Lotka-Volterra systems with stochastic resetting

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Computational Models for Complex Systems

Lotka-Volterra model

Purpose

Desription of prey-predator populations interaction

The (basic) model

$$\begin{cases} \frac{\partial a(t)}{\partial t} = -\mu a(t) + \lambda a(t) b(t) \\ \frac{\partial b(t)}{\partial t} = \sigma b(t) - \lambda' a(t) b(t) \end{cases}$$

- $a(t)$ density of the population of predators
- μ mortality rate of predators
- λ reproductive rate of predators
- $b(t)$ density of the population of prey
- σ reproductive rate of prey
- λ' predation rate

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Reinterpretation of the model

Rapid population growth $+$ limited resources $\implies$ scarcity and risk of extinction

How to survive?

Two things have an important role in populations surviving/persistence under unfavorable conditions:

- Spatial structure of the environment
- Movements

Our model

Fragile ecosystem, prey are scarce, i.e. confined to the origin cell (patch).

- Prey confined to a single patch
- Predators only reproduce in the prey patch
- Predators movements modeled by *Lévy flights*
- Predators subject to resetting to the prey patch

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Motivations behind the model

Single patch

It is a limiting case of fragile system and it allows us to study the effect of predator mobility on species survival, within and outside the patch

Predators movements and resetting

- Standard models uses *Brownian diffusion* (Markovian random walks)
- Low prey density $\Longrightarrow$ foraging uncertainty $\Longrightarrow$ larger displacements and site fidelity

Random walk ignores multiscale movements and site fidelity and causes vanishing densities

- Lévy flights $\Longrightarrow$ more sites visited without preventing returns to previous sites
- Stochastic resetting to prey patch models spatial memory, traplining and cropping
- Resetting $\Longrightarrow$ stationary probability density around resetting point (home range behavior)

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Focus and expectations

We want to analyze the strategies which maximize the predator populations

Efficient reproduction and foraging $\not\Rightarrow$ population maximization [42]

Predictions

- Low predator's reproductive rate + NO resetting $\stackrel{(?)}{\Longrightarrow}$ low abundance or extinction
- Low reproductive rate + large resetting rate $\stackrel{(?)}{\Longrightarrow}$ increasing density around prey patch

But...

- High density around the patch $\stackrel{(?)}{\Longrightarrow}$ high competition for prey $\stackrel{(?)}{\Longrightarrow}$ decrease density

So, we expect that predators population reaches a maximum at some finite resetting rate

Similarly, fixing resetting rate, predators density could probably be maximized by adjusting Lévy flights parameters

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Setup

Environment

- D-dimensional lattice of square cells with length $R > 1$
- The center of each cell is represented by $\boldsymbol{n} \in \mathbb{Z}^D$

Movements

- Predators perform independent random steps of length > 1
- Probability distribution of dispersal of a predator between cells:

$$p(\boldsymbol{l}) = p_0 \delta_{\boldsymbol{l},\mathbf{0}} + (1 - p_0)\, f\,(\boldsymbol{l}) \ , \quad \boldsymbol{l} \in \mathbb{Z}^D$$

- $p_0 := \mathbb{P}(\text{predator remains in the same cell after moving})$
- f dispersal distribution ($\approx$ inverse power-law with exponent β), such that $f(0) = 0$ and:

$$\sum_{\boldsymbol{l}, |\boldsymbol{l}| \neq 0} f(\boldsymbol{l}) = 1$$

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New model

Predators equation

$$\frac{\partial a(\boldsymbol{n},t)}{\partial t} = -\overbrace{\alpha(1-p_0)a(\boldsymbol{n},t)}^{\text{1st term}} + \overbrace{\alpha \sum_{\boldsymbol{l},|\boldsymbol{l}|\neq 0} p(\boldsymbol{l})a(\boldsymbol{n}-\boldsymbol{l},t)}^{\text{2nd term}}$$

$$+ \underbrace{\lambda a_0(t)b(t)\delta_{\boldsymbol{n},\mathbf{0}}}_{\text{3rd term}} - \underbrace{\mu a(\boldsymbol{n},t)}_{\text{4th term}} - \underbrace{r a(\boldsymbol{n},t)}_{\text{5th term}} + \underbrace{\left[r\sum_{\boldsymbol{m}} a(\boldsymbol{m},t)\right]\delta_{\boldsymbol{n},\mathbf{0}}}_{\text{6th term}}$$

Prey equation

$$\frac{\partial b(t)}{\partial t} = \sigma b(t)\left(1-\frac{b(t)+a_0(t)}{K}\right) - \lambda' a_0(t)b(t)$$

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Steady states

Trivial case: no movements

Absence of movements: $\alpha = r = 0$

$$\frac{\partial a(\boldsymbol{n}, t)}{\partial t} = \lambda a_0(t) b(t) \delta_{\boldsymbol{n},\mathbf{0}} - \mu a(\boldsymbol{n}, t)$$

- Populations vanishing outside prey patch at large t
- Inside the prey patch:

$$\frac{\partial a(\boldsymbol{n}, t)}{\partial t} = \lambda a_0(t) b(t) - \mu a_0(t) = 0 \iff a_0(t) \left(\lambda b(t) - \mu \right) = 0$$

i $a_0(t) = 0 \implies \left[\frac{\partial b(t)}{\partial t} = \sigma b(t) \left(1 - \frac{b(t)}{K} \right) = 0 \iff b(t) = 0 \vee b(t) = K \right]$

ii $b(t) = \frac{\mu}{\lambda} \implies \left[\frac{\partial b(t)}{\partial t} = \sigma \frac{\mu}{\lambda} \left(1 - \frac{\mu/\lambda + a_0(t)}{K} \right) - \lambda' \frac{\mu}{\lambda} a_0(t) = 0 \iff a_0(t) = \frac{K - \mu/\lambda}{1 + \lambda' K/\sigma} \right]$

General case

Prey steady states

- $b(t) = 0$
- $b(t) \neq 0 \Rightarrow \left[\frac{\partial b(t)}{\partial t} = 0 \overset{\cdot\frac{1}{b}}{\iff} \sigma\left(1 - \frac{b+a_0}{K}\right) - \lambda' a_0 = 0 \iff b = K - a_0\left(1 - \frac{\lambda' K}{\sigma}\right)\right]$

Predators steady states

1. Define the Fourier series whose coefficients are the a_ns: $\hat{a}(\boldsymbol{k}) := \sum_{\boldsymbol{n}} a_{\boldsymbol{n}} e^{-i\boldsymbol{k}\cdot\boldsymbol{n}}$
2. Obtain an expression for a_n from $\frac{\partial a_n(t)}{\partial t} = 0$ and $b = K - a_0\left(1 - \frac{\lambda' K}{\sigma}\right)$
3. Replace it in $\hat{a}(\boldsymbol{k})$
4. Get a new equation for $\hat{a}(\boldsymbol{k})$: $\hat{a}(\boldsymbol{k}) = \frac{\lambda a_0\left[K - a_0(1 + K\lambda'/\sigma)\right] + rA}{\alpha(1-p_0)[1-\hat{f}(\boldsymbol{k})] + \mu + r}$, where $A := \hat{a}(\mathbf{0})$
5. $A = \hat{a}(\mathbf{0}) = \frac{\lambda a_0\left[K - a_0(1 + K\lambda'/\sigma)\right] + rA}{\mu + r} \implies A = \frac{\lambda a_0}{\mu}\left[K - a_0\left(1 + K\lambda'/\sigma\right)\right]$

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Stationary predators density at prey patch

- Fourier coefficients: $a_{\boldsymbol{n}} = \frac{1}{(2\pi)^D} \int_B \hat{a}(\boldsymbol{k}) e^{-i\boldsymbol{k}\cdot\boldsymbol{n}} d\boldsymbol{k}$, where $B := (-\pi, \pi)^D$
- $a_{\boldsymbol{0}} = \frac{1}{(2\pi)^D} \int_B \hat{a}(\boldsymbol{k}) d\boldsymbol{k} =$

$$= \frac{1}{(2\pi)^D} \int_B \frac{\lambda a_0 \left[K - a_0(1 + K\lambda'/\sigma)\right] + r \cdot \frac{\lambda a_0}{\mu} \left[K - a_0 \left(1 + K\lambda'/\sigma\right)\right]}{\alpha(1-p_0)[1-\hat{f}(\boldsymbol{k})] + \mu + r} d\boldsymbol{k}$$

1. $a_0 = 0$
2. $a_0 \neq 0$

$$\implies a_0 = \frac{1}{1 + K\lambda'/\sigma} \left[K - \left(\frac{\lambda}{\mu(2\pi)^D} \int_B \frac{\mu + r}{\alpha(1-p_0)[1-\hat{f}(\boldsymbol{k})] + \mu + r} d\boldsymbol{k}\right)^{-1}\right]$$

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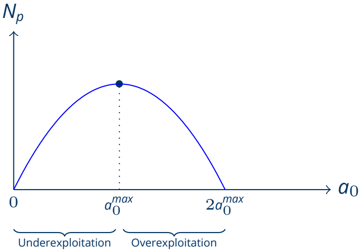
Total predators population

- Population in cell $\boldsymbol{n}$ = $R^D \cdot a_{\boldsymbol{n}}$
- Total population $N_p = \sum_{\boldsymbol{n}} R^D a_n = R^D \sum_{\boldsymbol{n}} a_n = R^D A = R^D \cdot \frac{\lambda a_0}{\mu} \left[K - a_0 \left(1 + K\lambda'/\sigma\right)\right]$
- $\frac{\partial N_p(a_0)}{\partial a_0} \implies a_0^{max} = \frac{K}{2(1+K\lambda'/\sigma)}$
- $N_p(a_0) = 0 \implies a_0 = 0 \vee a_0 = 2a_0^{max}$

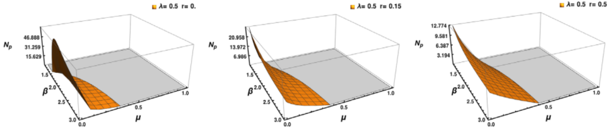


Experiments

Parameters setting

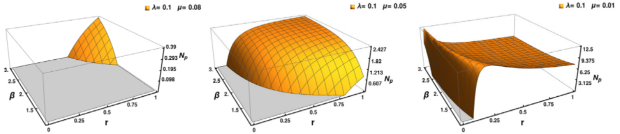
- $D = 1$
- $K = 1$
- $\sigma = 1$
- $R = 10$
- $f(x) = \begin{cases} \frac{\beta-1}{2}|x|^{-\beta} & |x| > 1 \\ 0 & |x| \leq 1 \end{cases}$
- $p_0 = \frac{2}{R}\int_0^R dr \int_0^r f(x)dx = \begin{cases} 1 - \dfrac{1}{R} + \dfrac{1 - R^{2-\beta}}{(2-\beta)R} & \beta \neq 2 \\ 1 - \dfrac{1}{R} - \dfrac{\log R}{R} & \beta = 2 \end{cases}$

Total predators population in the (μ, β)-plane



(a) (b) (c)

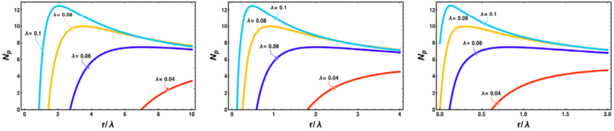
Total predators population in the (β, r)-plane



(a) (b) (c)

Total predators population as function of r/λ

- $\mu = 0.01$ $\beta = 1.1$ $\beta = 2$ $\beta = 3$



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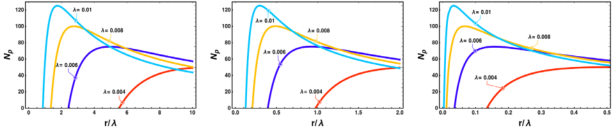
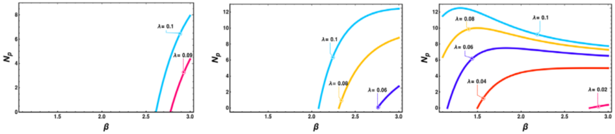


(a) (b) (c)

Total predators population as function of β

- $\mu = 0.01$ $\quad r = 0$ $\quad r = 0.01$ $\quad r = 0.15$



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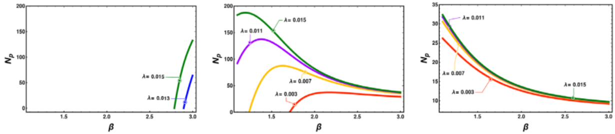

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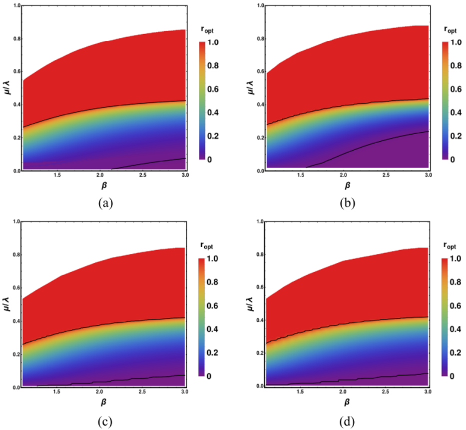
Optimal resetting rate



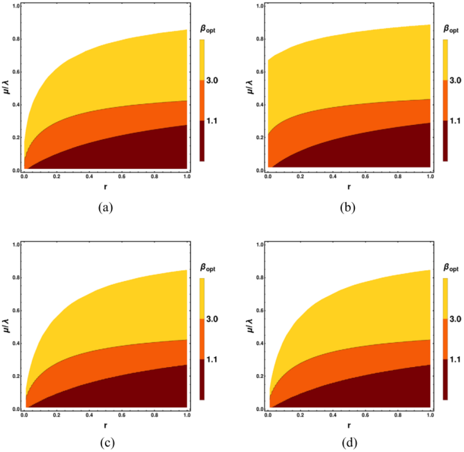
(a) $\lambda = 0.1$

(b) $\lambda = 0.5$

(c) $\lambda = 0.0001$

(d) $\lambda = 0.0005$

Optimal Lévy exponent



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(b) $\lambda = 0.5$

(c) $\lambda = 0.0001$

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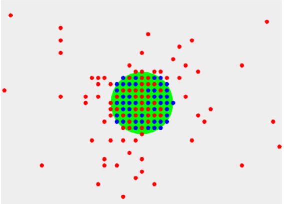
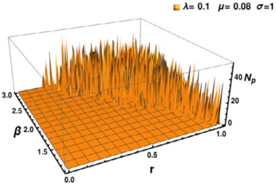
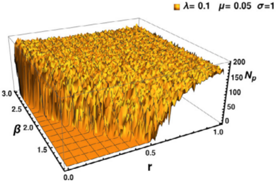
Monte Carlo simulations of 2D stochastic population model



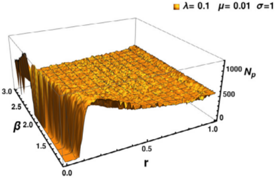
(a) $\lambda = 0.1$, $\mu = 0.01$, $r = 0.05$, $\beta = 2$



(b) $\lambda = 0.1$, $\mu = 0.08$ and $\sigma = 1$

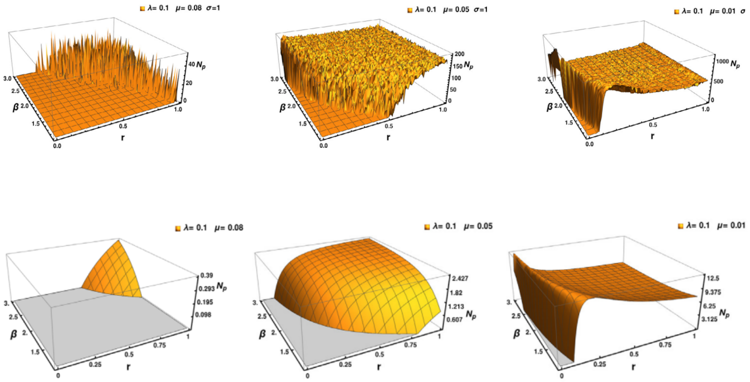


(c) $\lambda = 0.1$, $\mu = 0.05$ and $\sigma = 1$



(d) $\lambda = 0.1$, $\mu = 0.01$ and $\sigma = 1$

2D stochastic model VS 1D deterministic model



(a) (b) (c)

Grazie per l’attenzione!

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$$\sigma \cancel{b(t)}\left(1-\frac{b(t)+a_0(t)}{K}\right)-\lambda' a_0(t)\cancel{b(t)}=0$$

$$\sigma K-\sigma b(t)-\sigma a_0(t)-\lambda' K a_0(t)=0$$

$$\Rightarrow \quad a_0(t)\cancel{(\sigma+\lambda' K)}=\frac{\sigma K-\sigma b(t)}{\sigma+\lambda' K}=\frac{K-b(t)}{1+\lambda'\frac{K}{\sigma}}$$

$$\lambda a_0 b\,\delta_{m,0}-\mu a(m,t)=0 \quad \begin{cases} m=0 & (\lambda b-\mu)\dfrac{(K-b(t))}{1+\lambda'\frac{K}{\sigma}}=0 \Rightarrow b=\mu/\lambda \\ & \Rightarrow a_0(t)=\dfrac{K-\mu/\lambda}{1+\lambda'\frac{K}{\sigma}} \\ m\neq 0 & \mu a(m,t)=0 \Rightarrow a=0 \end{cases}$$

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$$\frac{\mathrm{d}b}{\mathrm{d}t}=\sigma b\left(1-\frac{b+a_0}{K}\right)-\lambda' a_0 b=0$$

- $b=0 \Rightarrow \frac{db}{dt}=0 \rightsquigarrow$ fixed point
- $b\neq 0 \Rightarrow \Big[\frac{db}{dt}=0 \iff \sigma\left(1-\frac{b+a_0}{K}\right)-\lambda' a_0=0 \iff \sigma-\frac{\sigma}{K}b-\frac{\sigma}{K}a_0-\lambda' a_0=0$
  $\iff K-b-a_0-\frac{\lambda' K}{\sigma}a_0=0 \iff \boxed{b=K-a_0\left(1-\frac{\lambda' K}{\sigma}\right)}\Big]$

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$$\frac{\partial a(\mathbf{n},t)}{\partial t} = -\overbrace{\alpha(1-p_0)a(\mathbf{n},t)}^{\text{1st term}} + \overbrace{\alpha \sum_{\mathbf{l},|\mathbf{l}|\neq 0} p(\mathbf{l})a(\mathbf{n}-\mathbf{l},t)}^{\text{2nd term}}$$

$$+ \underbrace{\lambda a_0(t)b(t)\delta_{\mathbf{n},\mathbf{0}}}_{\text{3rd term}} - \underbrace{\mu a(\mathbf{n},t)}_{\text{4th term}} - \underbrace{r a(\mathbf{n},t)}_{\text{5th term}} + \underbrace{\left[r \sum_m a(\mathbf{m},t) \right] \delta_{\mathbf{n},0}}_{\text{6th term}} .$$

$$(*) = -\alpha(1-p_0)a_n + \alpha \sum_l p(l) a_{n-l} + \lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right)\delta_{n,0}$$

$$-\mu a_n - r a_n + \left(r \sum_m a_m\right)\cdot \delta_{n,0} = 0$$

$$\overset{n\neq 0}{\Longrightarrow} a_n\left(\alpha(1-p_0)+\mu+r\right) = \alpha \sum_{l\neq 0} p(l) a_{n-l}$$

$$p(\mathbf{l}) = p_0\delta_{\mathbf{l},\mathbf{0}} + (1-p_0) f(\mathbf{l})$$

$$\Rightarrow a_n = \begin{cases} \dfrac{\alpha \sum_{l\neq 0} p(l) a_{n-l}}{\alpha(1-p_0)+\mu+r} = \dfrac{\alpha \sum_{l\neq 0} (1-p_0) f(l)\, a_{n-l}}{\alpha(1-p_0)+\mu+r} & \text{if } n\neq 0 \\[2ex] \dfrac{\alpha \sum_{l\neq 0} (1-p_0) f(l)\, a_{-l} + \lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum a_m}{\alpha(1-p_0)+\mu+r} & \text{if } n = 0 \end{cases}$$

$$\hat{a}(\tilde{\mathbf{k}}) \equiv \sum_{\mathbf{n}} a_{\mathbf{n}} e^{-i\tilde{\mathbf{k}}\cdot\mathbf{n}}$$

$$= \underbrace{\sum_{n\neq 0} \frac{\alpha \sum_{\ell\neq 0}(1-p_0) f(\ell)\, a_{n-\ell}}{\alpha(1-p_0)+\mu+r}\, e^{-i\tilde{k}n}}_{1)} + \underbrace{\frac{\alpha\sum_{\ell\neq 0}(1-p_0) f(\ell)\, a_\ell + \lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)+\mu+r}}_{2)}$$

1)

$$e^{-i\tilde{k}n} = e^{-i\tilde{k}(n-\ell)}\, e^{-i\tilde{k}\ell}$$

$$1) = \sum_{n\neq 0} \frac{\alpha(1-p_0)\sum_{\ell\neq 0} f(\ell)\, a_{n-\ell}\, e^{-i\tilde{k}(n-\ell)} e^{-i\tilde{k}\ell}}{\alpha(1-p_0)+\mu+r}$$

$$= \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r} \sum_{\ell\neq 0} f(\ell)\, e^{-i\tilde{k}\ell} \sum_{n\neq 0} a_{n-\ell}\, e^{-i\tilde{k}(n-\ell)}$$

2)

$$2) = \frac{\alpha(1-p_0)\sum_{\ell\neq 0} f(\ell)\, a_\ell + \lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)+\mu+r}$$

$$= \underbrace{\frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r} \sum_{\ell\neq 0} f(\ell)\, a_{-\ell}\, e^{-i\tilde{k}\ell}\, e^{-i\tilde{k}(0-\ell)}}_{3)} + \underbrace{\frac{\lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)+\mu+r}}_{4)}$$

1) + 3)

$$1)+3) = \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\left(\sum_{\ell\neq 0} f(\ell)e^{-i\tilde{k}\ell}\sum_{n\neq 0} a_{n-\ell}e^{-i\tilde{k}(n-\ell)} + \sum_{\ell\neq 0} f(\ell)e^{-i\tilde{k}\ell} a_{-\ell}e^{-i\tilde{k}(0-\ell)}\right)$$

$$= \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\left[\sum_{\ell\neq 0} f(\ell)e^{-i\tilde{k}\ell}\left(\sum_{n\neq 0} a_{n-\ell}e^{-i\tilde{k}(n-\ell)} + a_{-\ell}e^{-i\tilde{k}(0-\ell)}\right)\right]$$

$$= \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\left[\sum_{\ell\neq 0} f(\ell)e^{-i\tilde{k}\ell}\underbrace{\sum_{n} a_{n-\ell}e^{-i\tilde{k}(n-\ell)}}_{\hat{a}(\tilde{k})}\right]$$

(translation is the identity since we are summing over $\mathbb{Z}$).

$f(0)=0$

$$\overset{\downarrow}{=} \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\hat{a}(\tilde{k})\underbrace{\sum_{\ell} f(\ell)e^{-i\tilde{k}\ell}}_{\hat{f}(\tilde{k})} = \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\hat{a}(\tilde{k})\hat{f}(\tilde{k})$$

4 + 5

$$\Longrightarrow \hat{a}(\tilde{k}) = \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\,\hat{f}(\tilde{k})\,\hat{a}(\tilde{k}) + \frac{\lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)+\mu+r}$$

$$\Longrightarrow \hat{a}(\tilde{k})\left(1 - \frac{\alpha(1-p_0)}{\alpha(1-p_0)+\mu+r}\,\hat{f}(\tilde{k})\right) = \frac{\lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)+\mu+r}$$

$$\Longrightarrow \hat{a}(\tilde{k})\left(\frac{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r}{\alpha(1-p_0)+\mu+r}\right) = \frac{\lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)+\mu+r}$$

$$\Longrightarrow \hat{a}(\tilde{k}) = \frac{\lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + r\sum_m a_m}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r} = \frac{\lambda a_0\left[K - a_0(1+K\lambda'/\sigma)\right] + rA}{\alpha(1-p_0)\left[1-\hat{f}(\mathbf{k})\right]+\mu+r},$$

$$\square$$

$$A := \sum_m a_m = \hat{a}(0) = \frac{\lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + rA}{\mu+r}$$

$$\Longrightarrow \mu A + \cancel{rA} = \lambda a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right) + \cancel{rA}$$

$$\Longrightarrow A = \frac{\lambda a_0}{\mu}\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right)$$

$$\sqrt{2\pi}\, a_n = \left\langle \hat{a}(k), \frac{e^{ink}}{\sqrt{2\pi}} \right\rangle = \frac{1}{\sqrt{2\pi}} \int_{-\pi}^{\pi} \hat{a}(k)\, e^{-ink}\, dk$$

$$\Longrightarrow a_n = \frac{1}{2\pi} \int_{-\pi}^{\pi} \hat{a}(k)\, e^{-ink}\, dk$$

$$a_0 = \frac{1}{(2\pi)^D}\int_B \hat{a}(\tilde{k})\,d\tilde{k} = \frac{1}{(2\pi)^D}\int_B \frac{\lambda a_0\left[K - a_0(1+K\lambda'/\sigma)\right] + rA}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{\mathbf{k}})\right]+\mu+r}\,d\tilde{k}$$

$$= \frac{1}{(2\pi)^D}\int_B \frac{\lambda a_0\left[K - a_0(1+K\lambda'/\sigma)\right] + r\frac{\lambda}{\mu}a_0\left(K - a_0\left(1+\frac{K\lambda'}{\sigma}\right)\right)}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r}\,d\tilde{k}$$

- $a_0 = 0 \rightsquigarrow$ ok
- $a_0 \neq 0 \rightsquigarrow$

$$1 = \frac{\lambda}{(2\pi)^D}\left[\int_B \frac{K(1+r/\mu)\,d\tilde{k}}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r} - (1+K\lambda'/\sigma)\int_B \frac{\left(1+\frac{r}{\mu}\right)d\tilde{k}}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r}\,a_0\right]$$

$$\Longrightarrow 1 = \frac{\lambda}{\mu(2\pi)^D}\int_B \frac{\mu+r}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r}\,d\tilde{k}\cdot\left[K - (1+K\lambda'/\sigma)a_0\right]$$

$$\Longrightarrow a_0 = \frac{1}{1+K\lambda'/\sigma}\left[K - \left(\frac{\lambda}{\mu(2\pi)^D}\int_B \frac{\mu+r}{\alpha(1-p_0)\left[1-\hat{f}(\tilde{k})\right]+\mu+r}\,d\tilde{k}\right)^{-1}\right]$$