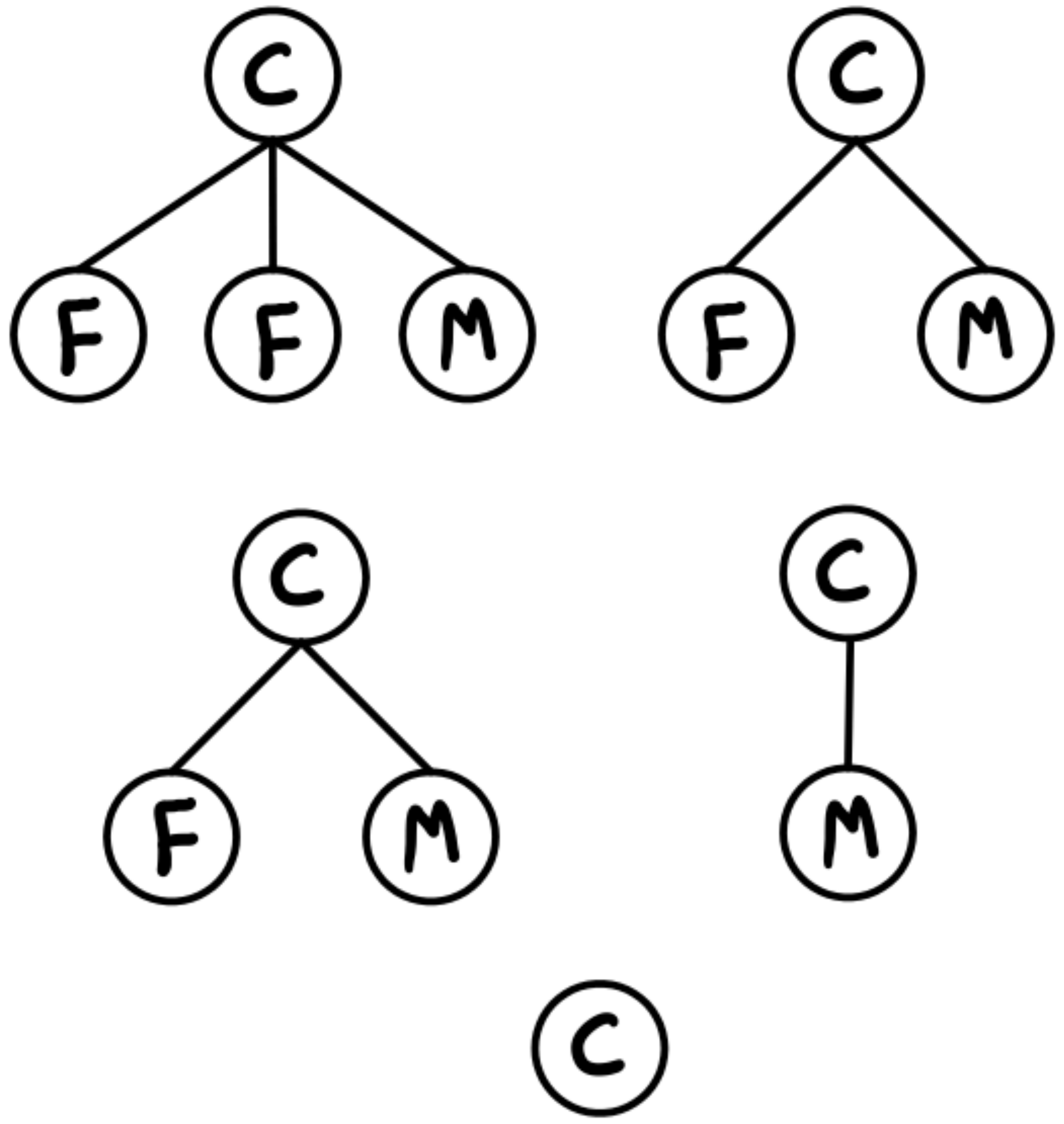

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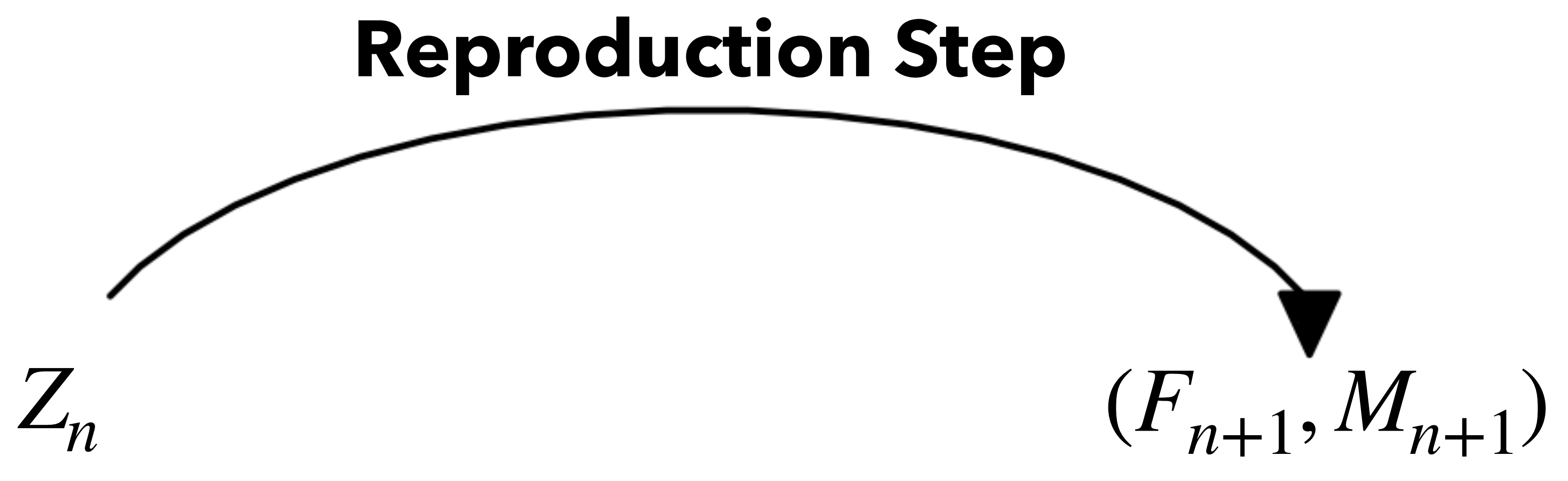

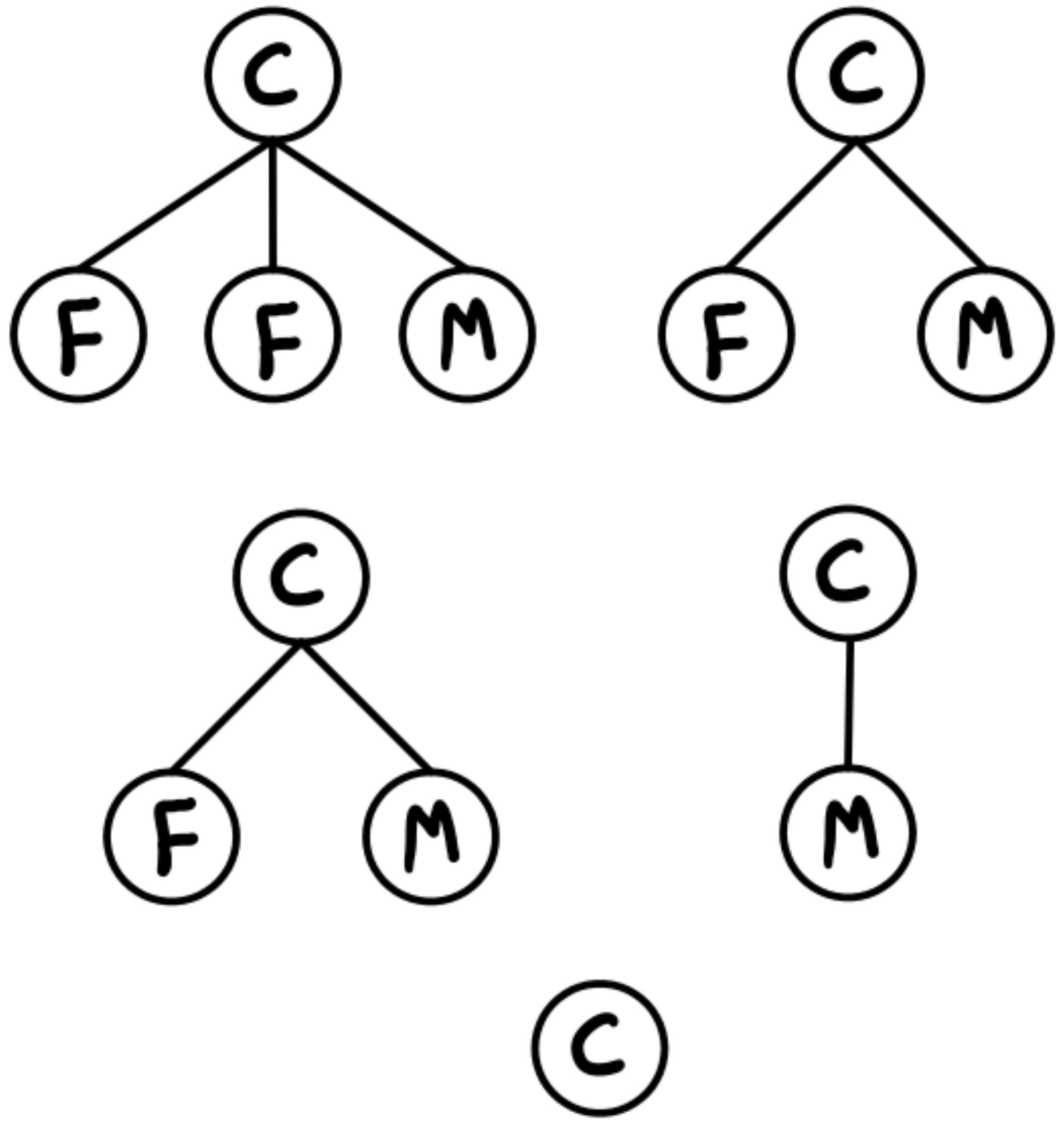

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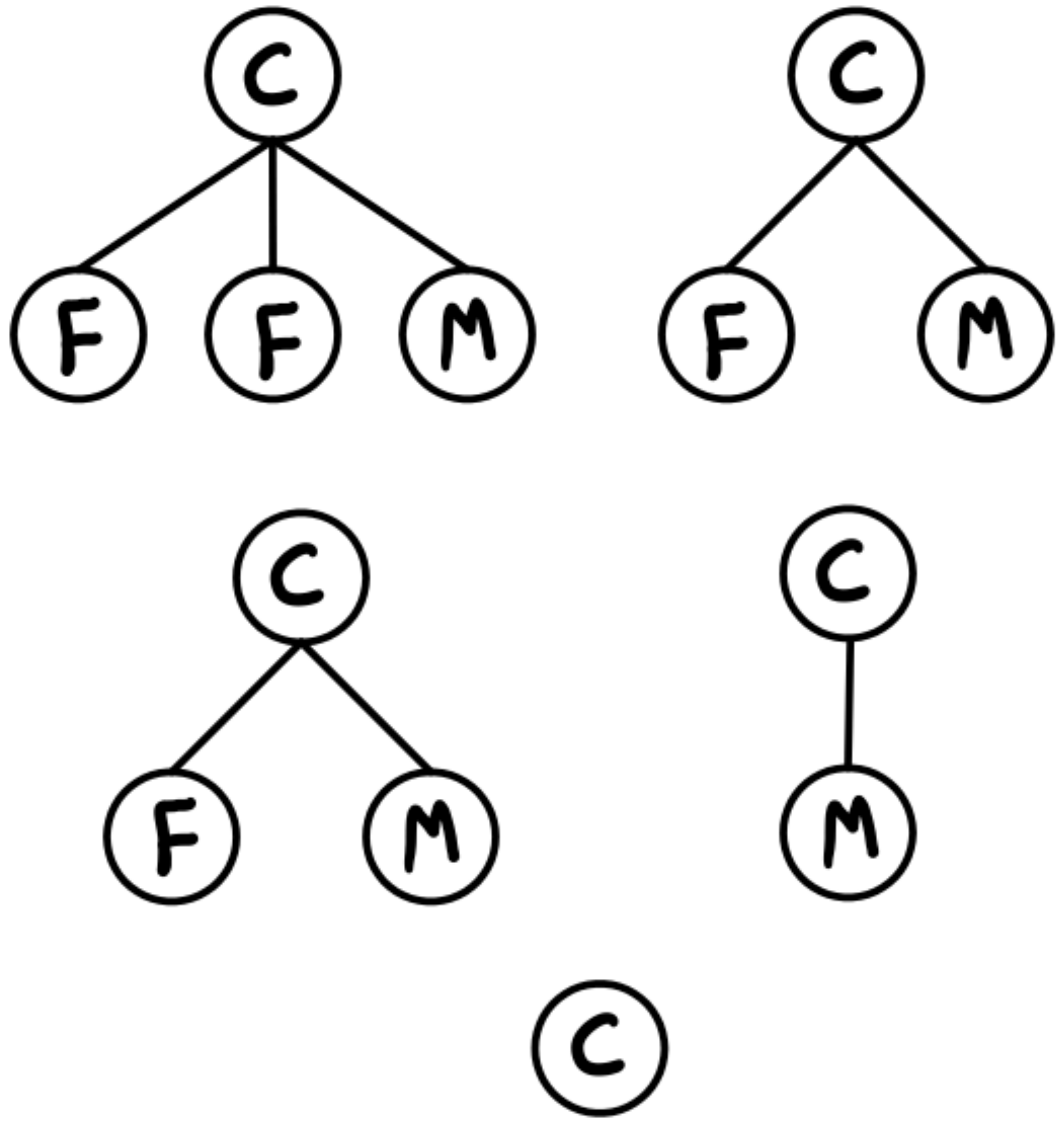

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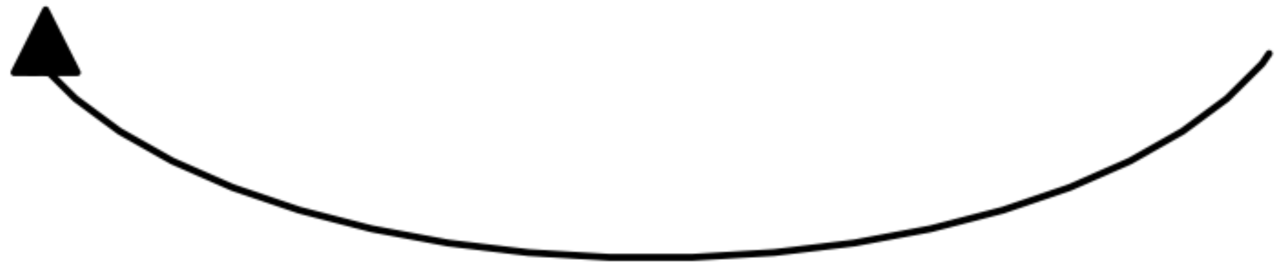
Z_{n+1} (F_{n+1}, M_{n+1})



Mating Step

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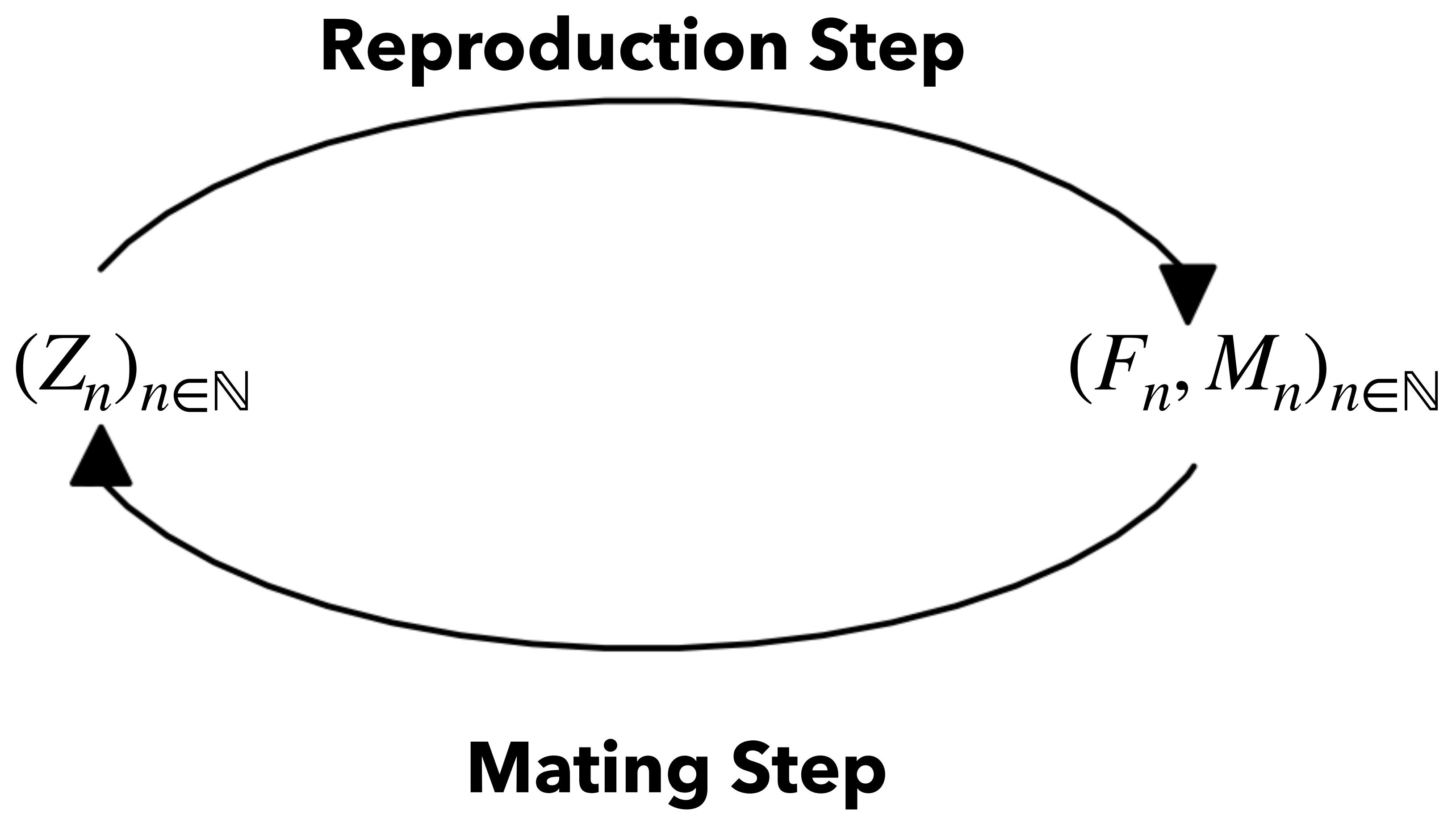

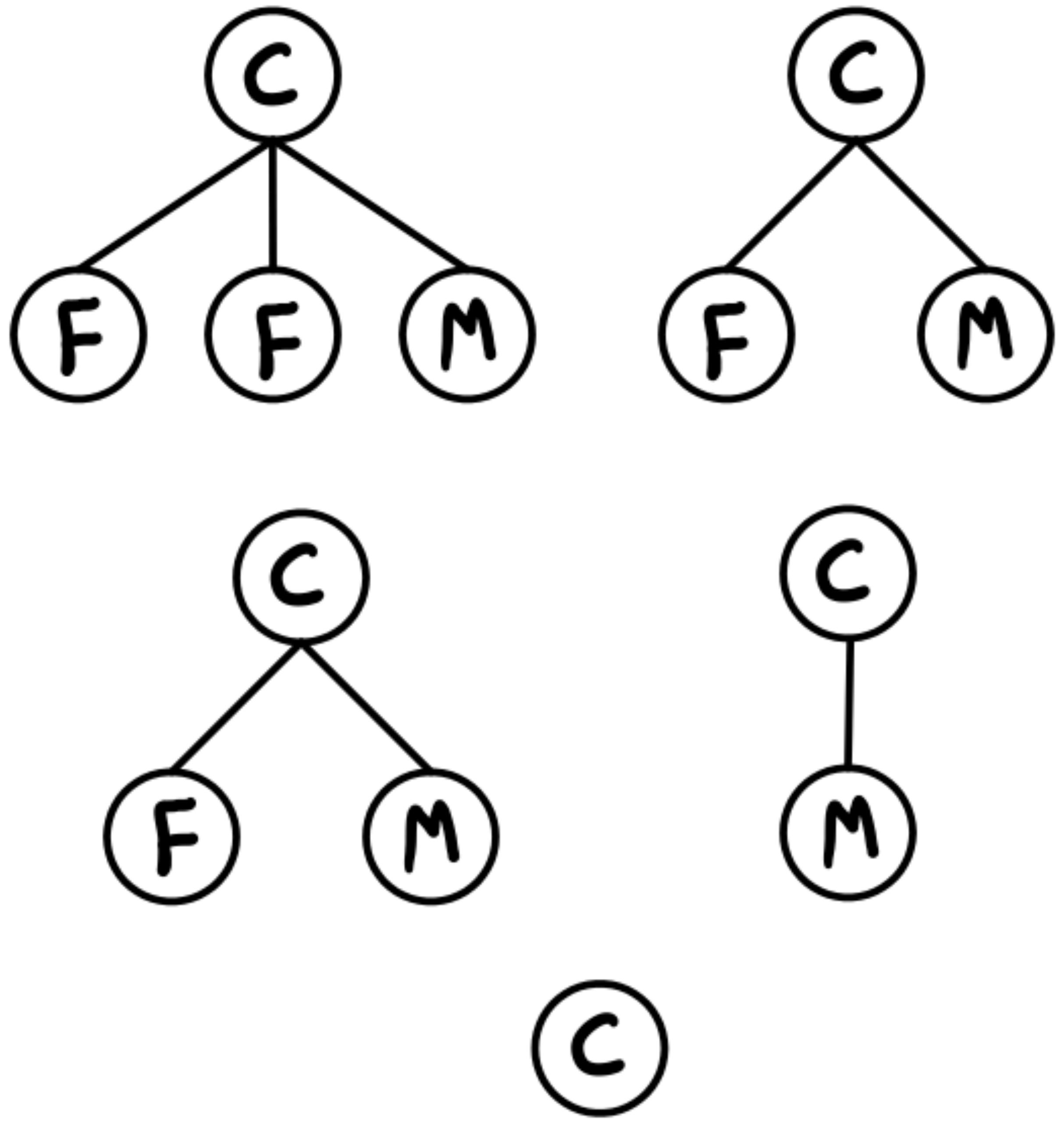

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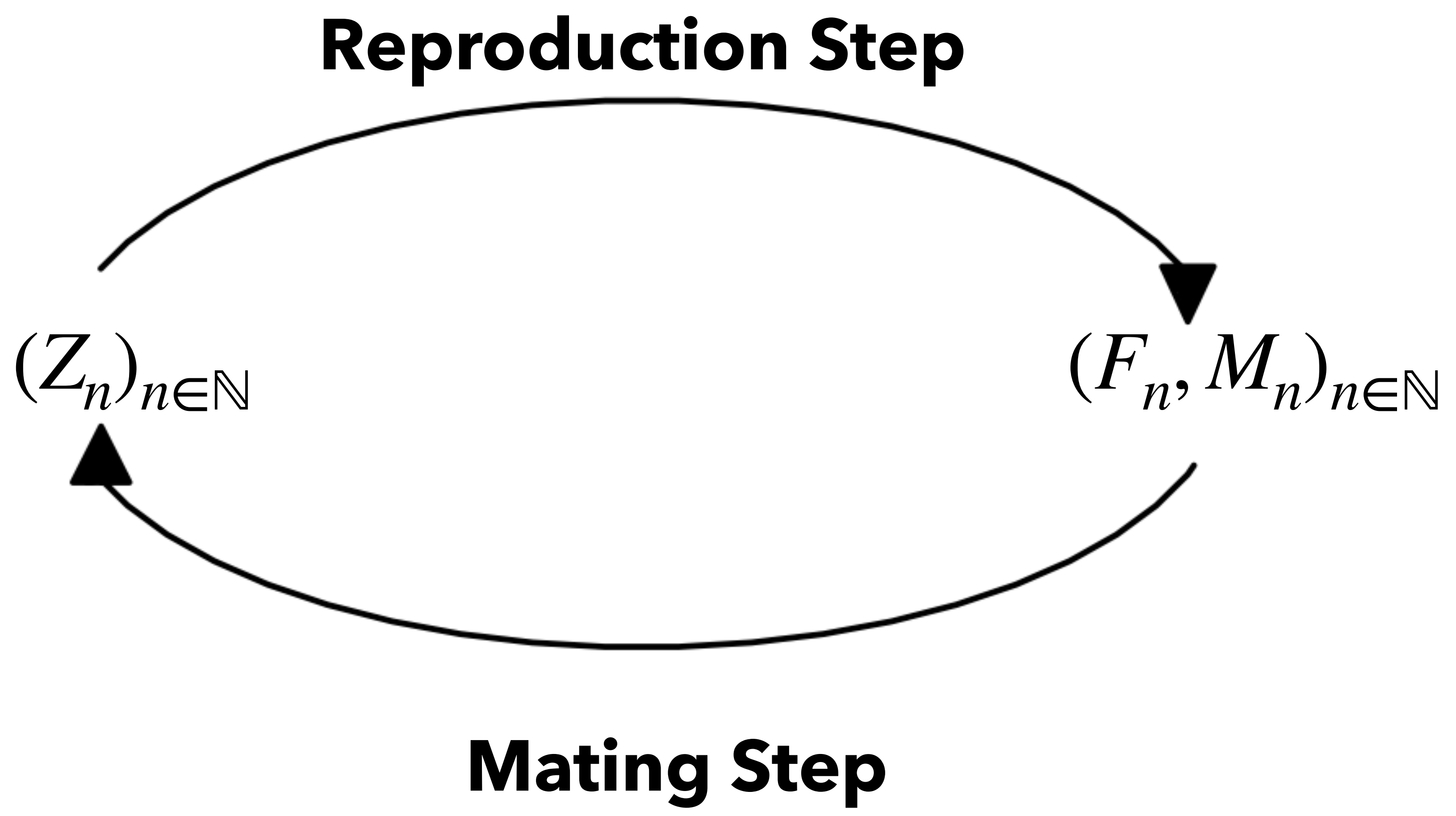

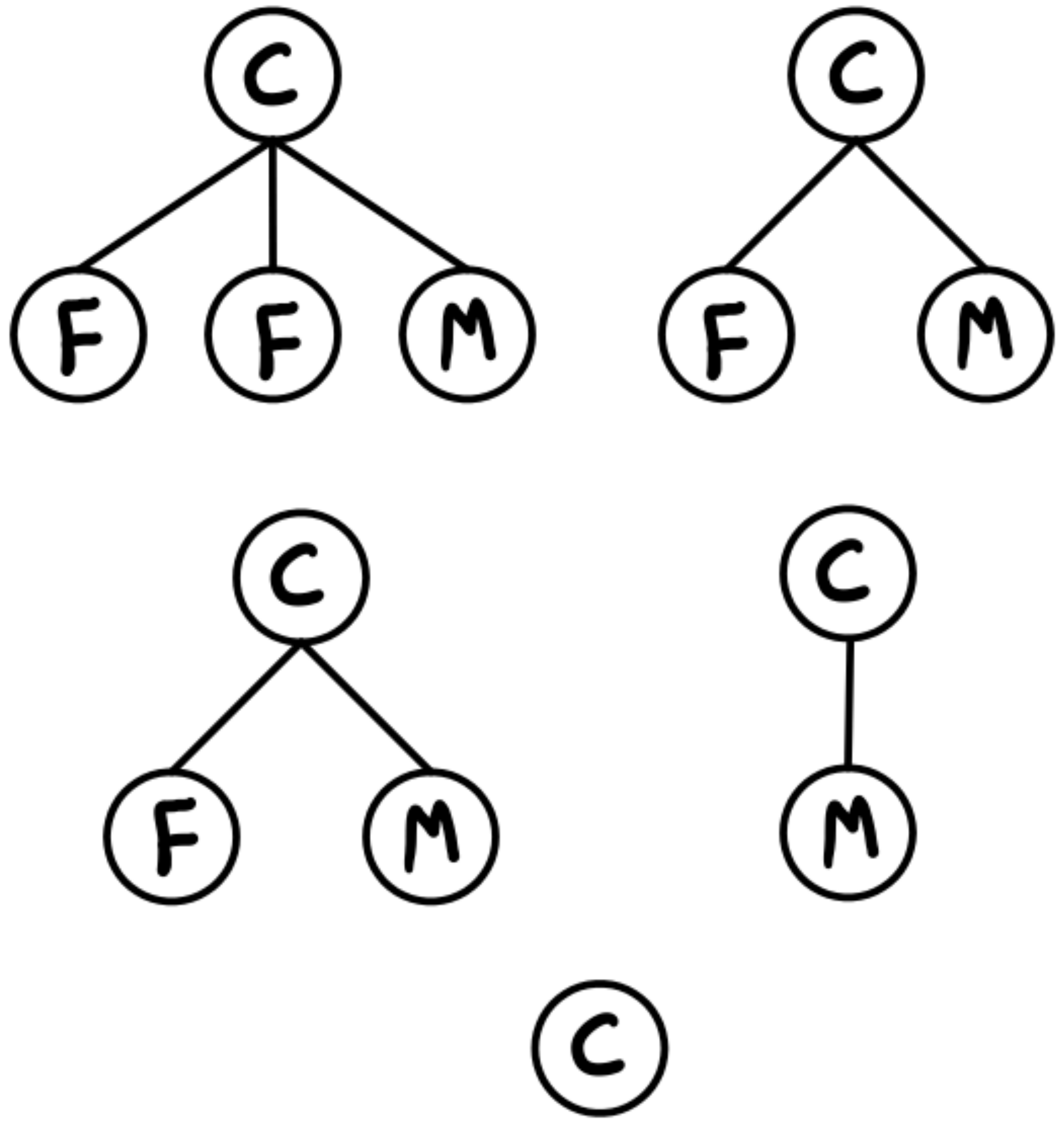

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No branching property

Some references on bisexual processes

General results on single-type process

[Daley, '68] First definition of the bisexual Galton-Watson process (bGWp)

[Daley, Hull & Taylor, '86] Extinction condition with superadditive mating function:

$$\exists r \in [0, +\infty] \text{ such that } \mathbb{P}(Z_n \to 0 \mid Z_0 = k) = 1, \forall k \in \mathbb{N} \Leftrightarrow r \leq 1.$$

What about multi-type?

[González, Hull, Martínez & Mota '06; González, Martínez & Mote '08 & '09; Alsmeyer, Gutíerrez & Martínez, '11]
A model with two types of males and one type of female in a genetic context.

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Mating step:

$$Z_{n+1} = \xi((F_{n+1,1}, \ldots, F_{n+1,q_f}), (M_{n+1,1}, \ldots, M_{n+1,q_m}))\,.$$

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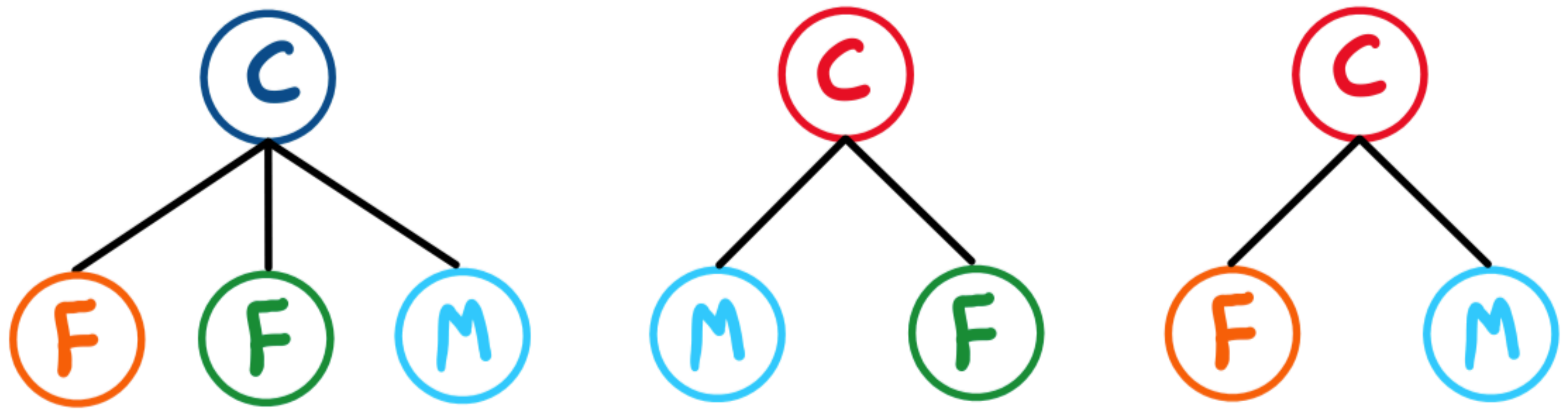

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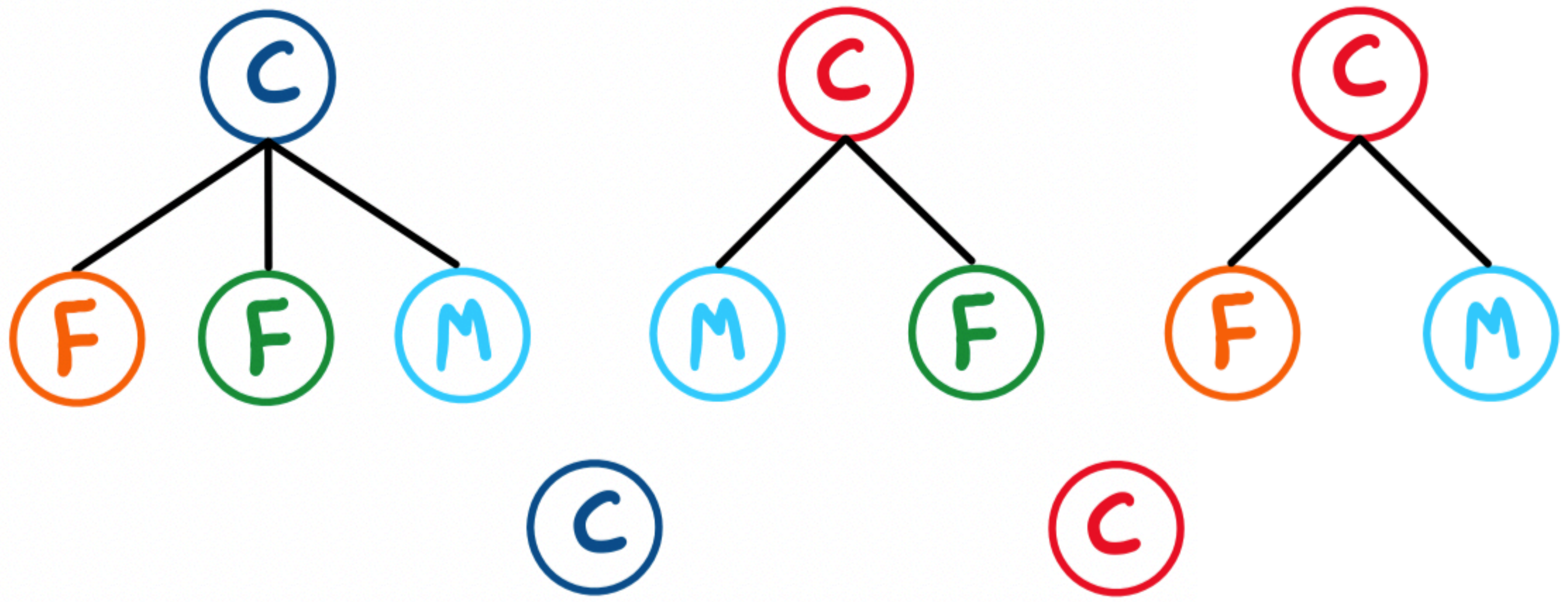

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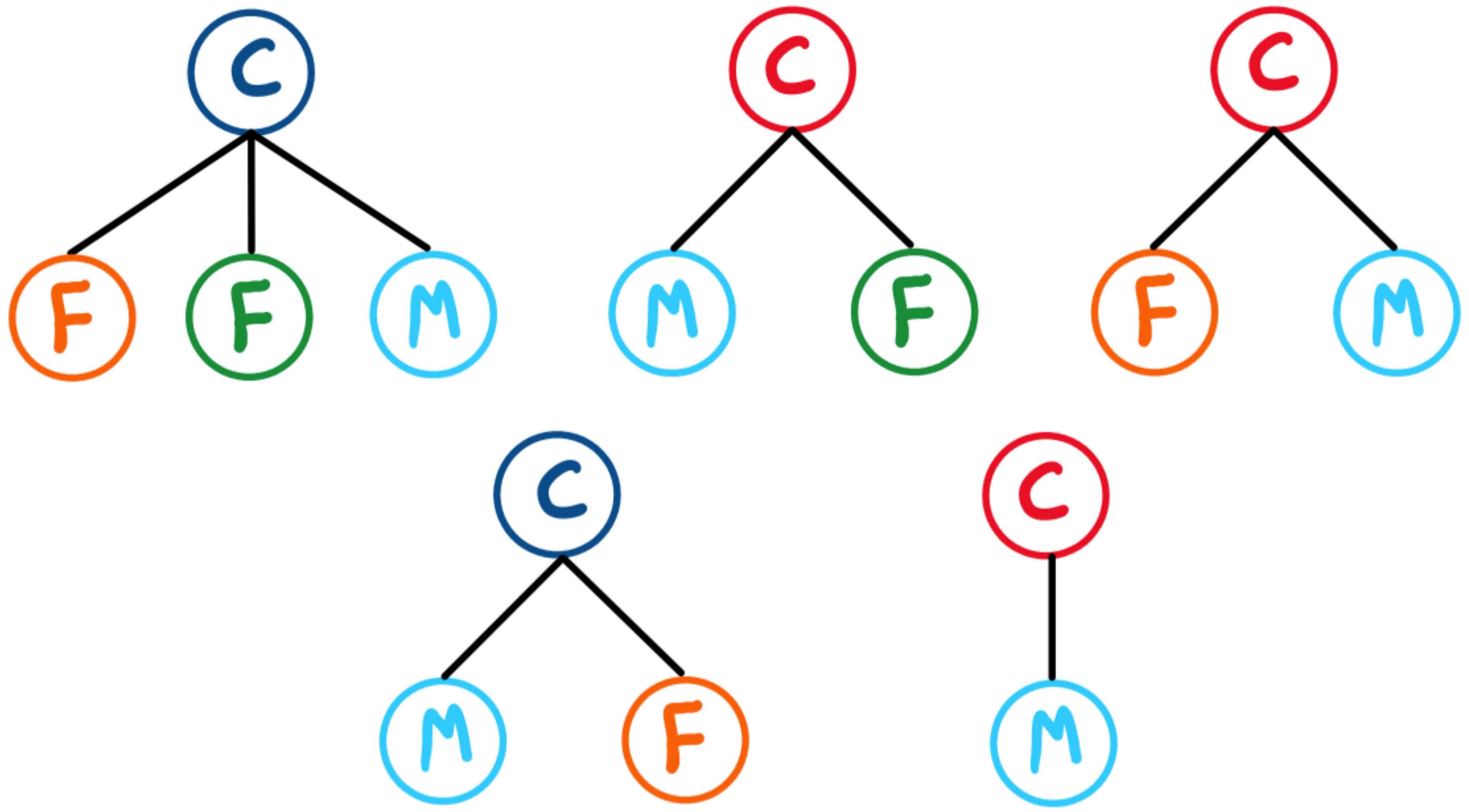

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$F_2 = (1,0),\ M_2 = 2$

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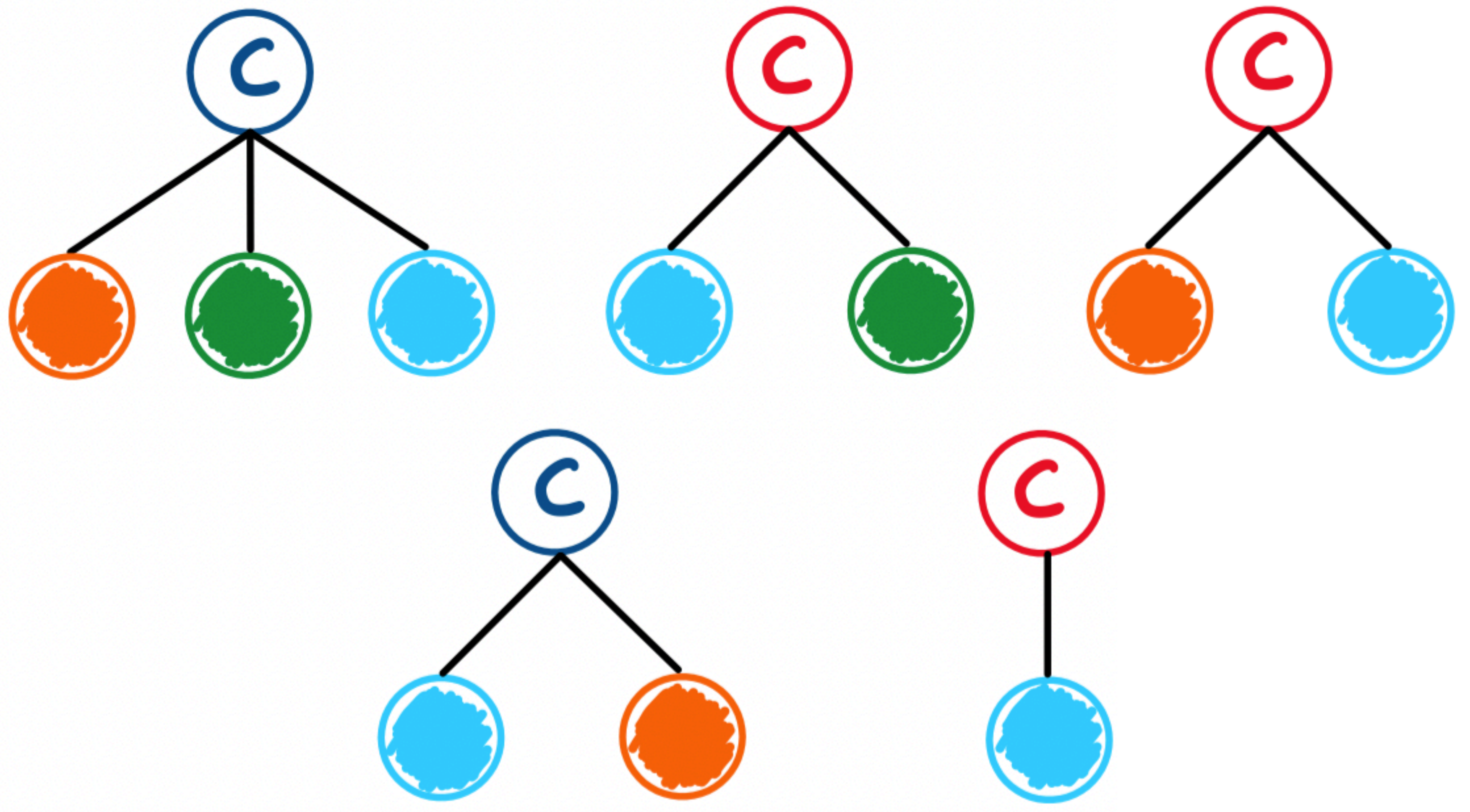
We can set $W_n = (F_n, M_n)$, and $q = q_m + q_f$.



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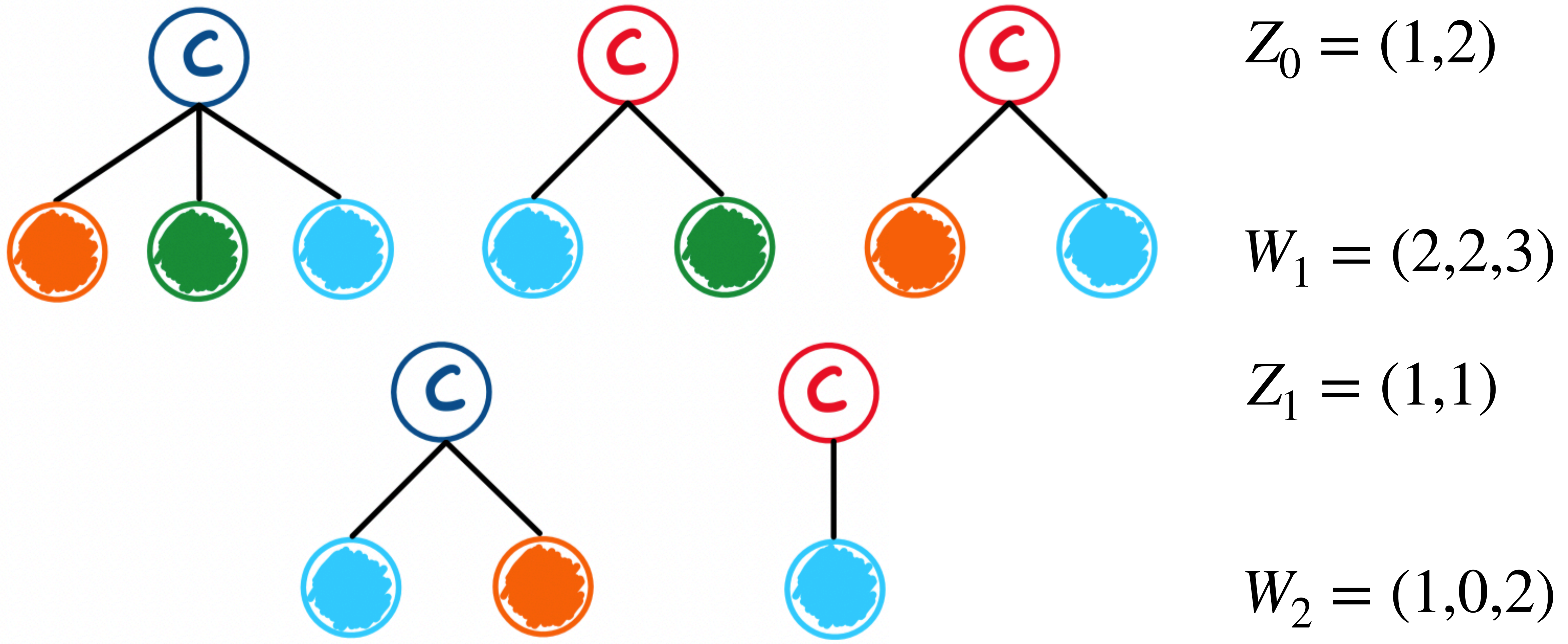

We can set $W_n = (F_n, M_n)$, and $q = q_m + q_f$.

Single-type asexual process
$p = q = 1,\ \xi(x) = x.$

Multi-type asexual process
$p = q > 1,\ \xi(x) = x.$

Single-type bisexual process
$p = 1,\ q = 2,\ \xi$ superadditive.

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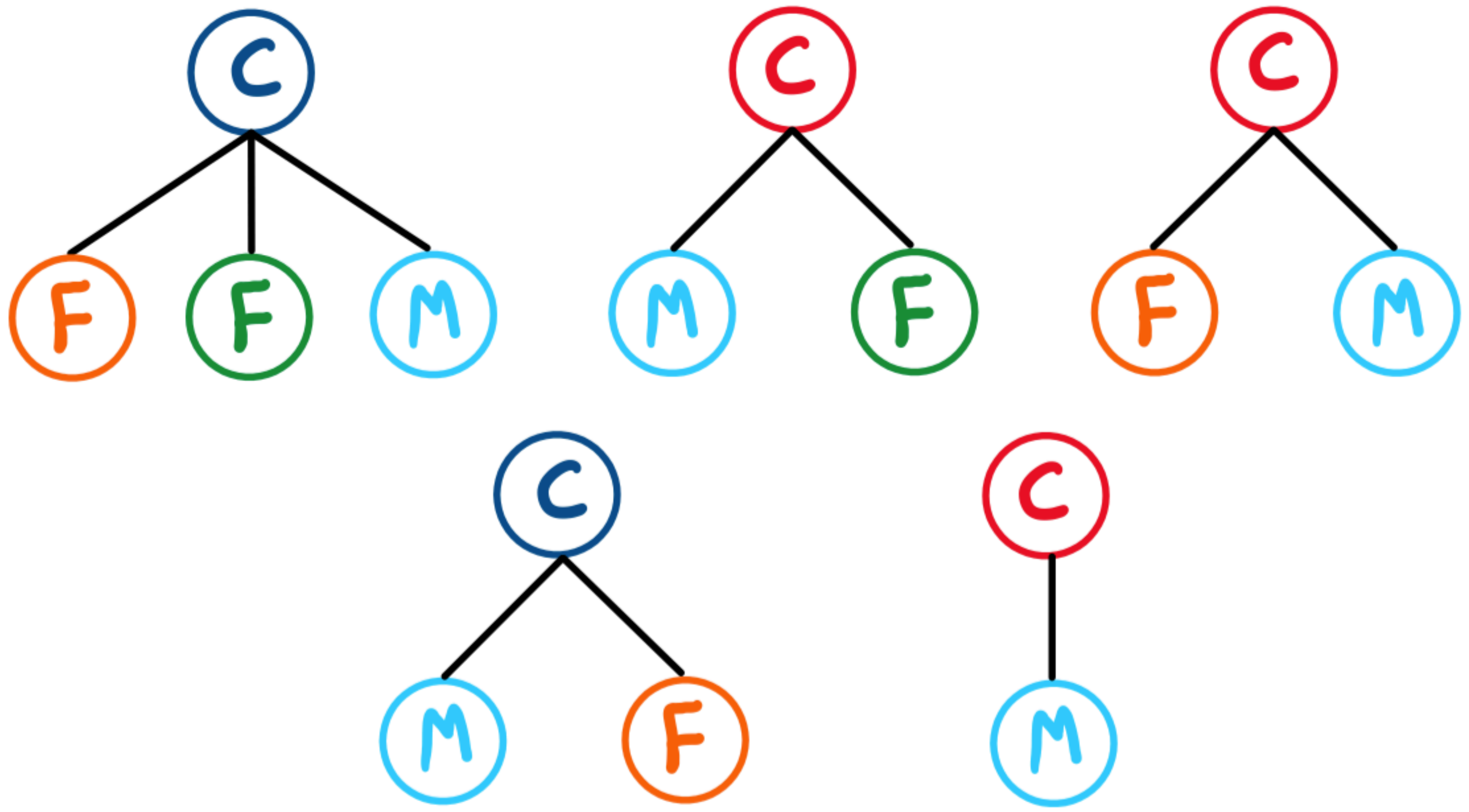

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Multi-type asexual process
$p = q > 1,\ \xi(x) = x.$

Single-type bisexual process
$p = 1,\ q = 2,\ \xi$ superadditive.

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Assumptions on the Offspring Distribution

Reproduction step:

$$F_{n+1,j} = \sum_{i=1}^{p} \sum_{k=1}^{Z_{n,i}} X_{i,j}^{(k,n)}, \quad \text{and} \quad M_{n+1,j} = \sum_{i=1}^{p} \sum_{k=1}^{Z_{n,i}} Y_{i,j}^{(k,n)}$$

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$$Z_{n+1} = \xi((F_{n+1,1}, \ldots, F_{n+1,q_f}), (M_{n+1,1}, \ldots, M_{n+1,q_m}))\,.$$

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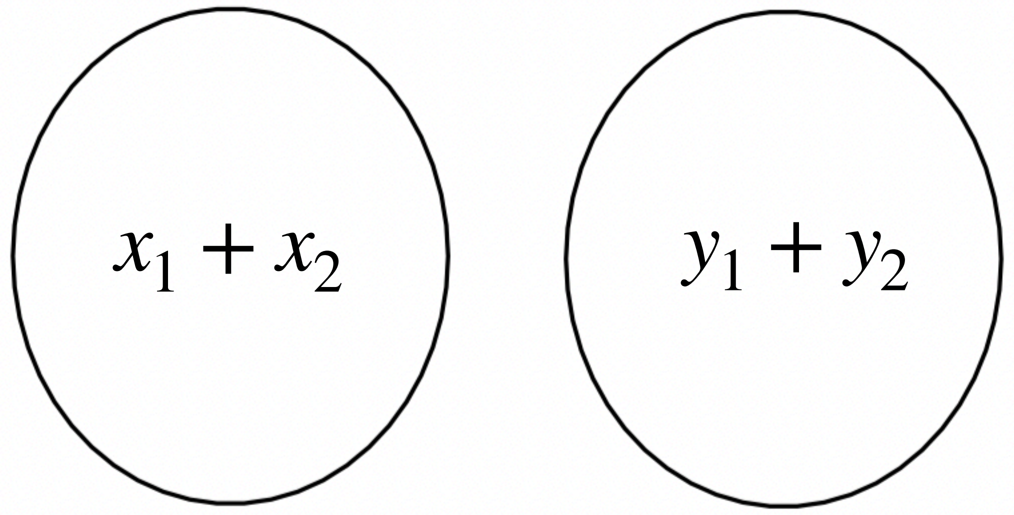

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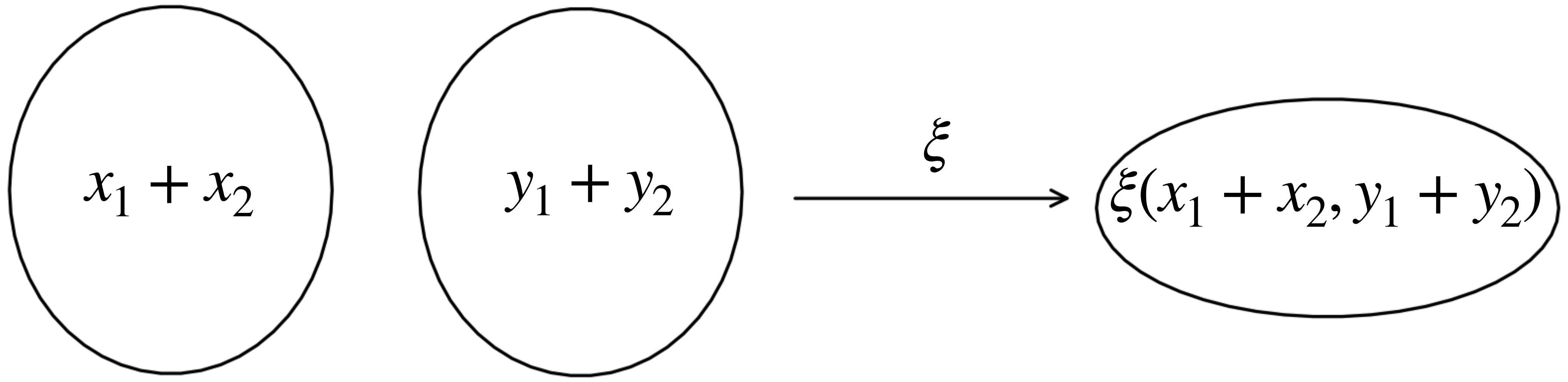

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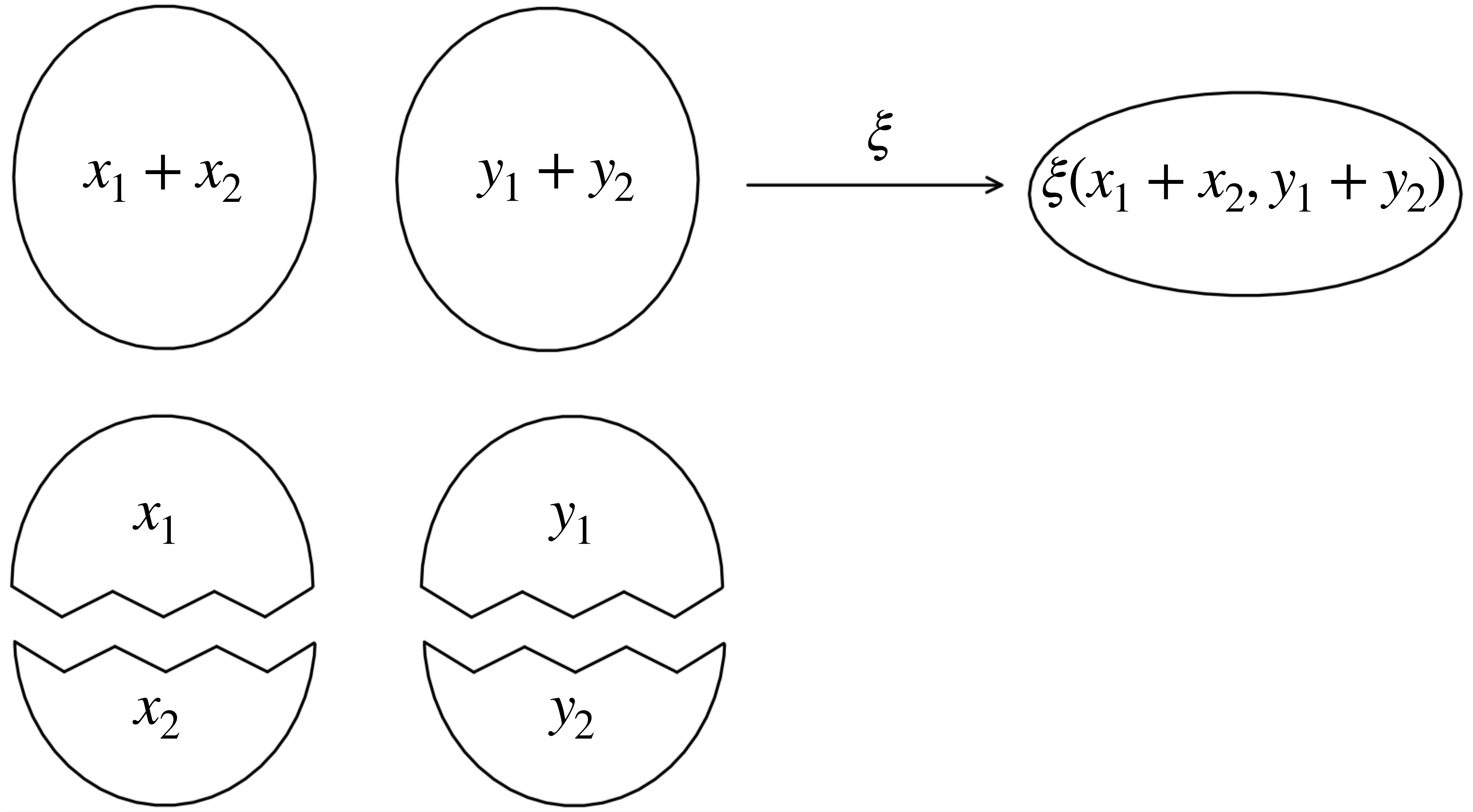

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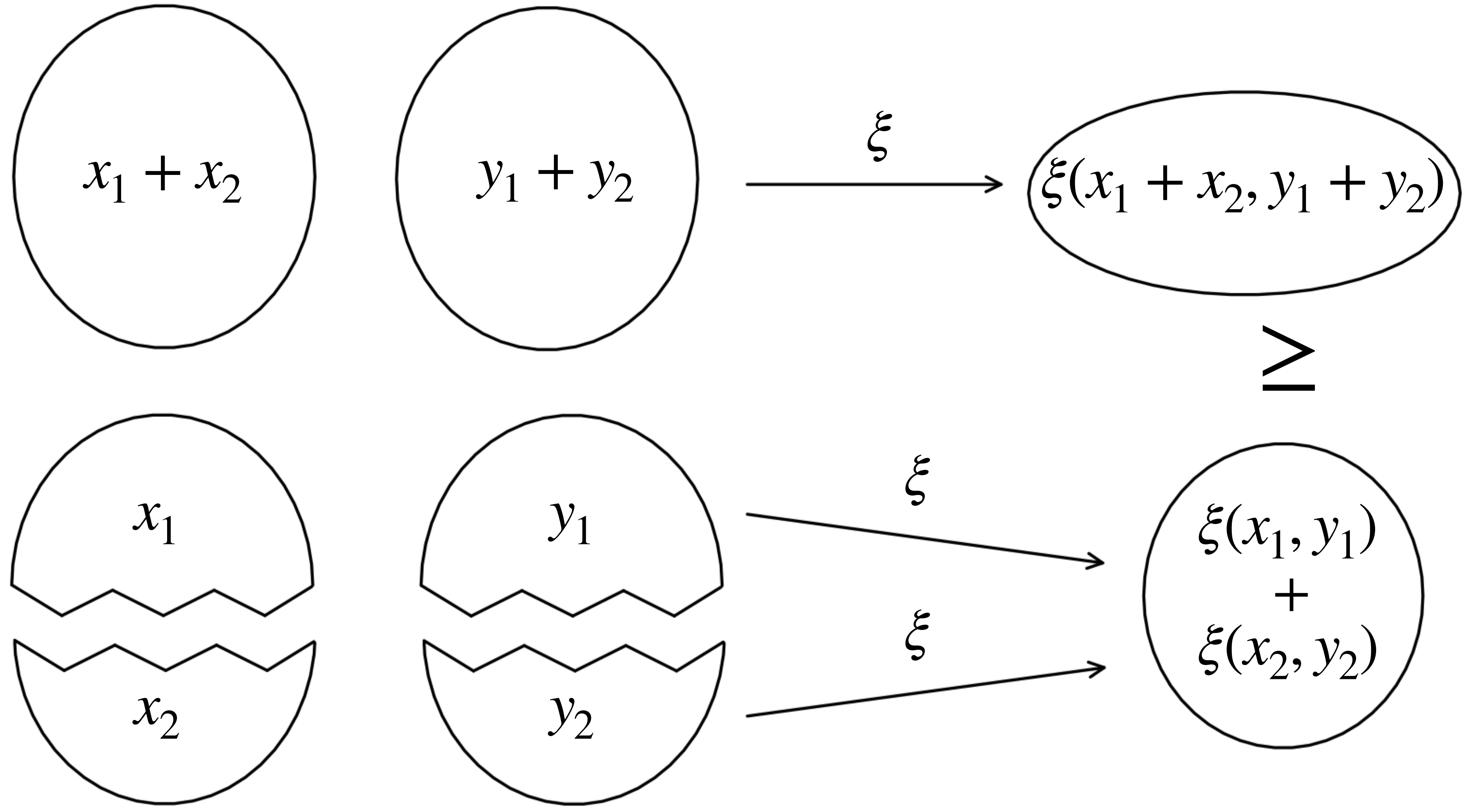

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Example: Multi-type perfect fidelity ($p = q_m = q_f$)

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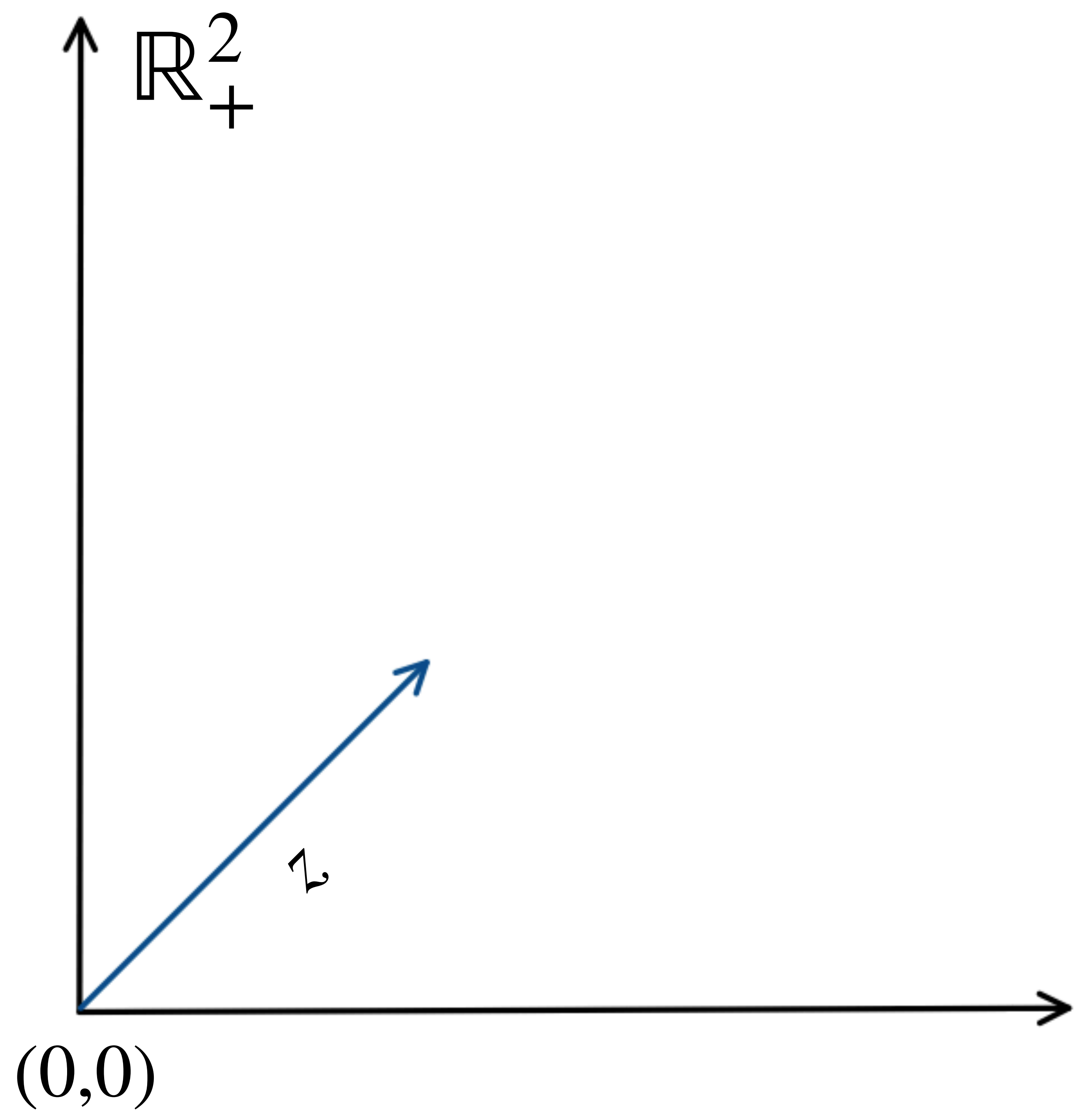
Definition

Consider $\mathfrak{M} : \mathbb{R}_+^p \longrightarrow (\mathbb{R}_+ \cup \{+\infty\})^p$ given by:

$$\mathfrak{M}(z) = \lim_{k \to +\infty} \frac{\mathbb{E}(Z_1 \mid Z_0 = \lfloor kz \rfloor)}{k}.$$



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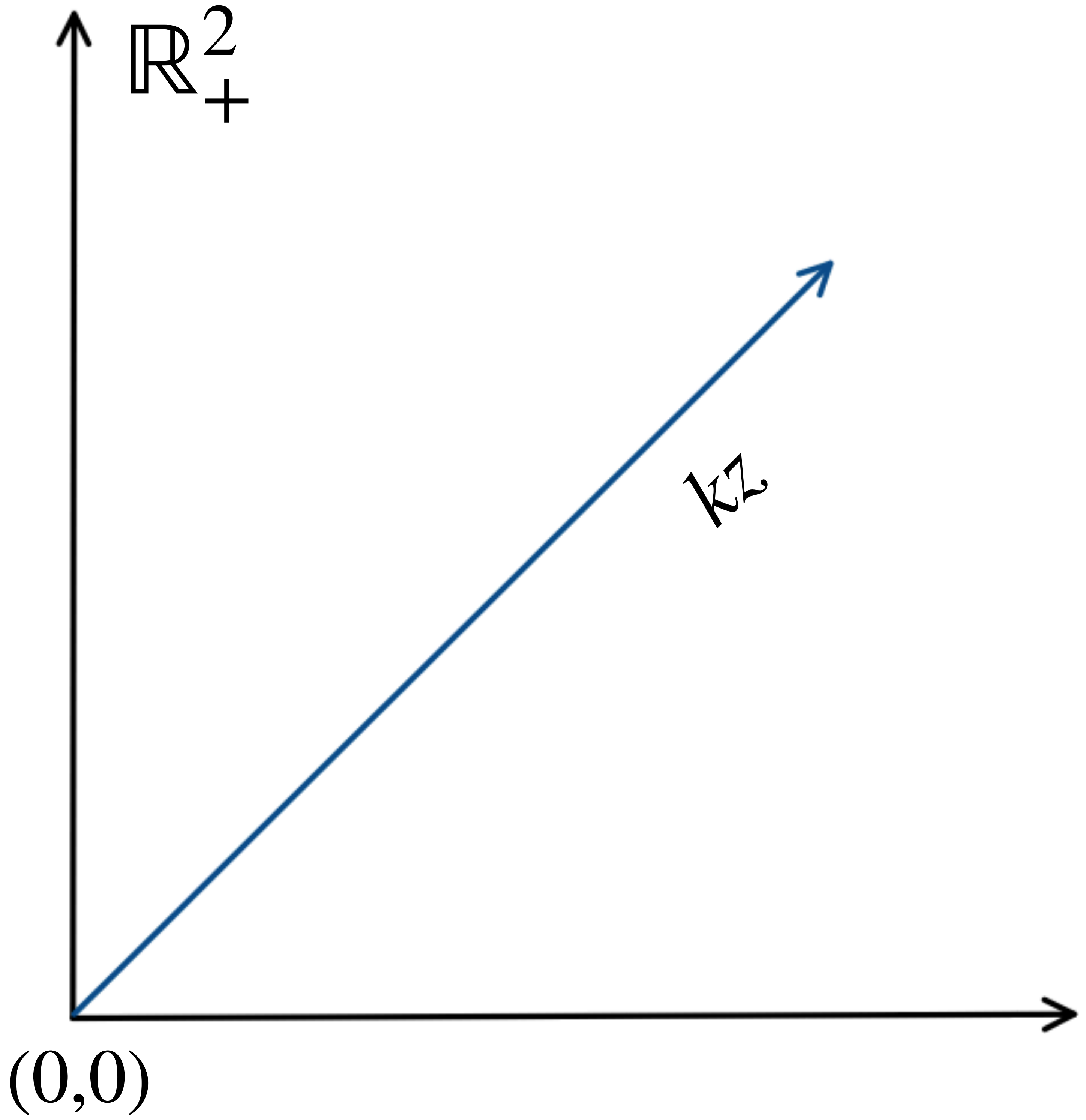

Examples

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	Asexual	Bisexual
Single-type		
Multi-type		

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First Properties

$$\mathfrak{M}(z) = \lim_{k\to+\infty} \frac{\mathbb{E}(Z_1 \mid Z_0 = \lfloor kz \rfloor)}{k}$$

$\mathfrak{M}$ is positively homogeneous:

$$\mathfrak{M}(\alpha z) = \alpha \mathfrak{M}(z),$$

for all $\alpha > 0$ and $z \in \mathbb{R}_+^p$.

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$\Rightarrow$

$\mathfrak{M}$ is a concave function:

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LLN for large initial population

Theorem I: Assume $\mathfrak{M} < +\infty$. Consider $z \in \mathbb{N}^p$ and denote for $k \geq 1$, $(Z_n(k))_{n\in\mathbb{N}}$ the process with initial condition $Z_0(k) = kz$. Then, for all $n \in \mathbb{N}$, we have

$$\frac{Z_n(k)}{k} \xrightarrow{k\to+\infty} \mathfrak{M}^n(z) \text{ a.s. and in } L^1 .$$

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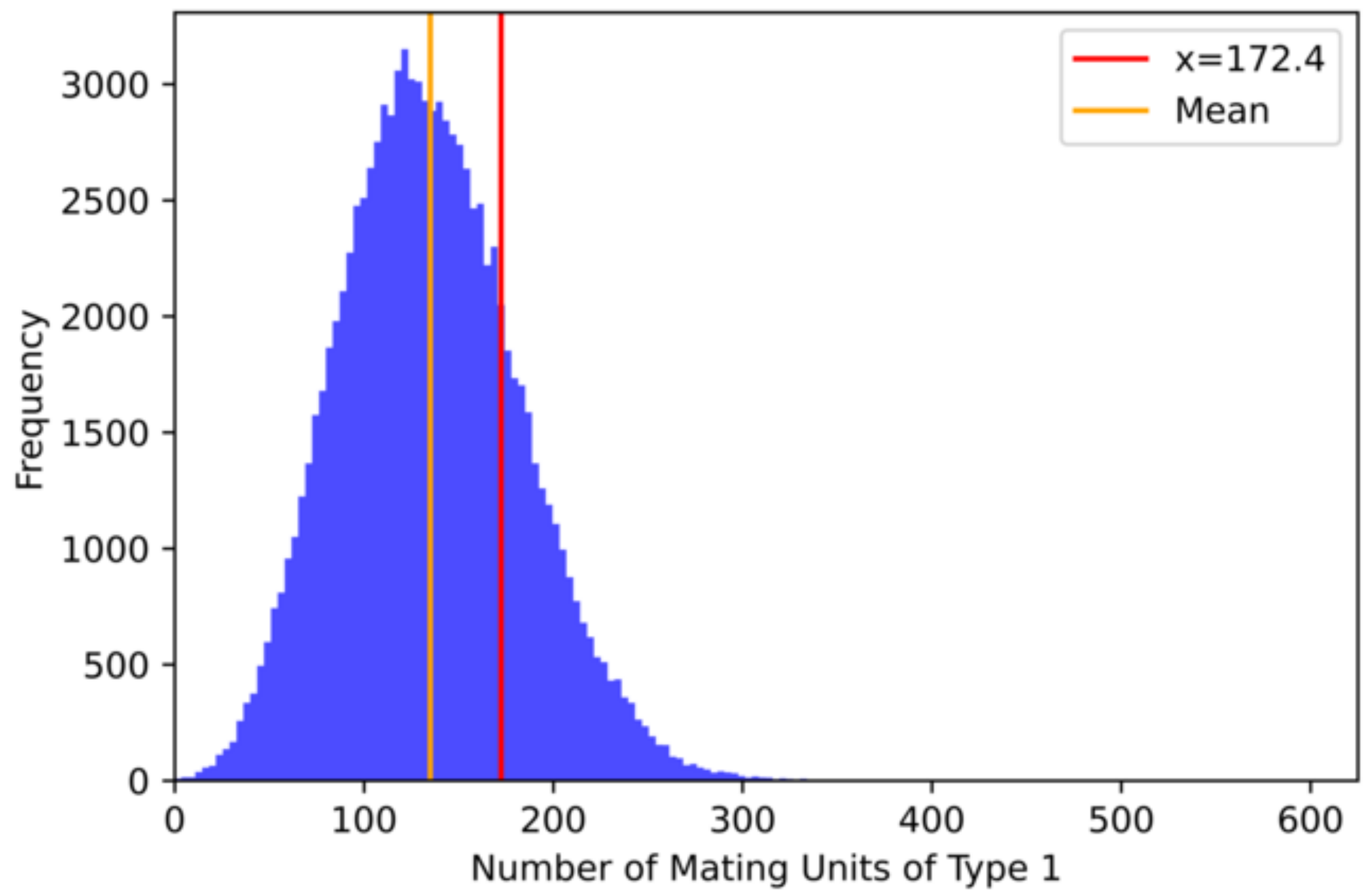
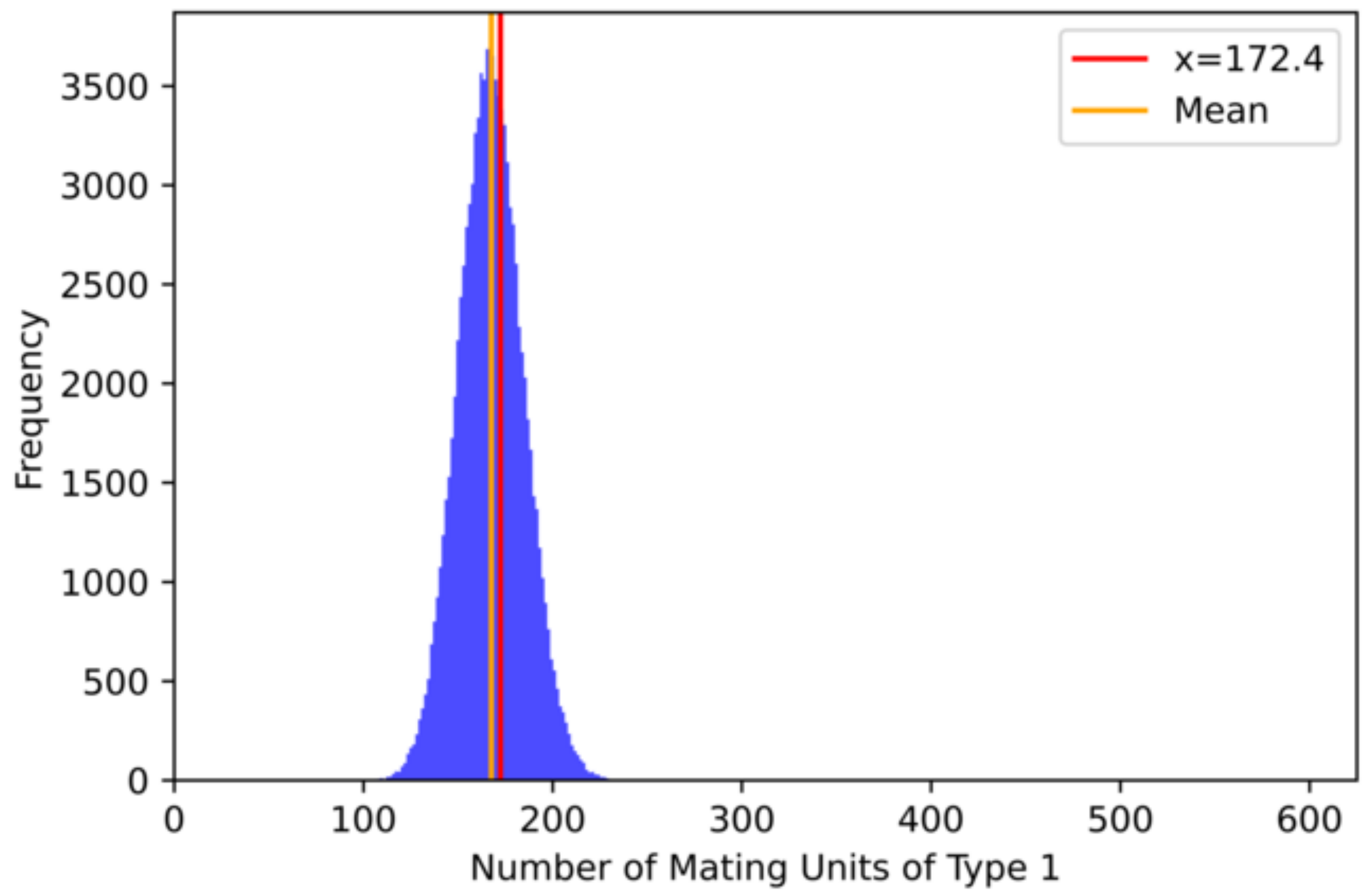


$n = 5,\ k = 5$



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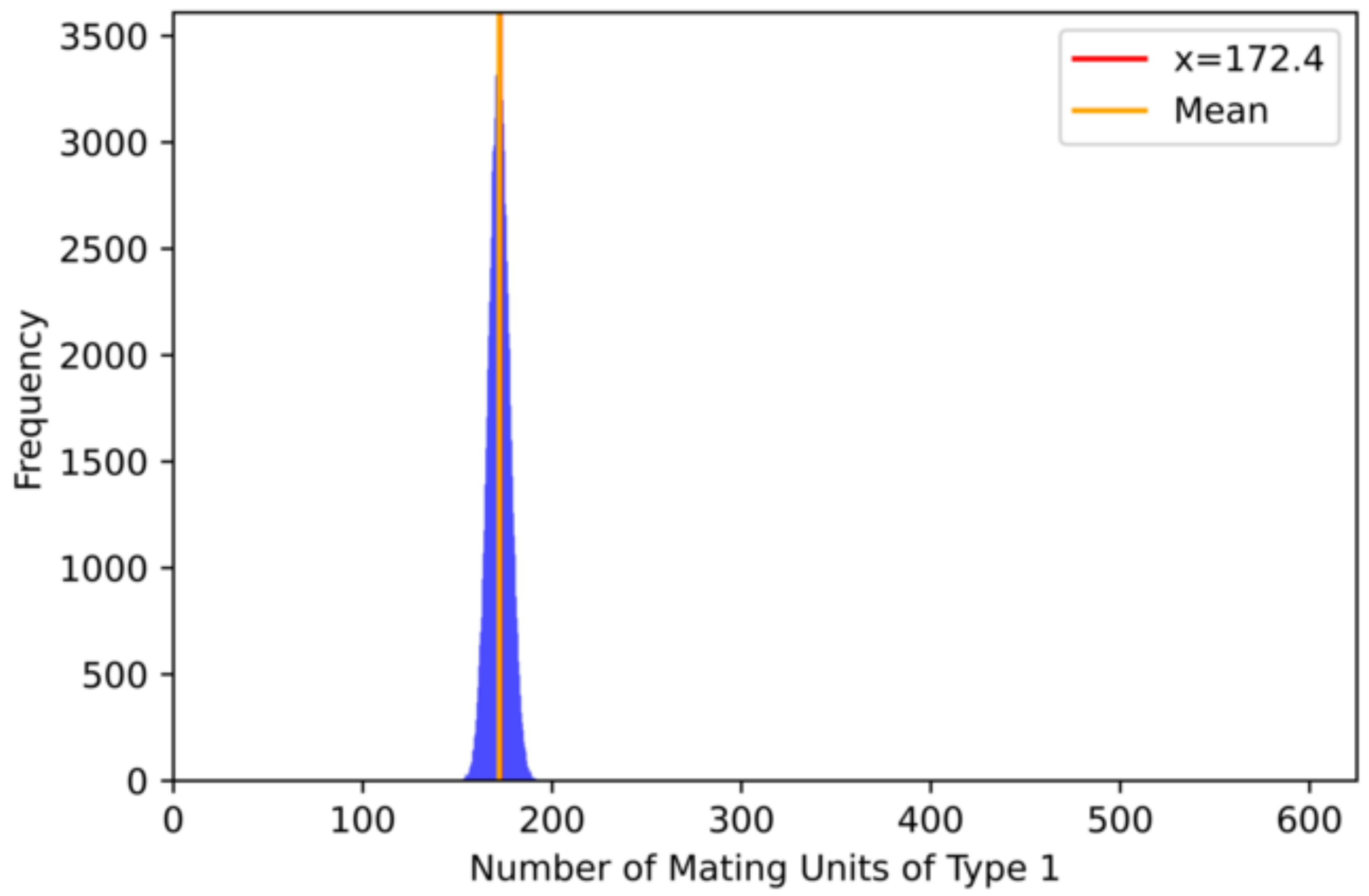

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LLN for large initial population: consequences

The iterations of $\mathfrak{M}$ will play a fundamental role in the asymptotic behaviour for large population. In addition:

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In particular for $k = 1$

$$\mathfrak{M}^n(z) \geq \mathbb{E}(Z_n \mid Z_0 = \lfloor z \rfloor).$$

In addition, we obtain a second definition for $\mathfrak{M}$ in terms of the mating function:

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Example: For the multi-type perfect fidelity mating, we have

$$\mathfrak{M}(z) = (\min\{(z\mathbb{X})_1, (z\mathbb{Y})_1\}, \dots \min\{(z\mathbb{X})_p, (z\mathbb{Y})_p\}).$$

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Concave Perron-Frobenius theory

We suppose that $\mathfrak{M}$ is a **primitive** function. That is, there exists $n_0 \in \mathbb{N}$ such that for all $n \geq n_0$, and all $z \in \mathbb{R}_+^p$, $\mathfrak{M}^n(z) > 0$.

Theorem [Krause, 1994]: If $\mathfrak{M} : \mathbb{R}_+^p \longrightarrow \mathbb{R}_+^p$ is a *concave*, *positively homogeneous* and *primitive* function, then the problem $\mathfrak{M}(z) = \lambda z$ has a unique solution $\lambda^* > 0$ and $z^* > 0,\ \|z^*\| = 1$.
There exists a function $\mathscr{P} : \mathbb{R}_+^p \longrightarrow \mathbb{R}_+$ such that

$$\lim_{k \to +\infty} \frac{\mathfrak{M}^n(z)}{(\lambda^*)^n} = \mathscr{P}(z) z^*$$

LLN for the complete trajectory

<u>Theorem II</u>: Assume $\mathfrak{M} < +\infty$ and that $\lambda^* > 1$. There exists $n_0 \in \mathbb{N}$, such that for all $\varepsilon, \eta \in (0,1)$, there exists $r > 0$ such that if $\|z\| > r$,

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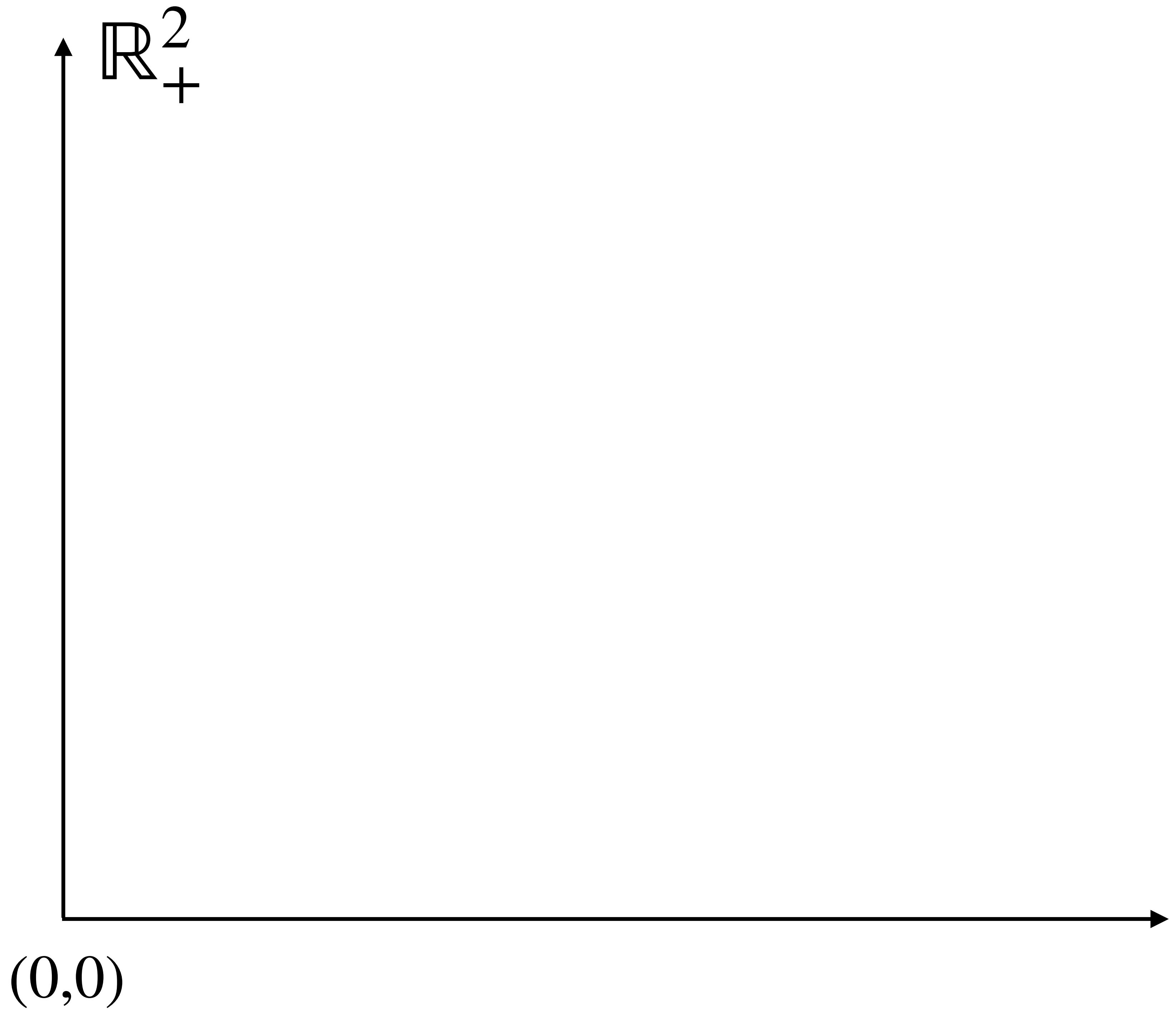

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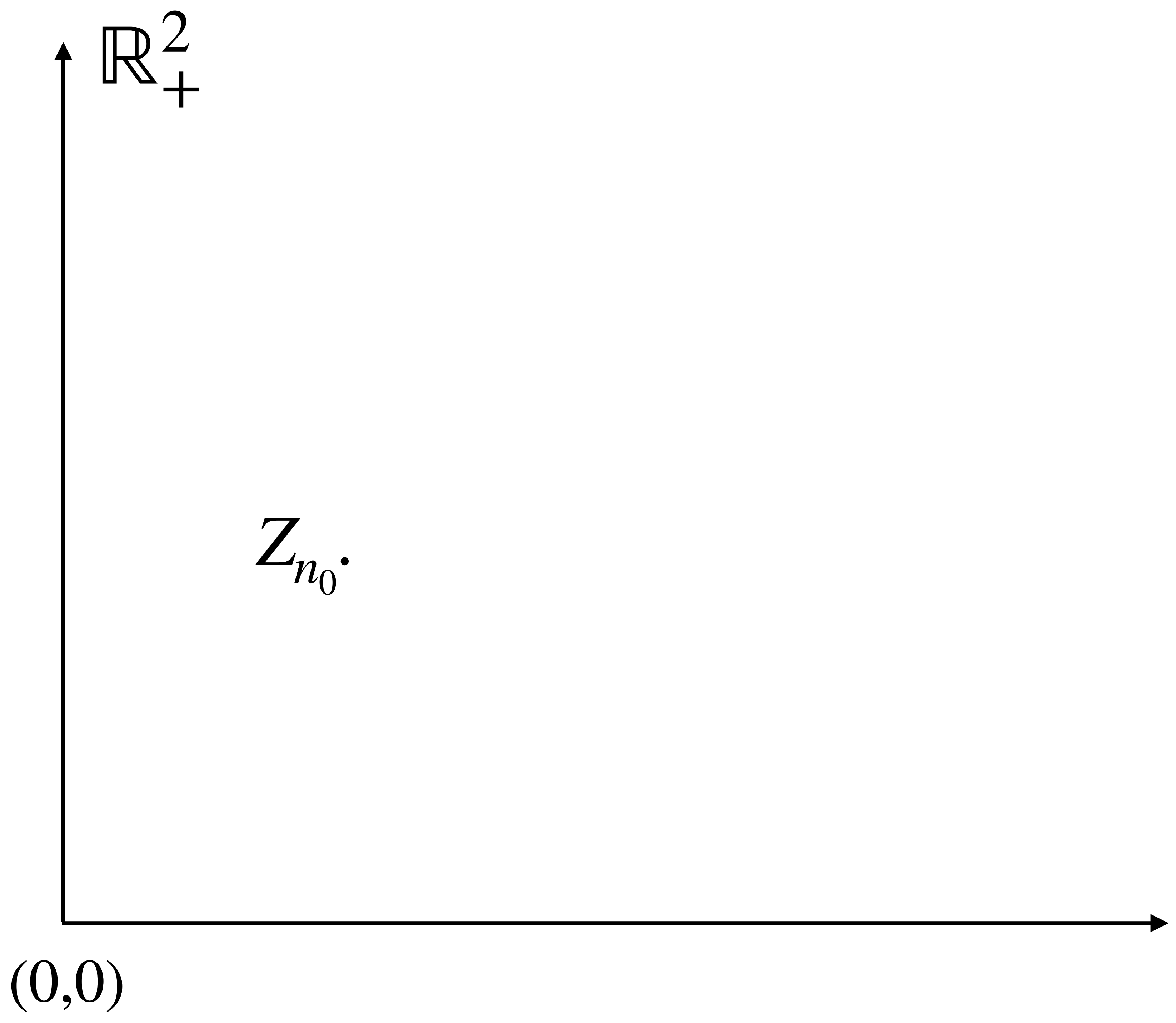

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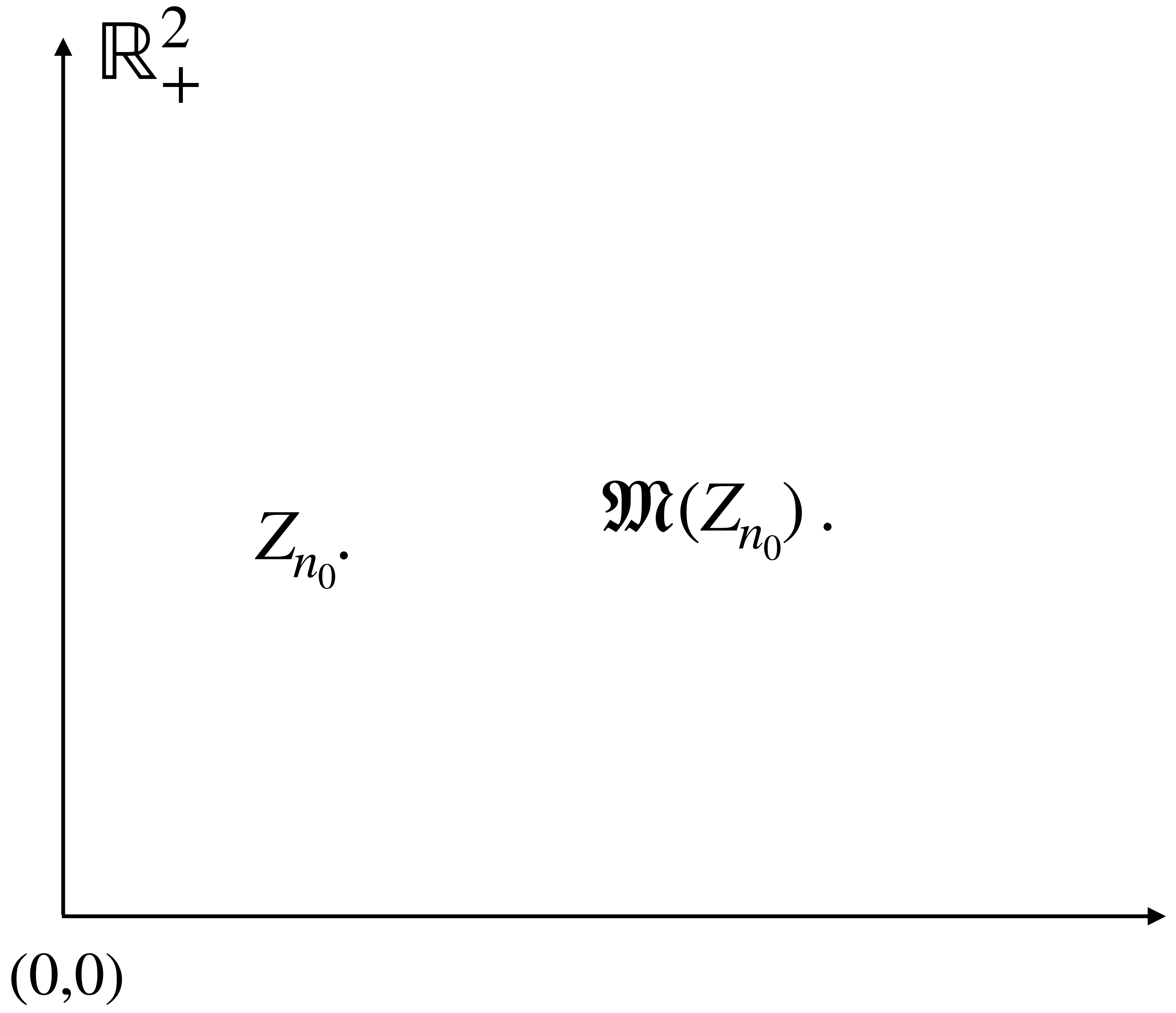

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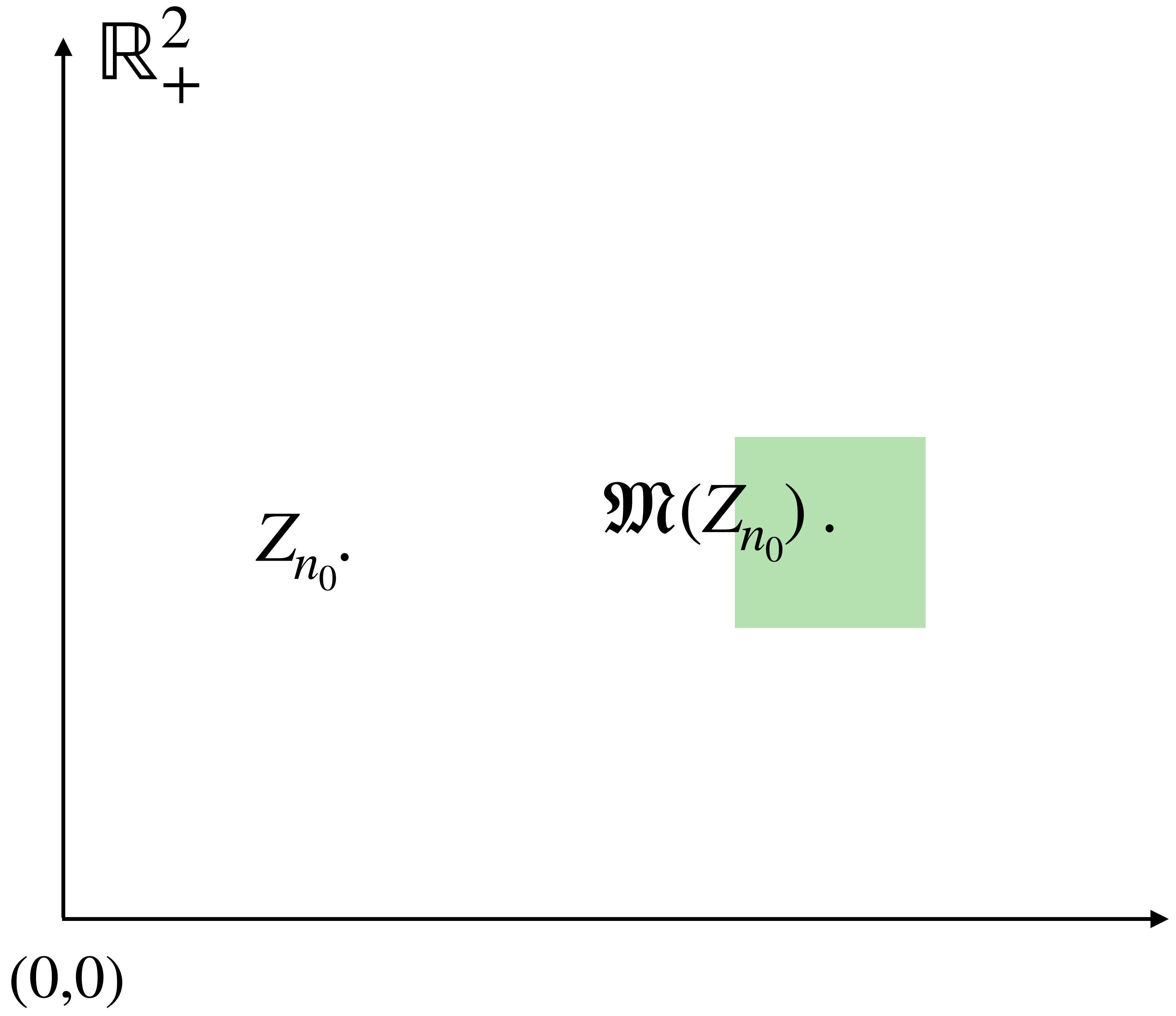

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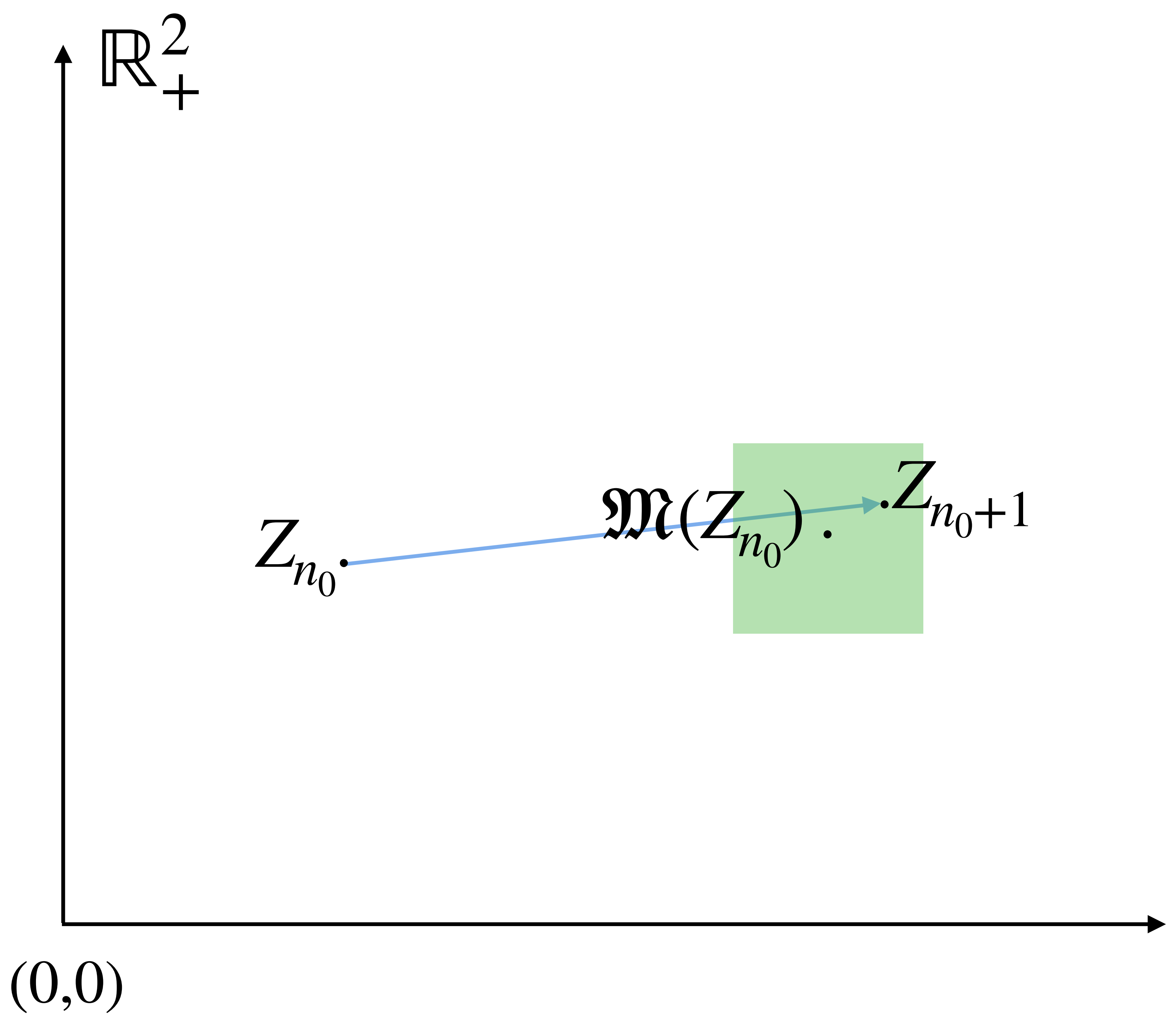

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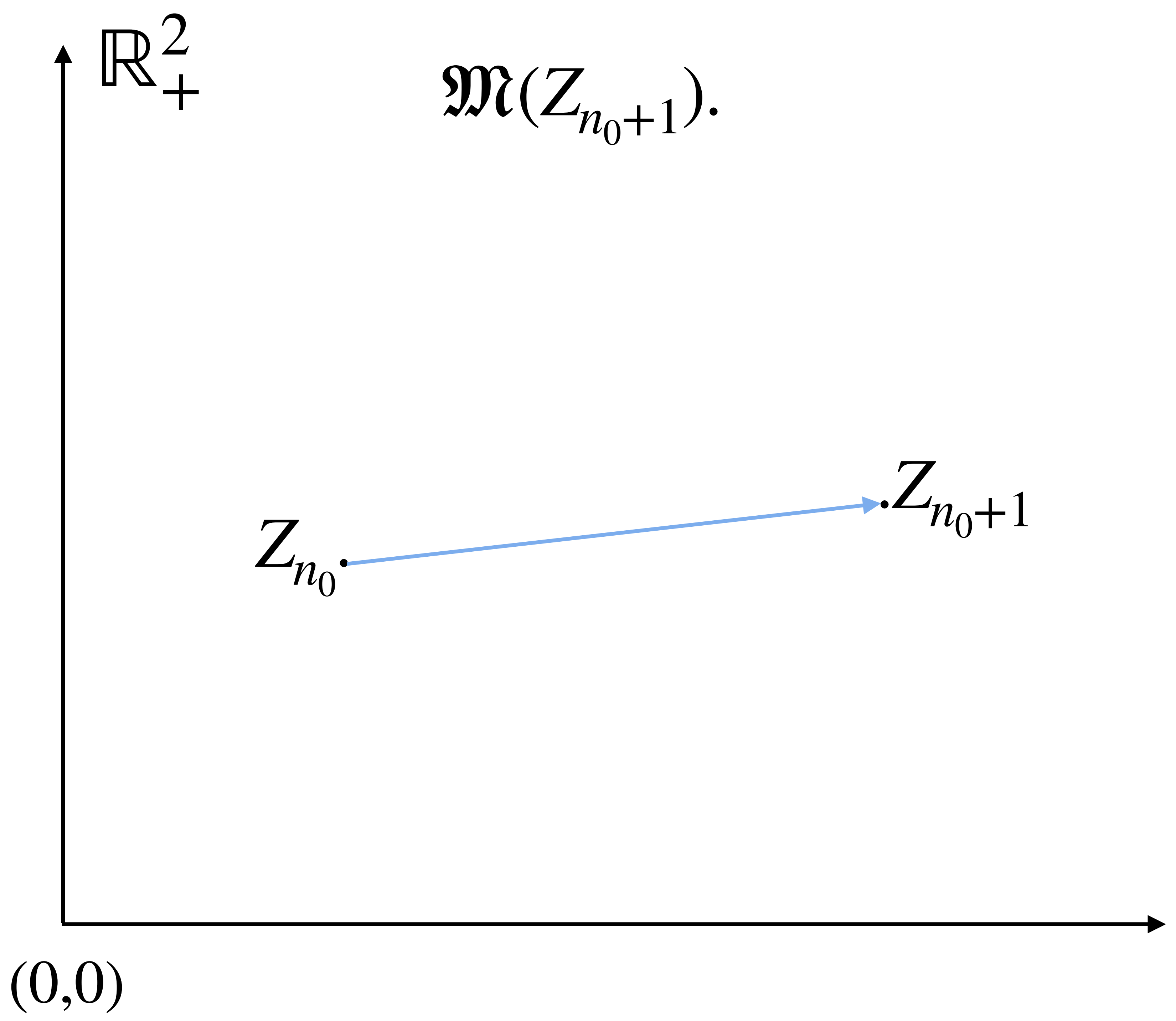

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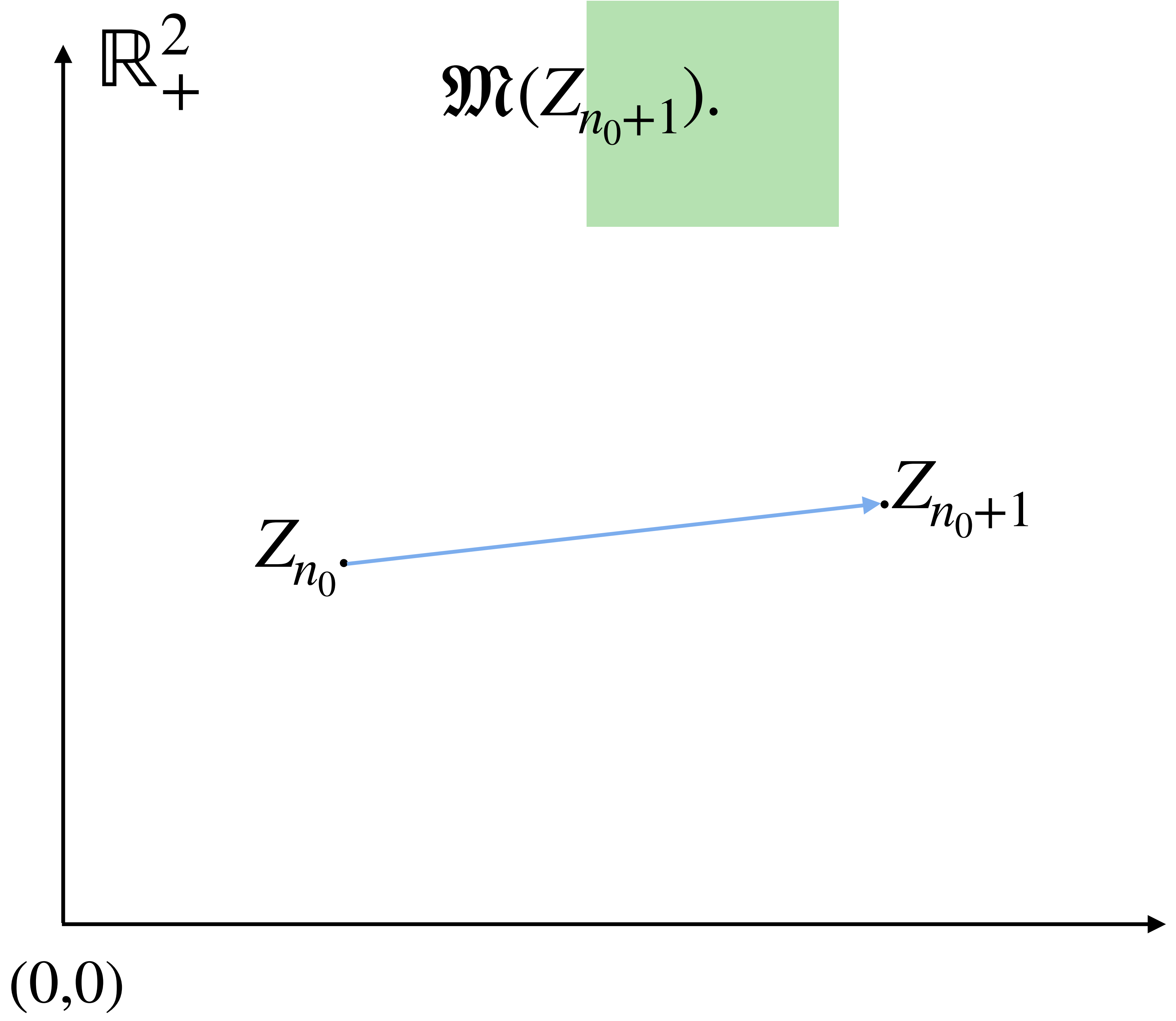

LLN for the complete trajectory

Theorem II: Assume $\mathfrak{M} < +\infty$ and that $\lambda^* > 1$. There exists $n_0 \in \mathbb{N}$, such that for all $\varepsilon, \eta \in (0,1)$, there exists $r > 0$ such that if $\|z\| > r$,

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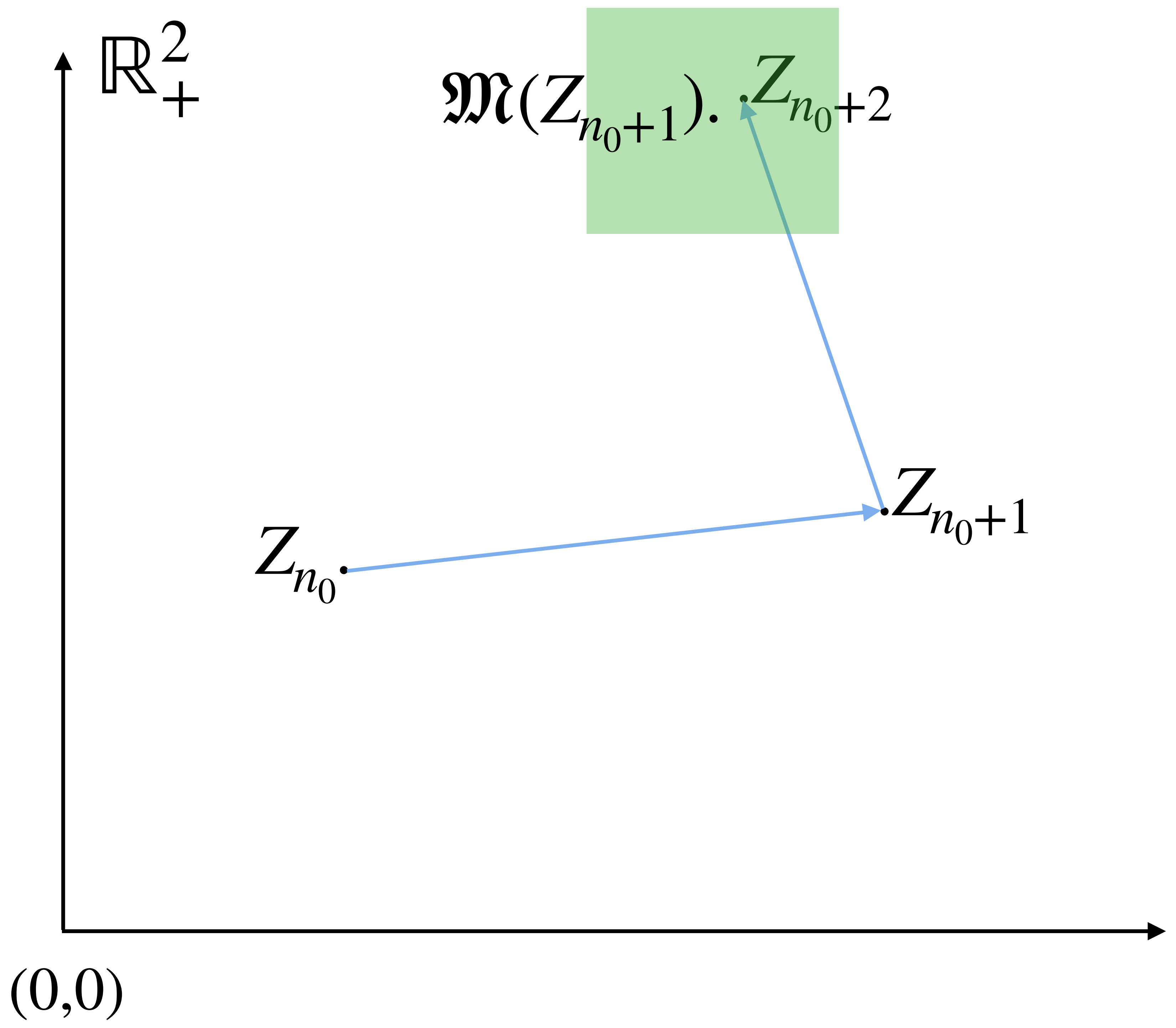

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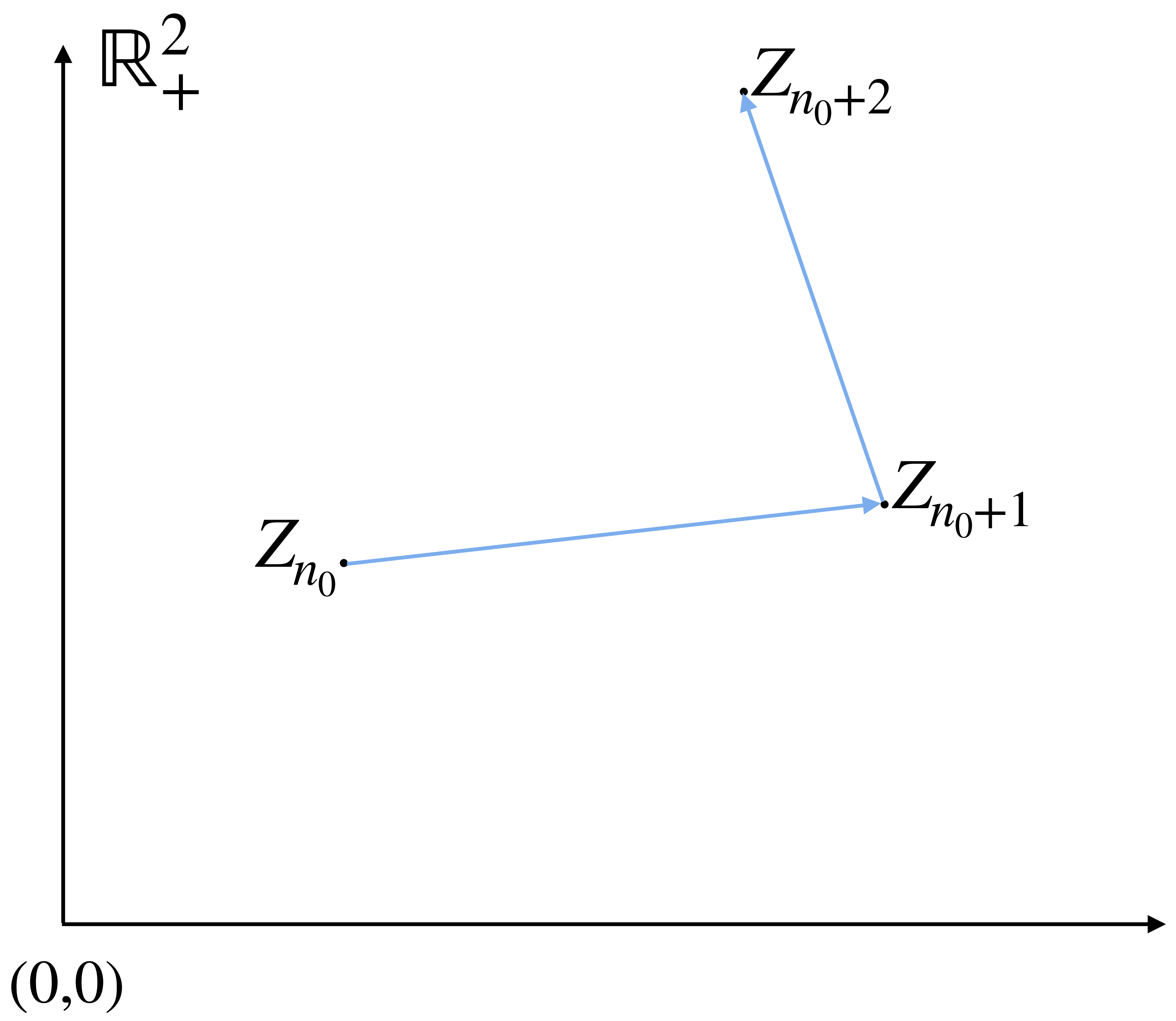

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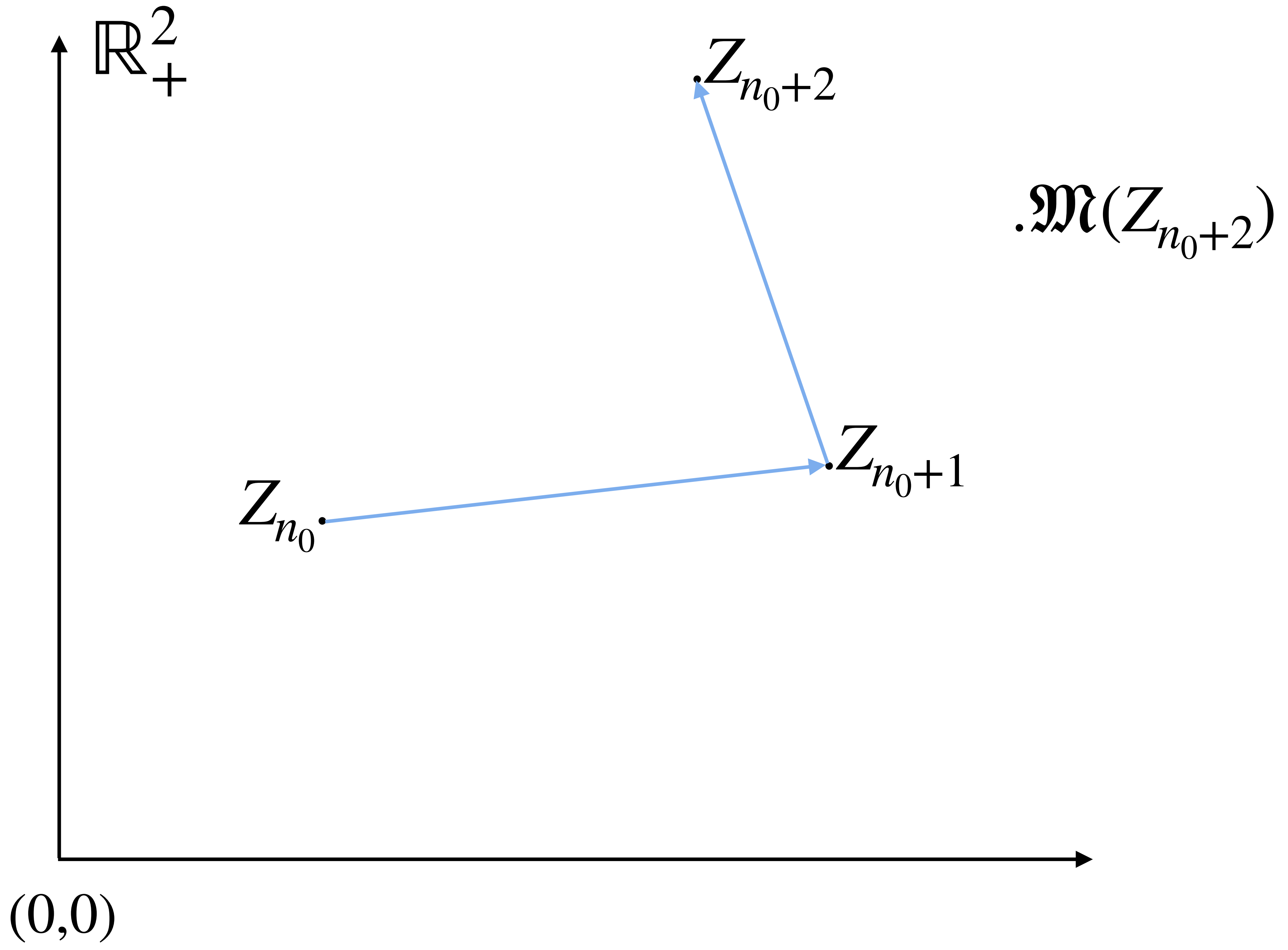

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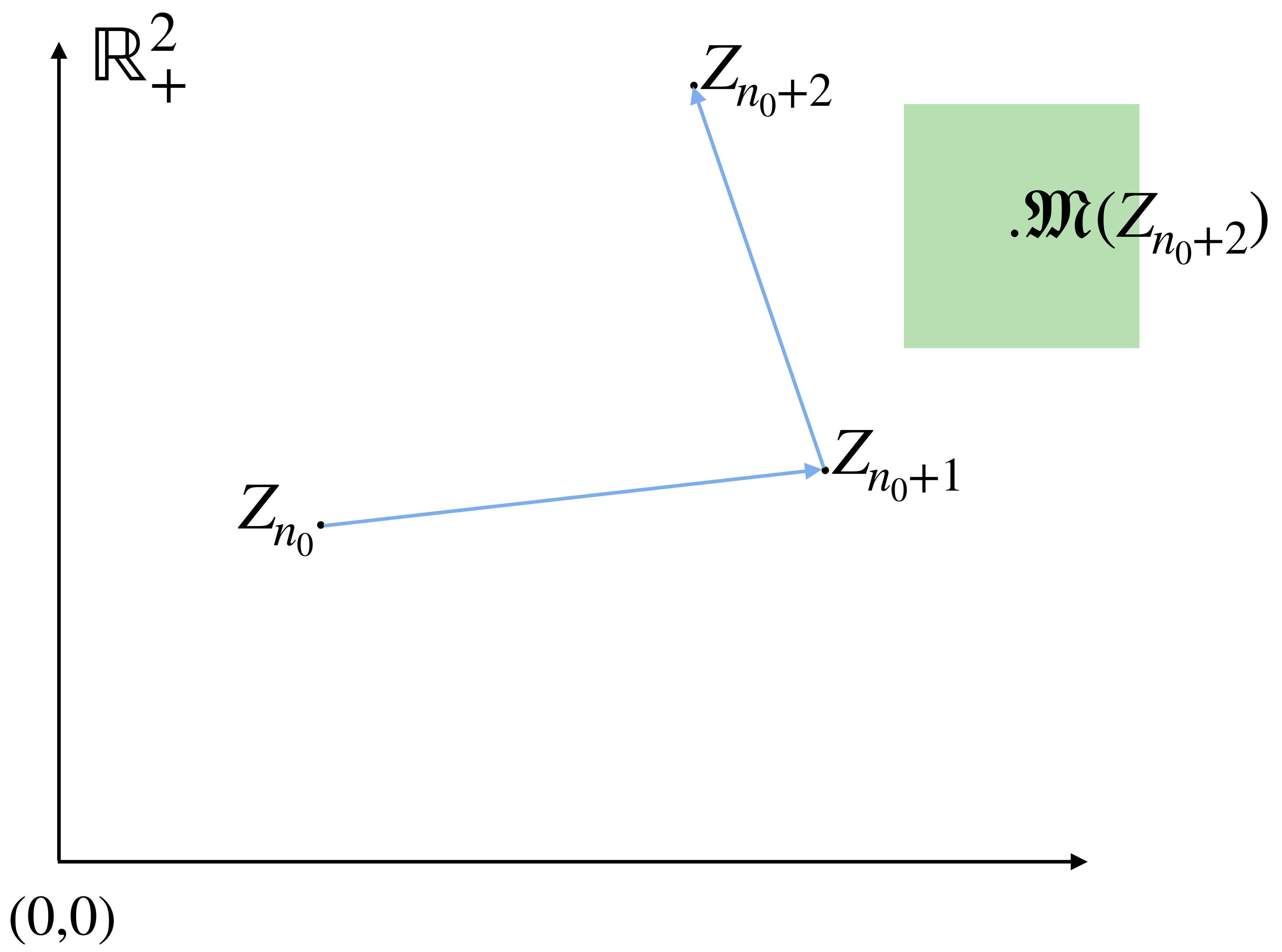

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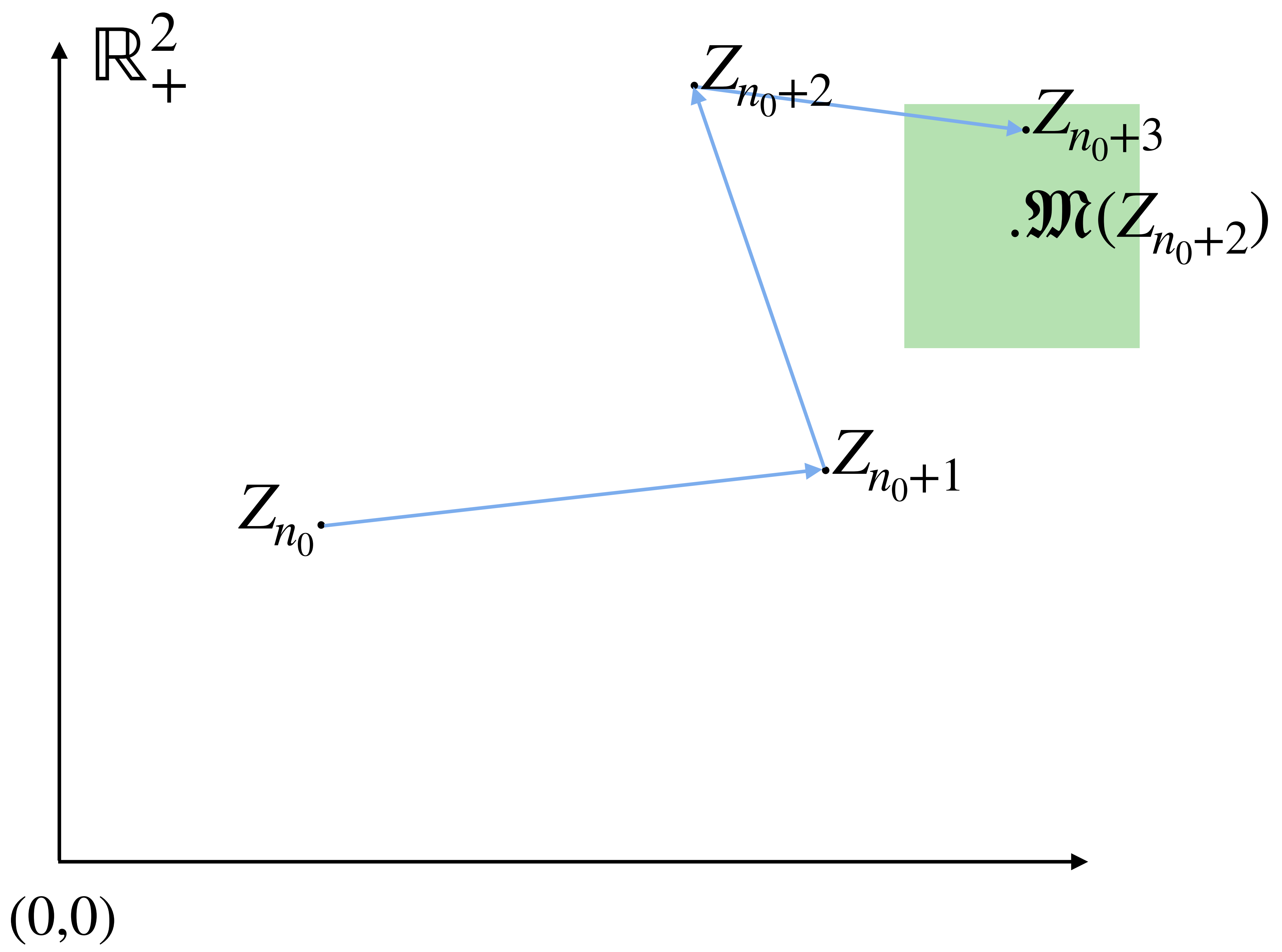

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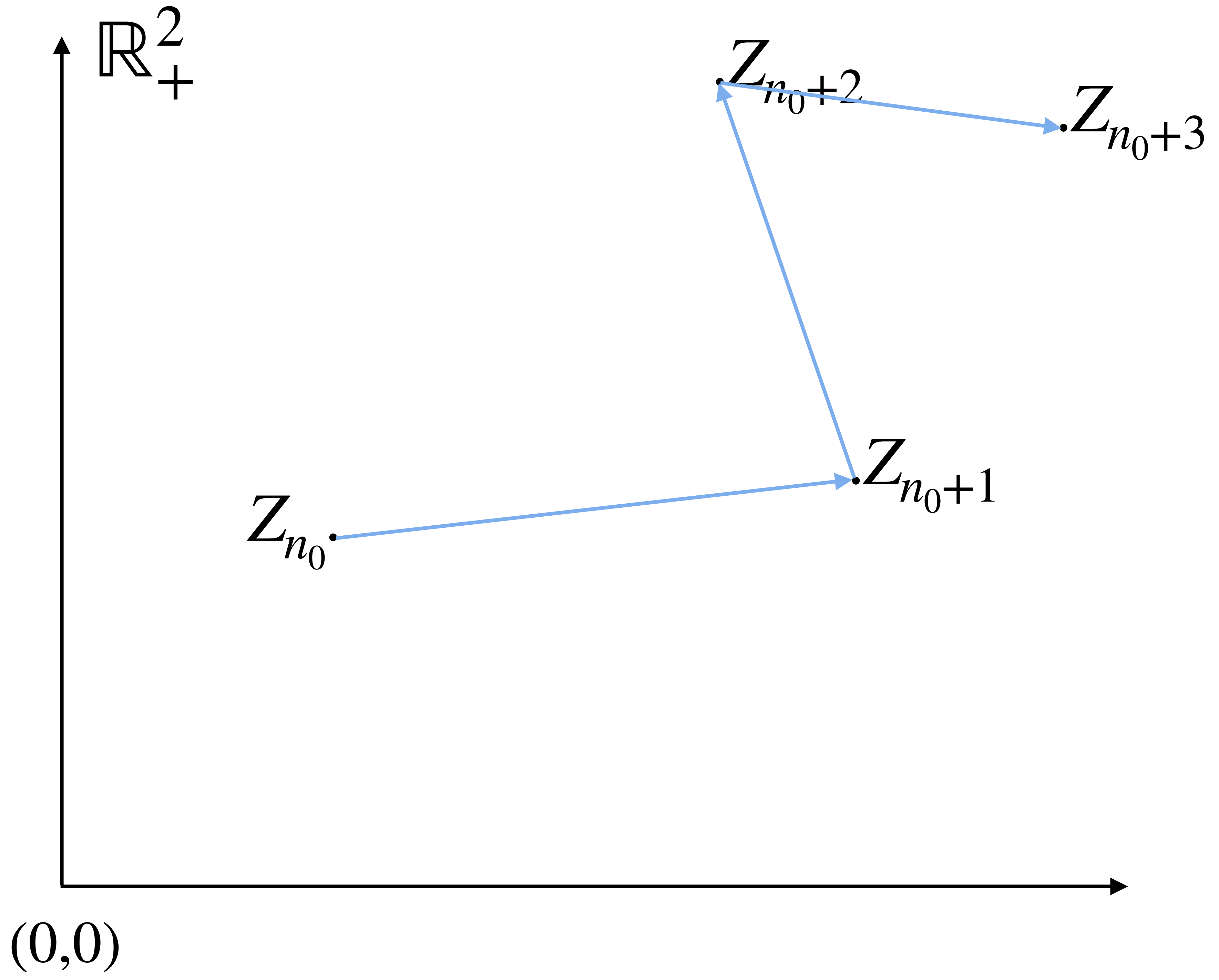

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With high probability

$$(1-\varepsilon)\mathfrak{M}(Z_n) \leq Z_{n+1} \leq (1+\varepsilon)\mathfrak{M}(Z_n).$$

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Positive probability of survival in the case where $\lambda^* > 1$.

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Positive probability of survival in the case where $\lambda^* > 1$.

In addition, under the event of non-extinction $\{Z_n \neq 0,\, \forall n \in \mathbb{N}\}$ we have $\mathbb{P}_z-$a.s..

$$\lim_{n \to +\infty} \frac{Z_n}{\|Z_n\|} = z^*.$$

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Extinction condition

We suppose $(Z_n)_{n\in\mathbb{N}}$. is transient. Then $\mathbb{P}\left(\lim_{n\to+\infty}\|Z_n\| \in \{0+\infty\}\right) = 1.$

We define the probability of extinction

$$q_z = \mathbb{P}(Z_n \xrightarrow{n\to+\infty} 0 \mid Z_0 = z)$$

<u>Theorem III</u>: Assume $\mathfrak{M}$ is finite. Then,

$$\lambda^* \leq 1 \Leftrightarrow q_z = 1,\ \forall z \in \mathbb{N}^p$$

If $\lambda^* > 1$ or if there exists $z' \in \mathbb{R}_+^p$ such that $\mathfrak{M}(z')$ is not finite, then there exists $r > 0$ such that $q_v < 1$ for all $v \in \mathbb{N}^p$ with $\|v\| \geq r$.

Asymptotic profile

Recall that we have

$$F_{n+1,j} = \sum_{i=1}^{p} \sum_{k=1}^{Z_{n,i}} X_{i,j}^{(k,n)} \quad \text{and} \quad M_{n+1,j} = \sum_{i=1}^{p} \sum_{k=1}^{Z_{n,i}} Y_{i,j}^{(k,n)},$$

and the matrices

$$\mathbb{X}_{i,j} = \mathbb{E}(X_{i,j}),\ \mathbb{Y}_{i,j} = \mathbb{E}(Y_{i,j})$$

Theorem IV: Assume $\mathfrak{M}$ is finite. For all $z \in \mathbb{N}^p$ there exists a non-negative random variable $\mathscr{C}$ such that

$$\frac{Z_n}{(\lambda^*)^n} \xrightarrow{n\to+\infty} \mathscr{C} z^*,\ \frac{F_n}{(\lambda^*)^{n-1}} \xrightarrow{n\to+\infty} \mathscr{C} z^* \mathbb{X},\ \frac{M_n}{(\lambda^*)^{n-1}} \xrightarrow{n\to+\infty} \mathscr{C} z^* \mathbb{Y},$$

$\mathbb{P}(\,\cdot \mid Z_0 = z)-$a.s.

If in addition $\mathscr{C}$ is non-degenerate at 0 for some $z \in \mathbb{N}^p$, then up to a $\mathbb{P}(\,\cdot \mid Z_0 = z)-$negligible event,

$$\{\mathscr{C} = 0\} = \{\,\exists n \in \mathbb{N}, Z_n = 0\}\,.$$

L^1 Convergence under a $VlogV-$condition

Proposition I: Assume that $\mathbb{E}(X_{i,j} \log X_{i,j}) < +\infty$, $\mathbb{E}(Y_{i,j} \log Y_{i,j}) < +\infty$ for all i, j, and that

$$\left| \frac{\xi(z\mathbb{X}, z\mathbb{Y})}{|z|} - \frac{\mathfrak{M}(z)}{|z|} \right| \leq C|z|^{-\alpha}, \forall z \in \mathbb{N}^p,$$

for some $C, \alpha > 0$. Then the convergence in **Theorem IV** holds in L^1 and the random variable $\mathscr{C}$ is non-degenerate at 0.

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Conclusions

- We studied a population model with superadditive mating and different types, achieving:
    - Two LLN in large population.
    - Sufficient and necessary condition for extinction.
    - Sufficient condition for exponential growth in the supercritical case.
    - Existence of a continuum of QSDs in the subcritical case.
- We studied some particular cases of:
    - Continuous time two-sex birth and death process.
    - Models with random mating.

Perspectives

- Methods to approximate λ^* and z^* need to be developed (work with D. Villemonais and J. Corujo).

- Continuous time versions of the model (work with E. Horton).

- Model with a continuum of traits (work S. Méléard and A. Véber)

- Different models with non-superadditive mating. Models that consider competition of individuals

- Study existence of QSDs in the critical case.

The multi-type bisexual Galton-Watson process

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Besançon Meeting on Probability, Ecology & Evolution - December, 2024

Existence of QSDs

We suppose that $\mathfrak{M}$ is finite and that $\lambda^* < 1$.

We are interested in the existence of probability measures ν over $\mathbb{N}^p \backslash \{0\}$ such that

$$\mathbb{P}_\nu(Z_n \in \cdot \mid Z_n \neq 0) = \nu(\,\cdot\,).$$

The exponential absorption parameter is $\theta \in [0,1]$ such that

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1. Existence of a continuum of QSDs.
2. Existence of a finite number of QSDs under a moment hypothesis.
3. Existence of a unique QSD under irreducibility assumption.

Existence of a Continuum of QSDs

<u>Theorem V</u>: The process $(Z_n)_{n\in\mathbb{N}}$ admits an infinite set of quasi-stationary distributions. More precisely, for any $\theta \in (\lambda^*, 1)$, there exists a quasi-stationary distribution ν_θ with absorption parameter θ.

A general result is proven for sub-Markovian kernels. Then applied for the kernel

$$K(x, dy) = \mathbb{P}_x(Z_1 \in dy, Z_1 \neq 0)\,.$$

Existence of finitely many QSDs

We define

$$\theta_0 = \sup_{z \in \mathbb{N}^p \setminus \{0\}} \sup \left\{ \theta > 0, \liminf_{n \to +\infty} \theta^{-n} \mathbb{P}_z(Z_n \neq 0) > 0 \right\}.$$

We assume there exists $\eta > 1$ s.t. $(\lambda^*)^\eta < \theta_0$ and that $\mathbb{E}(X_{i,j}^\eta) < +\infty$, $\mathbb{E}(Y_{i,j}^\eta) < +\infty$ for all i, j.

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Theorem VI: We assume $(Z_n)_{n \in \mathbb{N}}$ aperiodic and fix $a \in (1, \eta)$. There exist $\nu_1, \ldots, \nu_\ell$ QSDs with $\nu_i(\mathscr{P}^a) < +\infty$ and absorption parameter θ_0 such that for all $f \leq \mathscr{P}^a$,

$$\left| \theta_0^{-n} n^{-j(z)} \mathbb{E}_z(f(Z_n) 1_{Z_n \neq 0}) - \sum_{i=1}^{\ell} \eta_i(z) \nu_i(f) \right| \leq \alpha_n \mathscr{P}(z)^a,$$

with $\alpha_n \to 0$, j and η_i functions s.t. $\eta_i \leq K \mathscr{P}^a$ for some $K > 0$.

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<u>Theorem VII</u>: In addition, if $(Z_n)_{n\in\mathbb{N}}$ is irreducible, there exists a unique QSD ν_{QSD} with $\nu_{QSD}(\mathcal{P}^a) < +\infty$ and absorption parameter θ_0 such that for all measure $\mu(\mathcal{P}^a) < +\infty$ and $|f| \leq \mathcal{P}^a$.

$$|\mathbb{E}_\mu(f(Z_n) \mid Z_n \neq 0) - \nu_{QSD}(f)| \leq C\gamma^n \mu(\mathcal{P}^a).$$

with $\gamma \in (0,1)$.

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