The University of Texas at Austin
Oden Institute for Computational Engineering and Sciences

Life history strategies in an explicit patch age model

Coexistence generating trade-offs with the age of first reproduction

Jon Staggs[1], Mihn Chau N. Ho[2], Daniel Smith[1], Annette Ostling[1,2]
[1]Oden Institute at UT Austin, [2]Dept. of Integrative Biology at UT Austin

Email: jon.staggs@utexas.edu

Staggering Diversity

Tropical forests are hyper diverse ecosystems

Photos from STRIs website

Staggering Diversity

Tropical forests are hyper diverse ecosystems

Barro Colorado Island (BCI), Panama has ~300 tree species in 50 hectare

Photos from STRIs website

Life History Variation

We have lots of species that are limited by the same resources (e.g. everyone needs light)

Life History Variation

We have lots of species that are limited by the same resources (e.g. everyone needs light)

However, species differ in *when* and *how* they take advantage of resource availability

Life History Variation

We have lots of species that are limited by the same resources (e.g. everyone needs light)

However, species differ in *when* and *how* they take advantage of resource availability

This defines a species ***life history strategy***

- schedule and investment in survival, growth, and reproduction over a species lifetime

Successional Niche

A classical life history strategy in a disturbance driven environment is the ***successional niche*** (*Pacala & Rees 1998)*

Successional Niche

A classical life history strategy in a disturbance driven environment is the ***successional niche*** (*Pacala & Rees 1998)*

Successional niche is a species ability to specializing on particular patch age (age is amount of time since last disturbed)

Successional Niche

A classical life history strategy in a disturbance driven environment is the ***successional niche*** (*Pacala & Rees 1998)*

Successional niche is a species ability to specializing on particular patch age (age is amount of time since last disturbed)

Species differ in their success across the patch age gradient:
Some excel in newly disturbed, high resource patches;
Others in older, shaded patches

Successional Niche

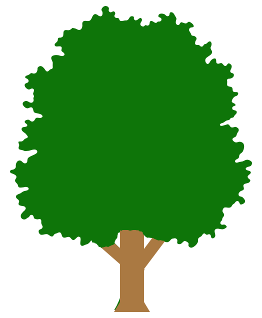
- Early successional: Fast growth in high light, high fecundity, shade intolerant

Successional Niche

- Early successional: Fast growth in high light, high fecundity, shade intolerant
- Late successional: Slow growth, low fecundity, shade tolerant, long lifespan

Successional Niche

 Early successional: Fast growth in high light, high fecundity, shade intolerant

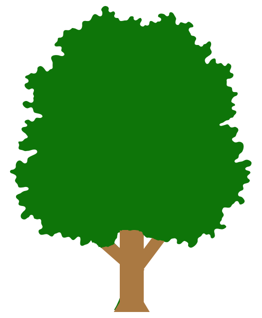
 Late successional: Slow growth, low fecundity, shade tolerant, long lifespan

Young Patch/Recently disturbed

Old Patch

Successional Niche

 Early successional: Fast growth in high light, high fecundity, shade intolerant

 Late successional: Slow growth, low fecundity, shade tolerant, long lifespan

Successional strategies originally formulated only as a verbal model so we lack modeling of specific demographic processes that drive successional niche

Young Patch/Recently disturbed

Old Patch

Reproductive Schedule as an important trade off axis

We add demographic specificity to the successional niche framework by proposing a concrete life history trait:
Age of first reproduction, τ

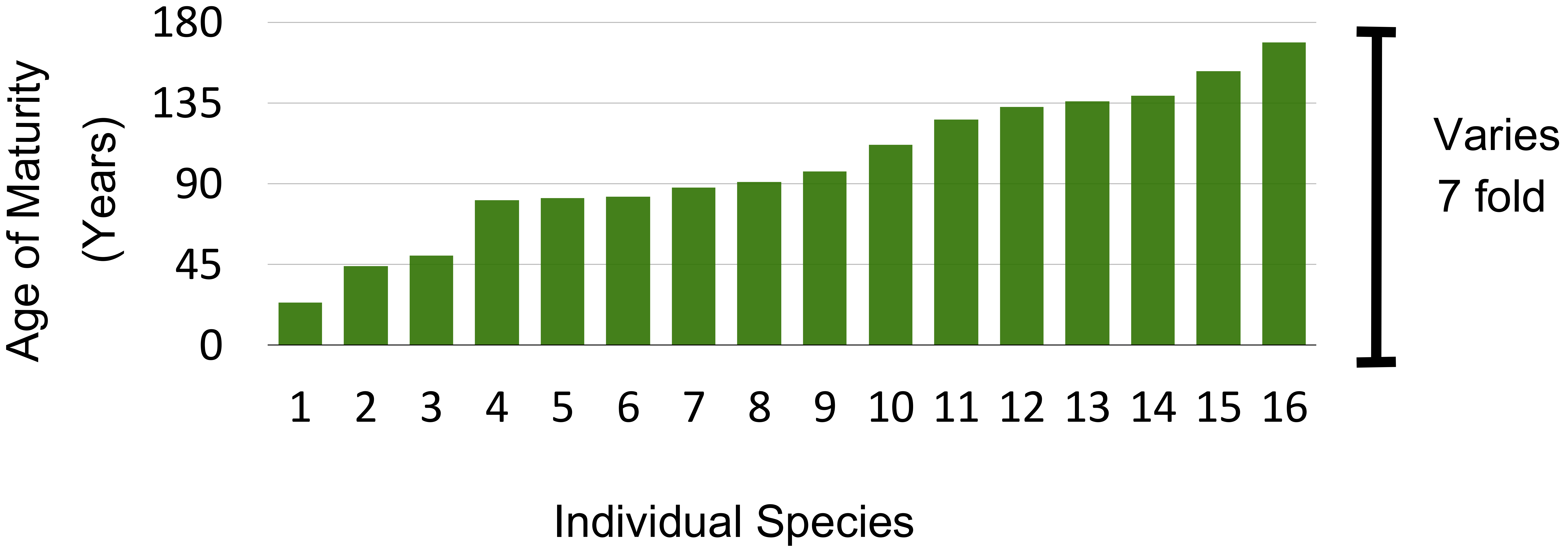
Reproductive Schedule as an important trade off axis

We add demographic specificity to the successional niche framework by proposing a concrete life history trait:
<u>Age of first reproduction, τ</u>

After a disturbance opens up access to high resource conditions,
the age of reproductive maturity controls who can capitalize first and who must invest longer before entering the reproductive pool

Reproductive Schedule as an important trade off axis

Age of first reproduction varies 7 fold for tree species on BCI (*Condit et al. 2025*)



Main Question:

How does the age of first reproduction shape trade offs that allow species to coexist under disturbance?

Main Question:

How does the age of first reproduction shape trade offs that allow species to coexist under disturbance?

i.e. What do species gain/give up when they accelerate/delay their reproductive schedule in an environment subject to disturbance?

Main Question - Key Parameters

We consider age of first reproduction, τ, to be the key trait we trade off against.

Main Question - Key Parameters

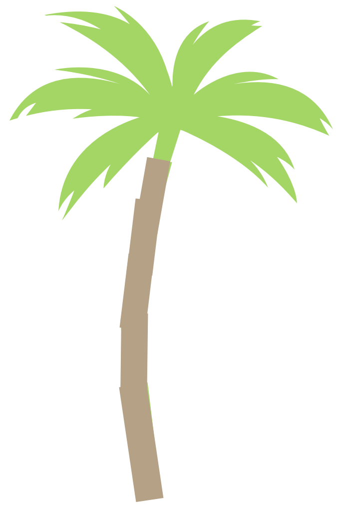
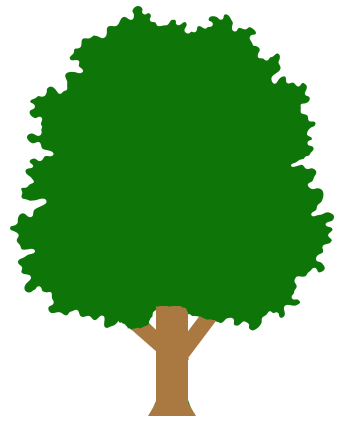
We consider age of first reproduction, τ, to be the key trait we trade off against.

Formulating a verbal model: what demographic rates should change as τ shifts?

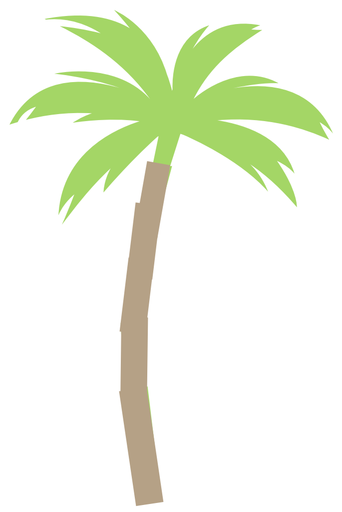
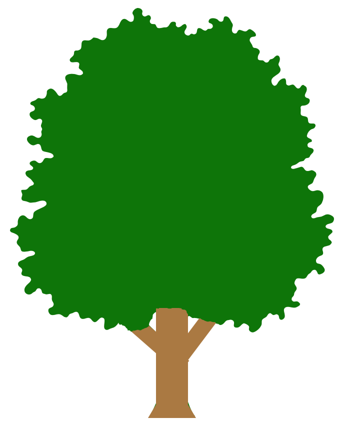
As $\tau \uparrow$ how does a species compensate for missed reproductive opportunity?

Main Question - Key Parameters

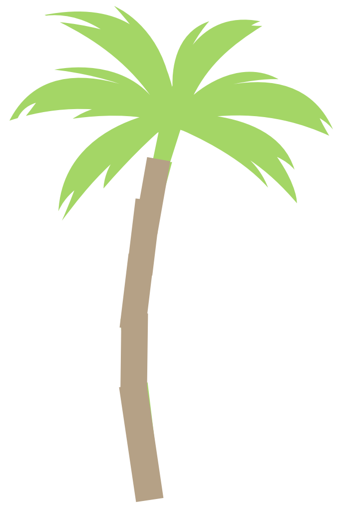
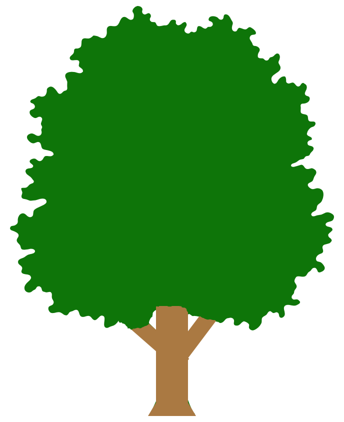
Age of first reproduction
τ

Early Successional 	Early Reproduction (Small τ)		
Late Successional 	Late Reproduction (Large τ)		

Main Question - Key Parameters

	Age of first reproduction τ	Recruitment to adulthood b	
Early Successional 	Early Reproduction (Small τ)	Low Recruitment (Small b)	
Late Successional 	Late Reproduction (Large τ)	High Recruitment (Large b)	

Main Question - Key Parameters

	Age of first reproduction τ	Recruitment to adulthood b	Adult Mortality μ
Early Successional 	Early Reproduction (Small τ)	Low Recruitment (Small b)	High Mortality (Large μ)
Late Successional 	Late Reproduction (Large τ)	High Recruitment (Large b)	Low Mortality (Small μ)

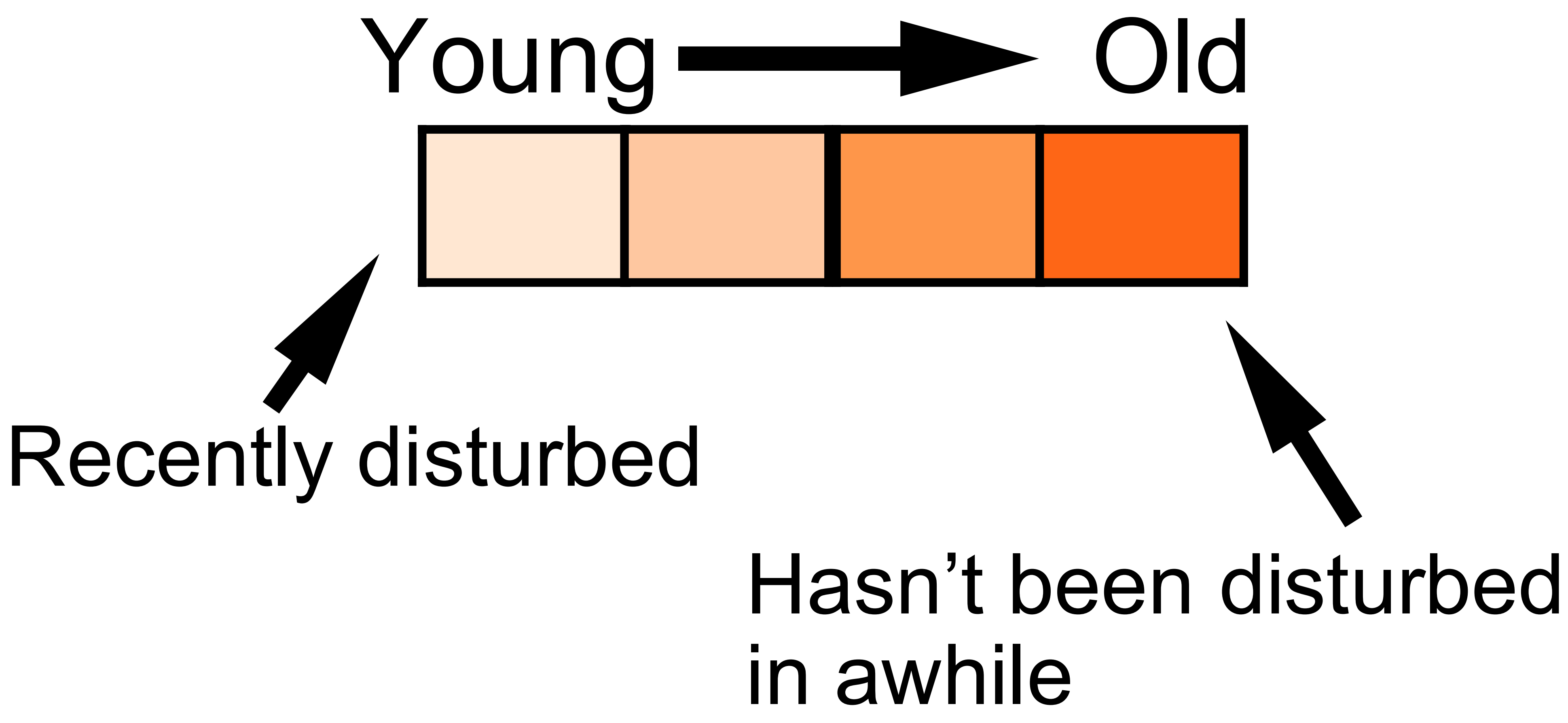
Our Model - Overview

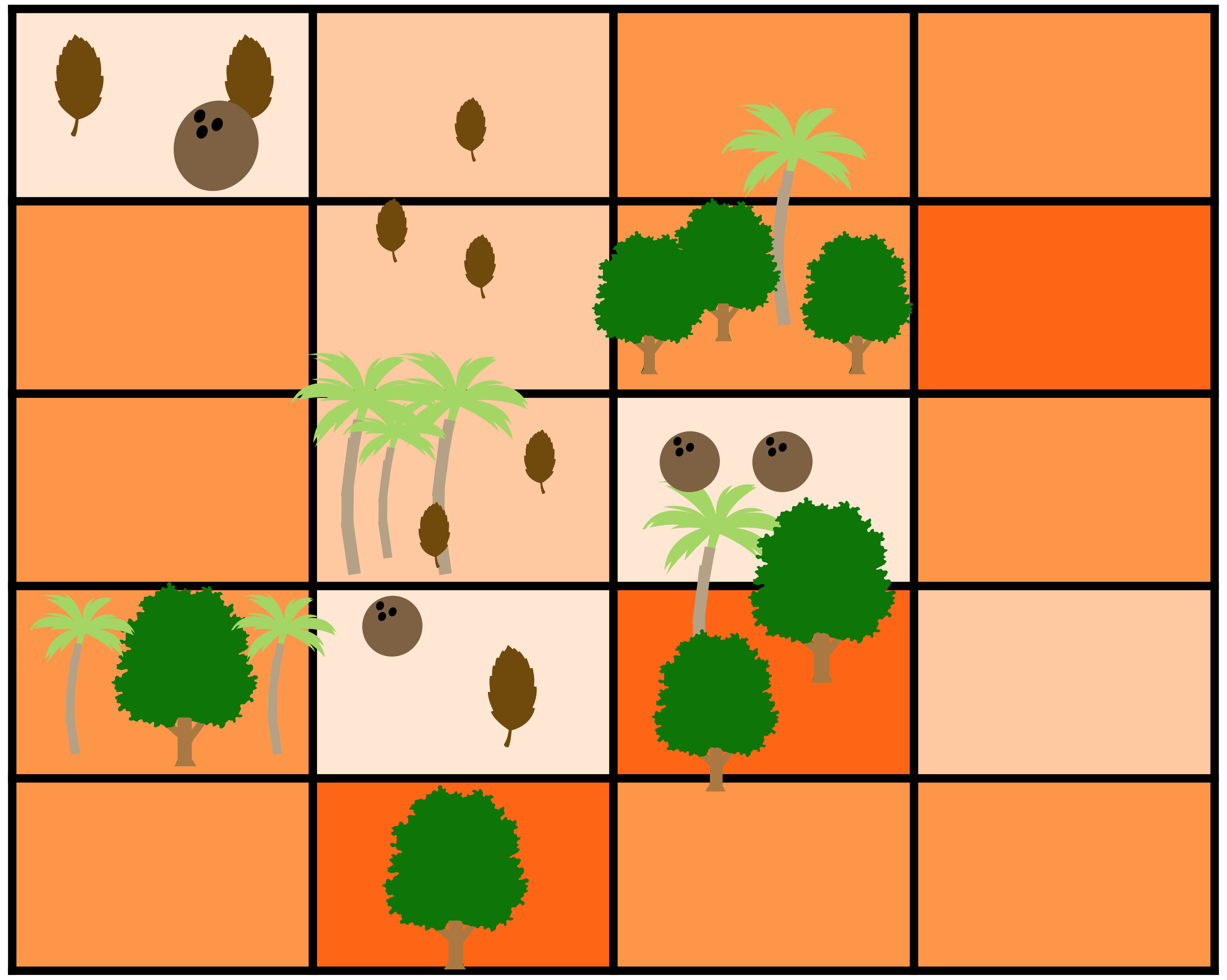
We will take the age structured metapopulation model introduced in *Trigos-Raczkowski et al. (preprint)* and extend it to include maturation time, τ.

Our Model - Overview

We will take the age structured metapopulation model introduced in *Trigos-Raczkowski et al. (preprint)* and extend it to include maturation time, τ.

We have a landscape made up of patches with different ages



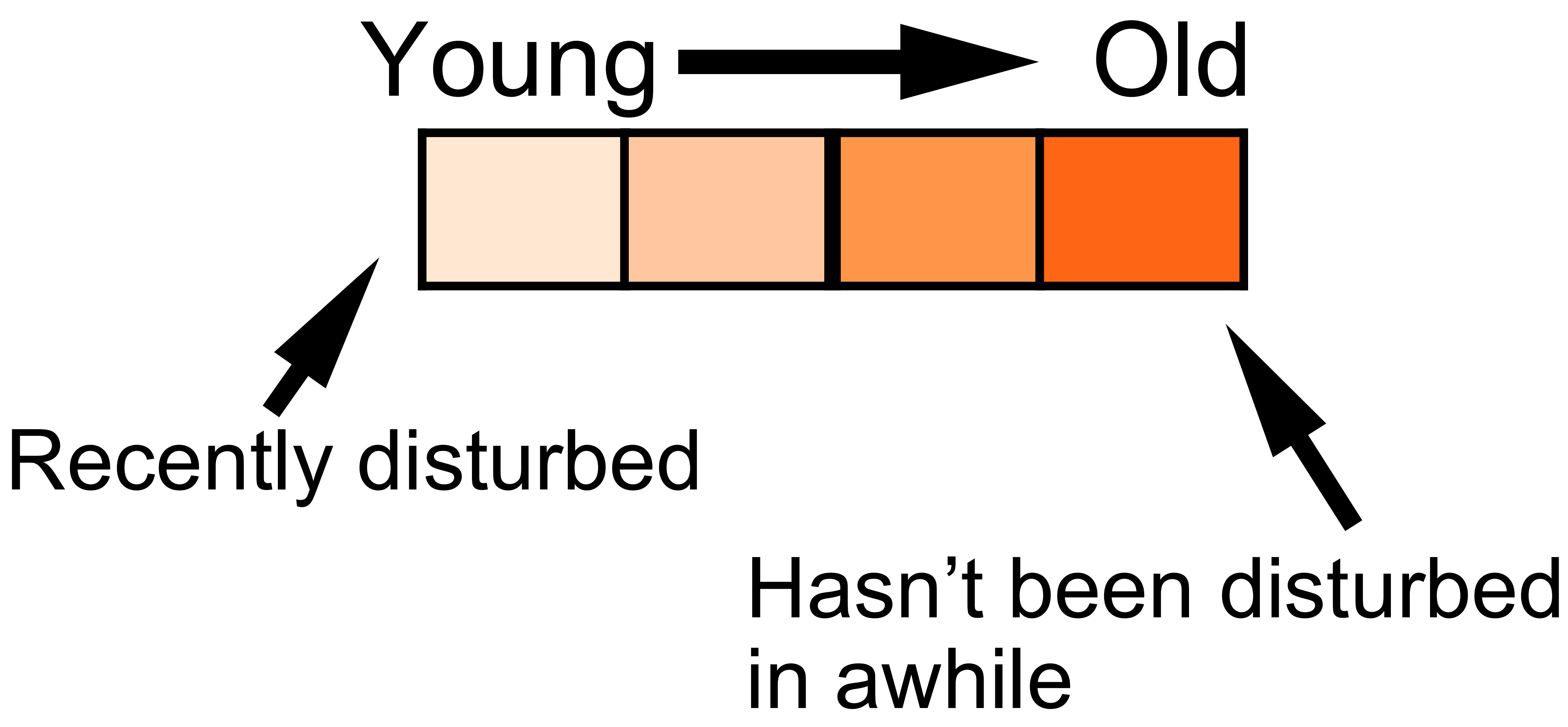


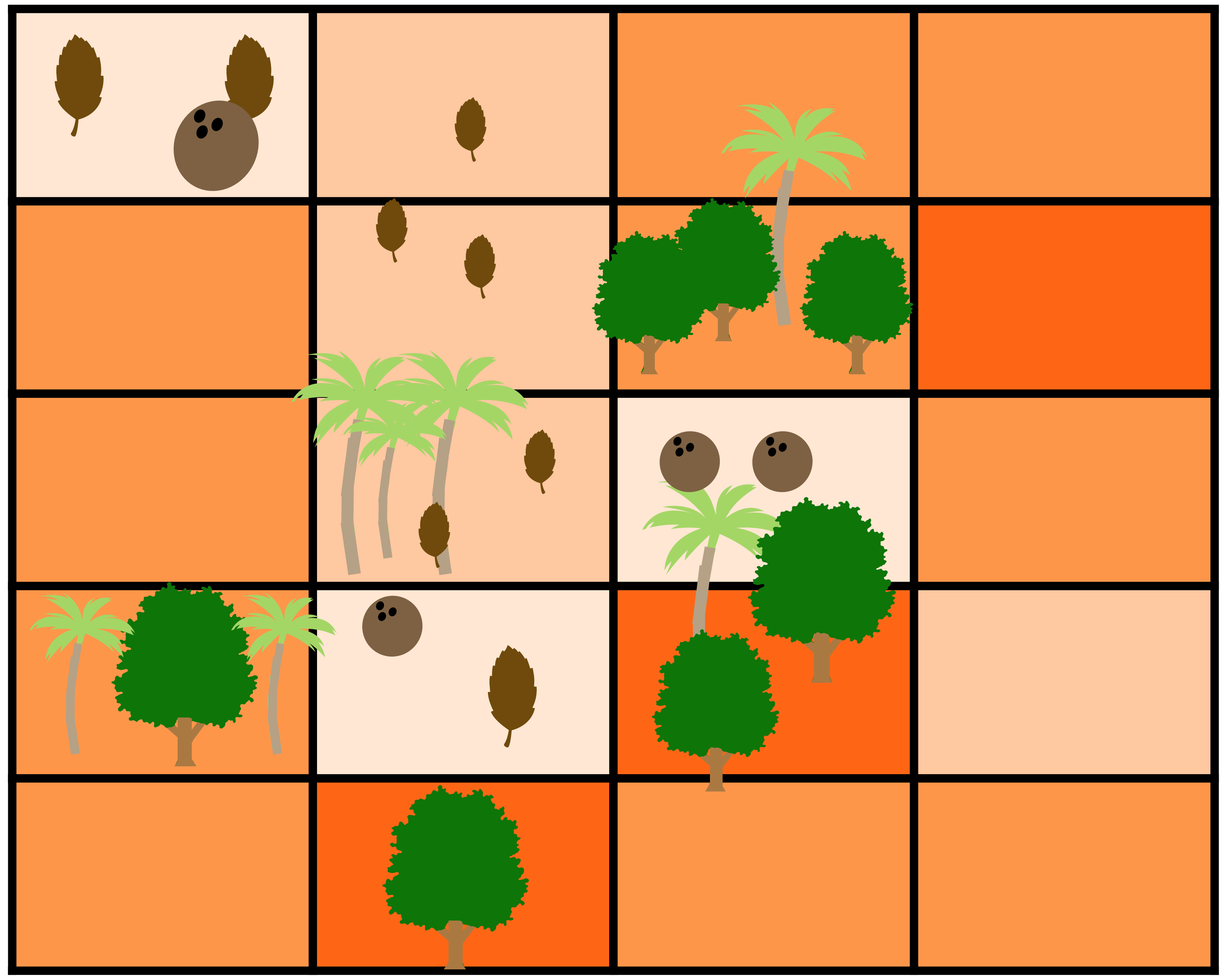
Our Model - Overview

We will take the <u>age structured metapopulation</u> model introduced in *Trigos-Raczkowski et al. (preprint)* and <u>extend it to include maturation time, τ.</u>

We have a landscape made up of patches with different ages

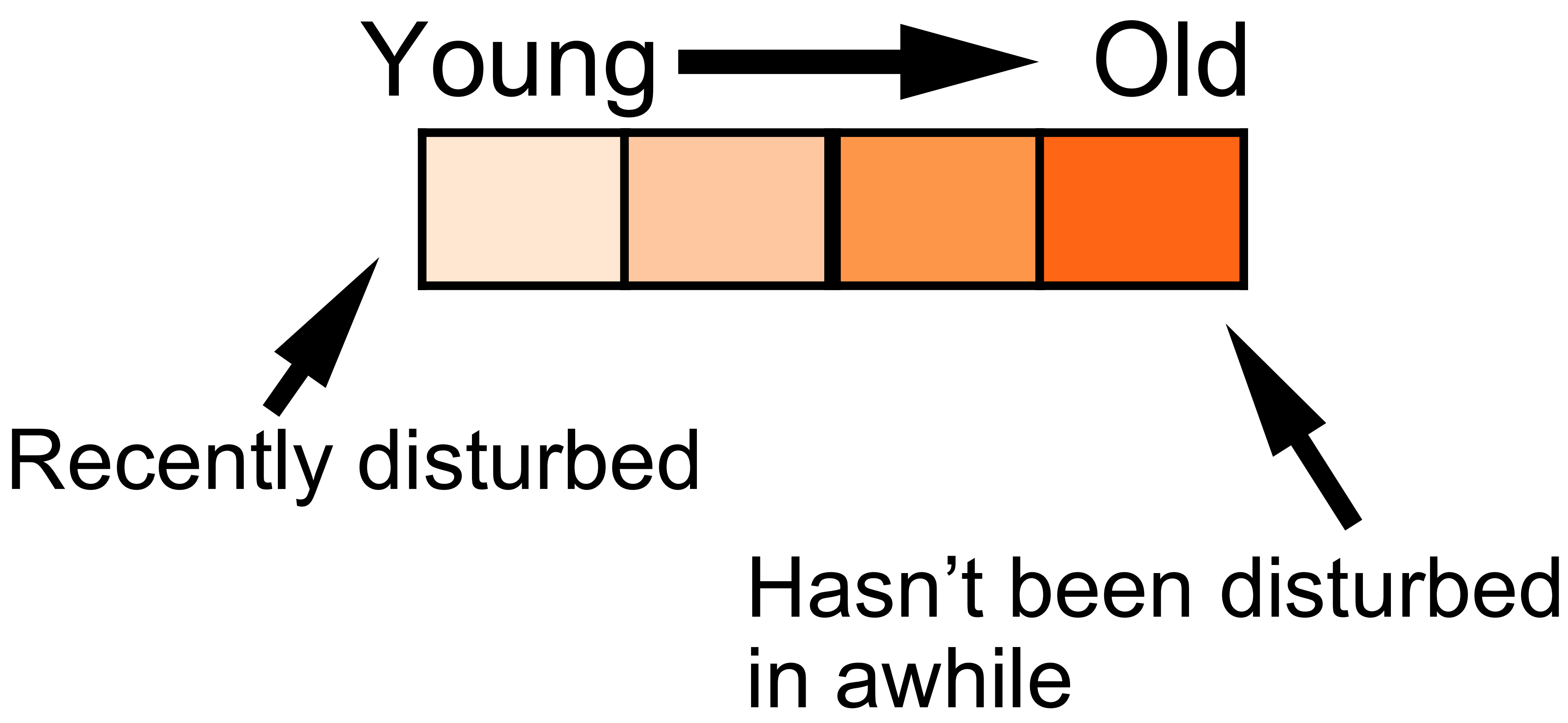
- Patch age means age since being disturbed

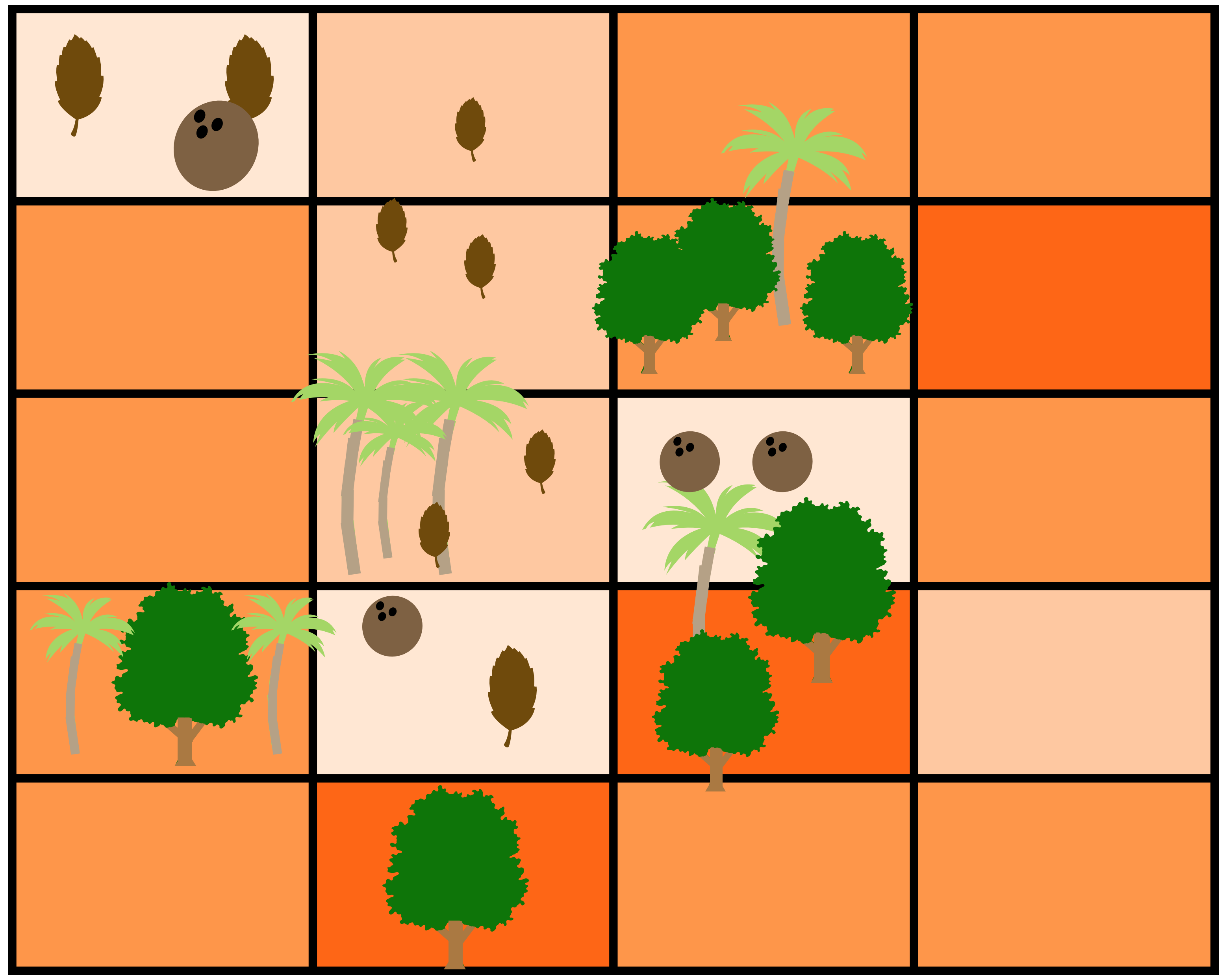




Our Model - Overview

On each patch we have a local population



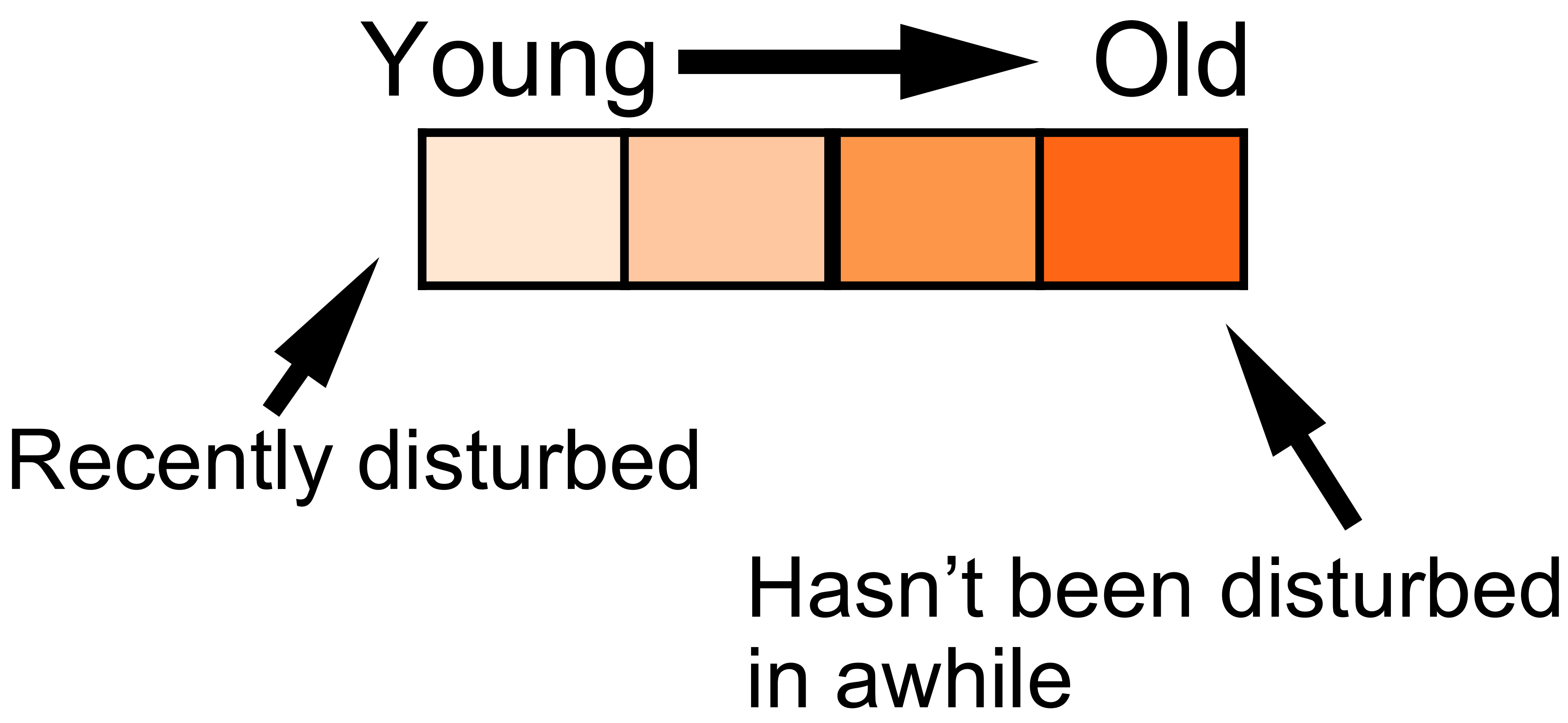


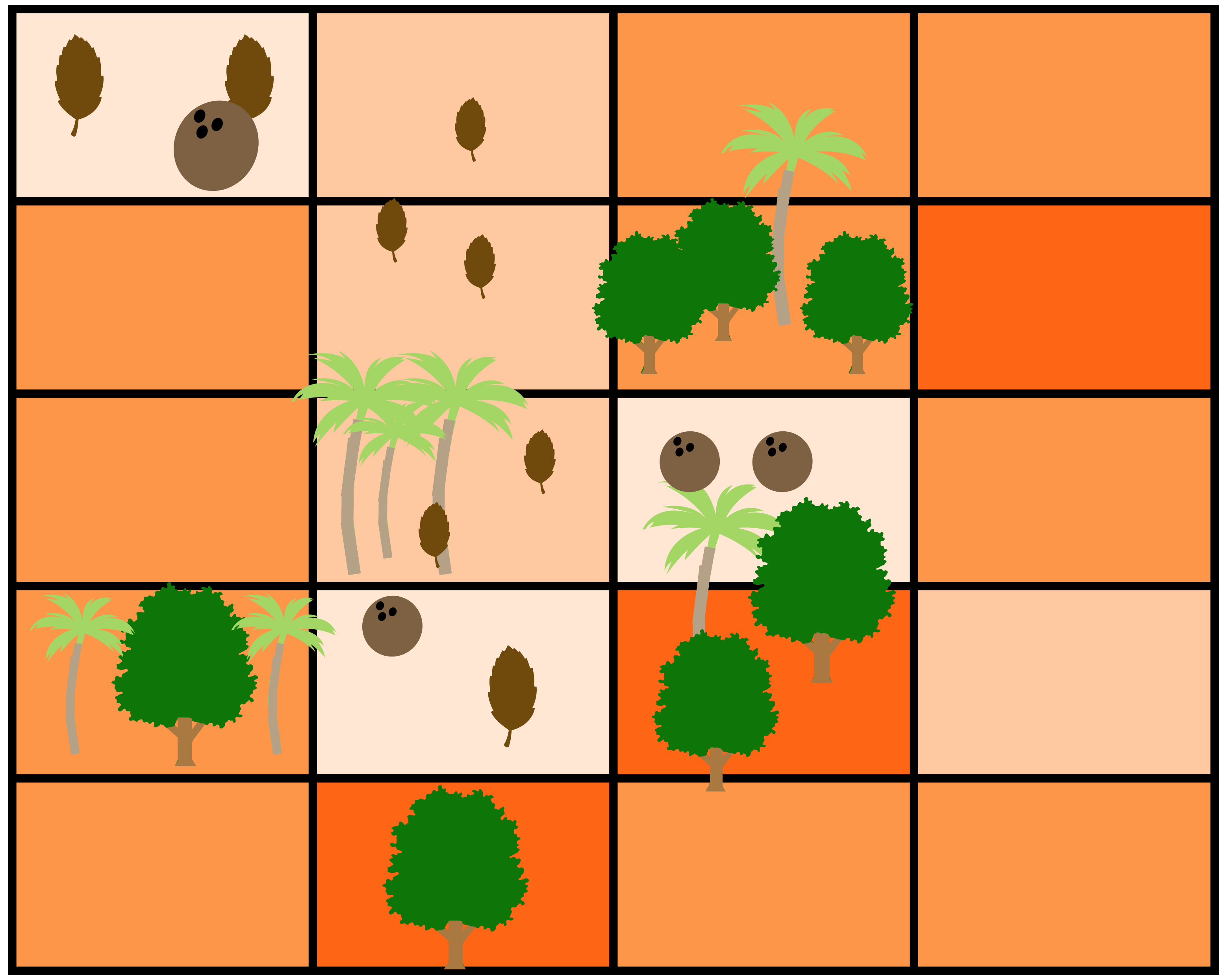
Our Model - Overview

On each patch we have a local population

Local populations will be governed by competitive dynamics

- *Individuals will age, reproduce, and die*



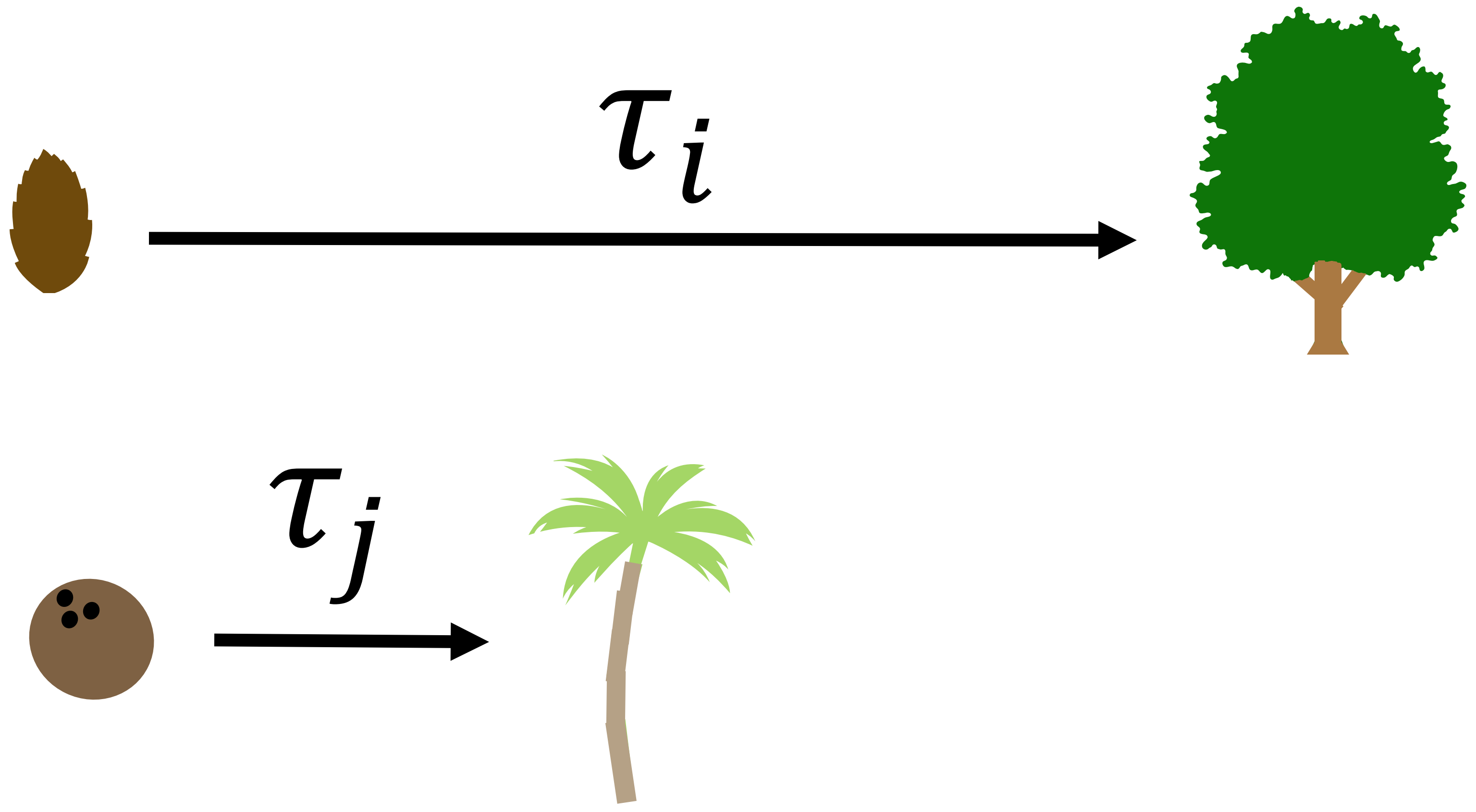


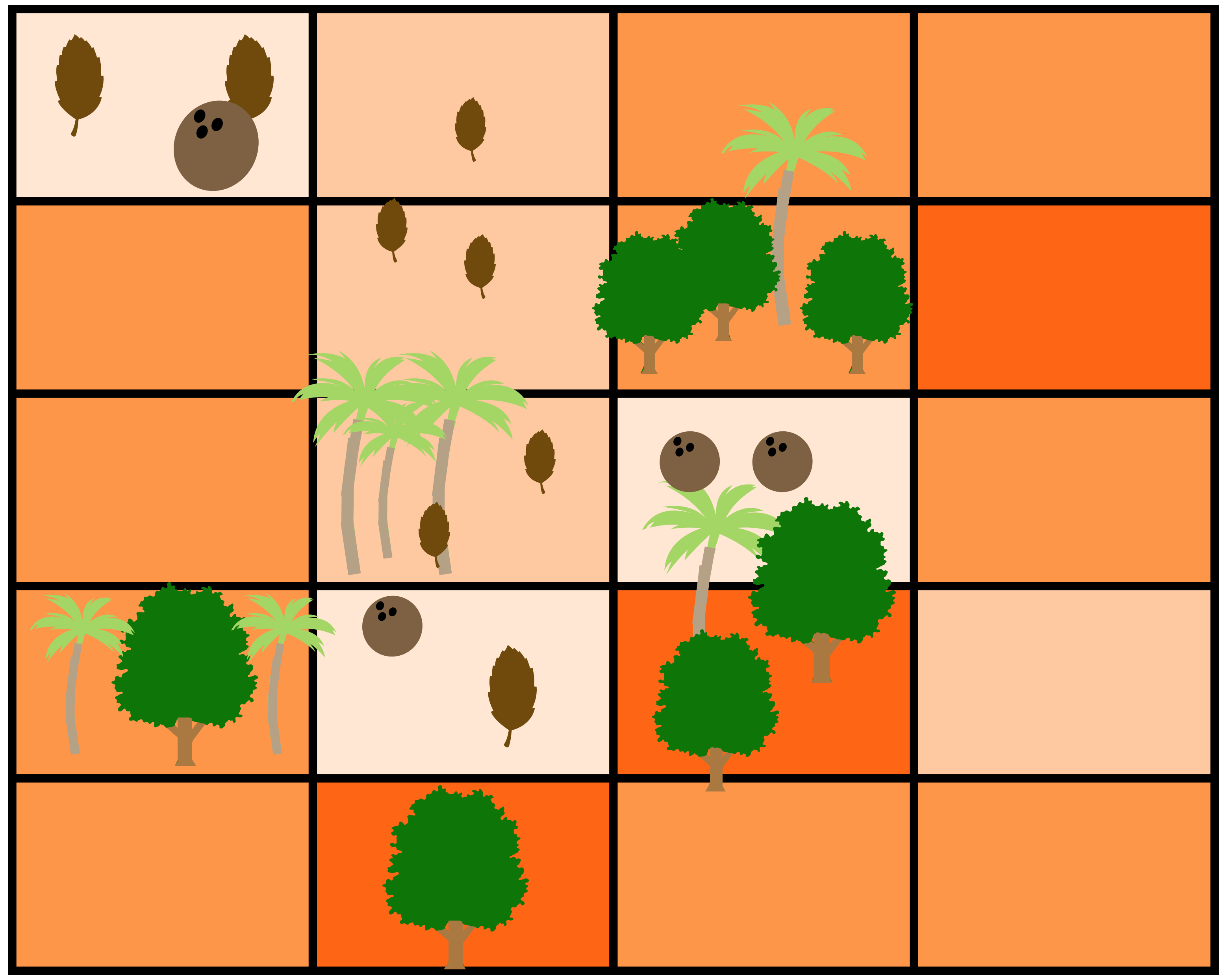
Our Model - Overview

On each patch we have a local population

Local populations will be governed by competitive dynamics

- *Individuals will age, reproduce, and die*
- <u>*Reaching reproductive maturity **takes time***</u>





Our Model - Overview

The model is a system of partial differential equations (PDEs) with two main components:

1. Patch Dynamics: McKendrick Von - Foerster PDE describing the change in the patch age frequencies.

2. Population Dynamics: Describes change (density dependent) in adult abundance of each species on each patch age

Our Model - Patch Dynamics

Let $\rho = \rho(a, t)$ be the density of patch ages. The evolution of this density is described by the following McKendrick Von - Foerster PDE:

$$\frac{\partial}{\partial t}\rho = -\frac{\partial}{\partial a}\rho - \gamma\rho$$

$$\rho(a, 0) = \rho_0(a)$$

$$\rho(0, t) = \int_0^\infty \gamma\rho(s, t)\mathrm{d}s$$

Our Model - Patch Dynamics

Let $\rho = \rho(a,t)$ be the density of patch ages. The evolution of this density is described by the following McKendrick Von - Foerster PDE:

Patches age

Patches get disturbed at rate γ

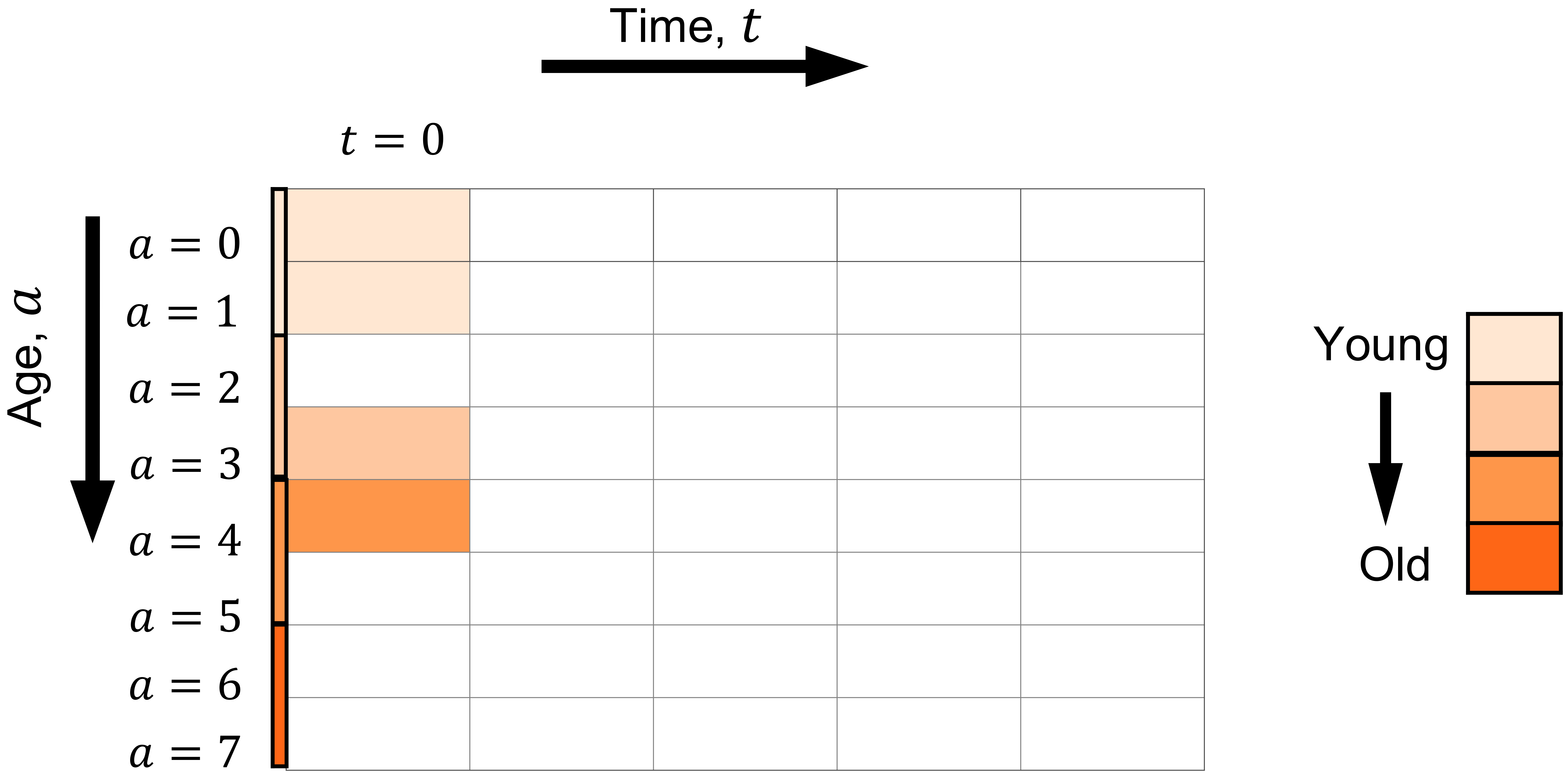
$$\frac{\partial}{\partial t}\rho = -\frac{\partial}{\partial a}\rho - \gamma\rho$$

$$\rho(a,0) = \rho_0(a)$$ Initial condition

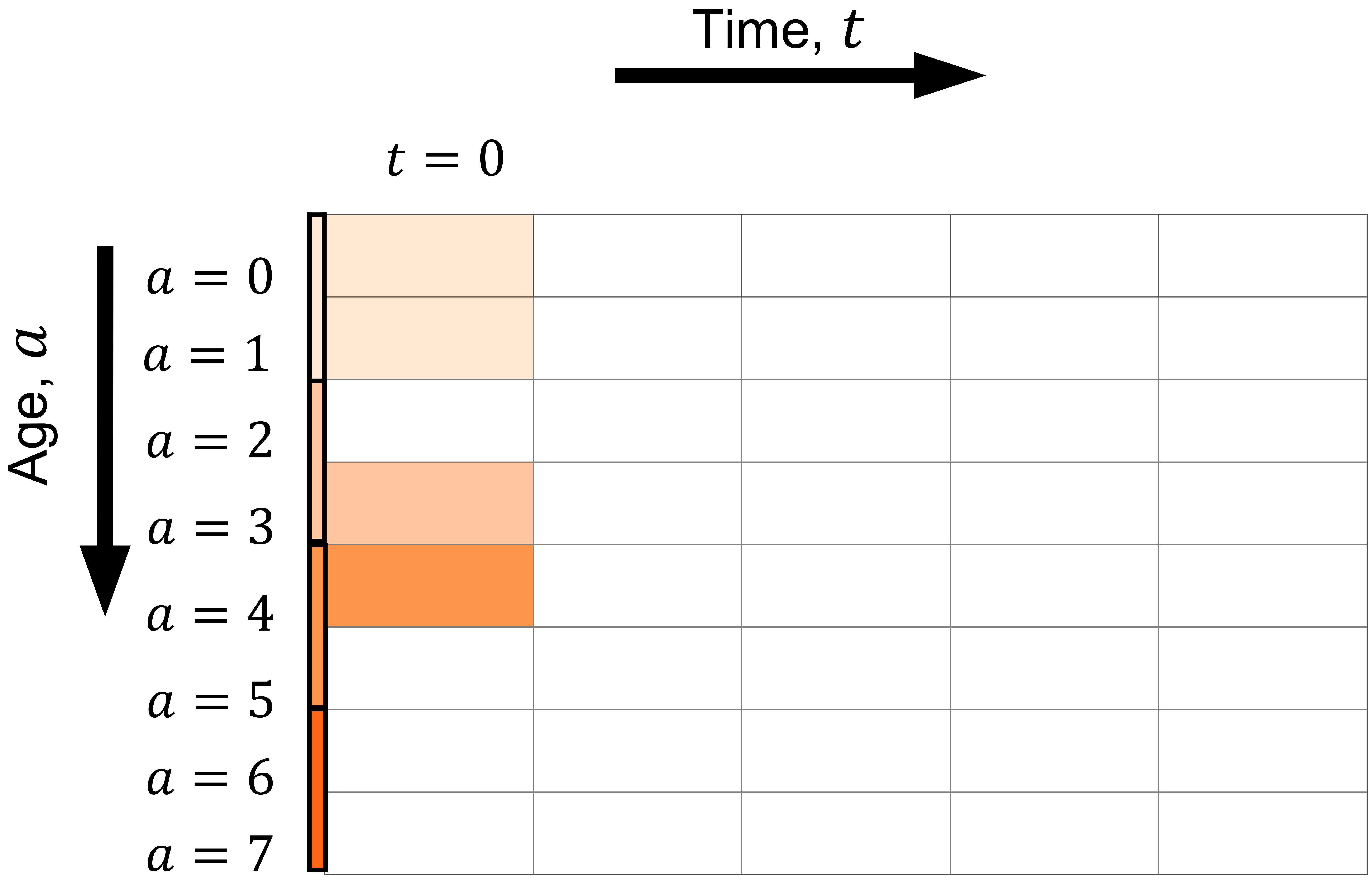
$$\rho(0,t) = \int_0^\infty \gamma\rho(s,t)\mathrm{d}s$$ Boundary condition

Get reset to age zero ← Patches that get disturbed

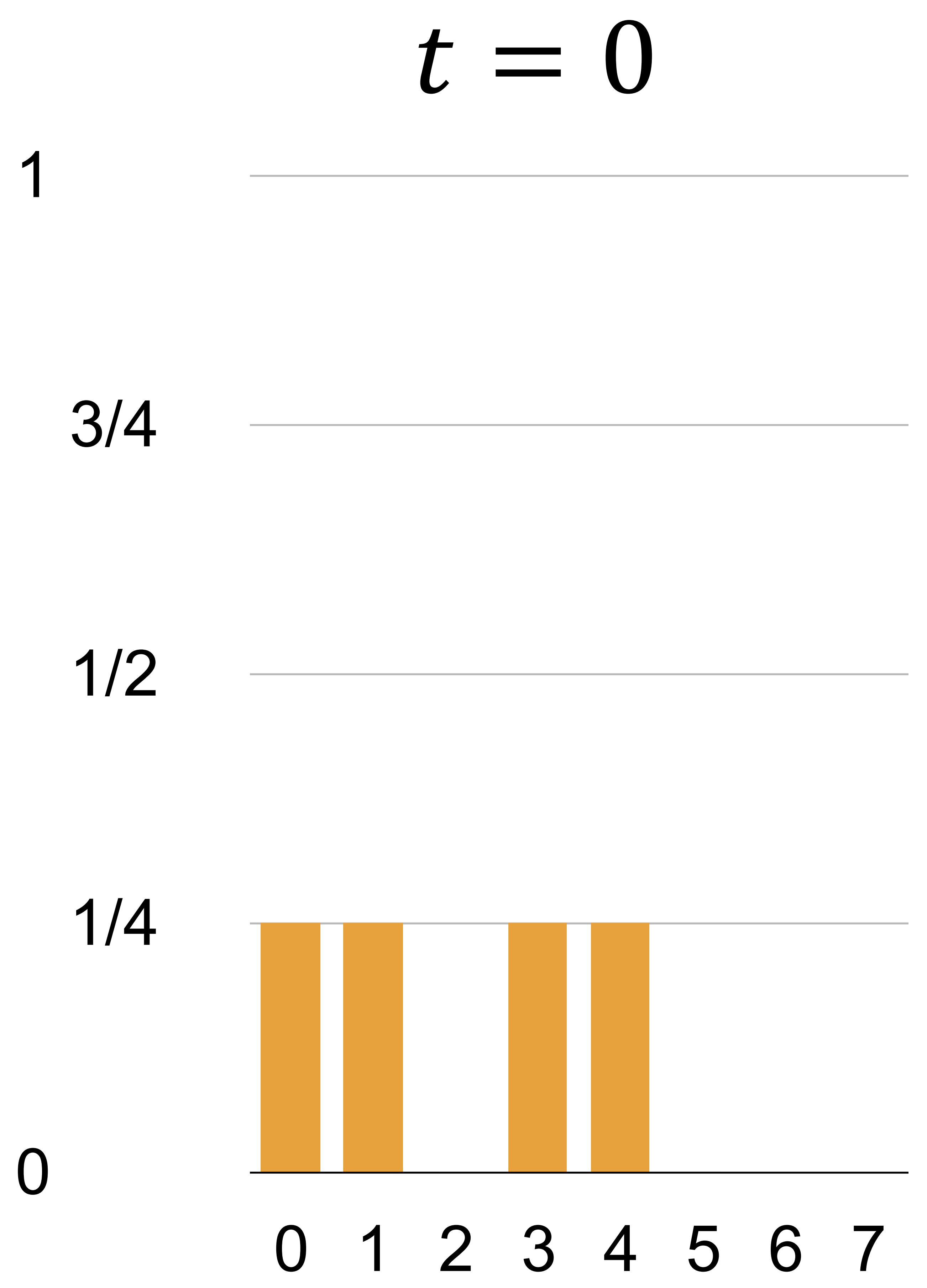
Our Model - Patch Dynamics



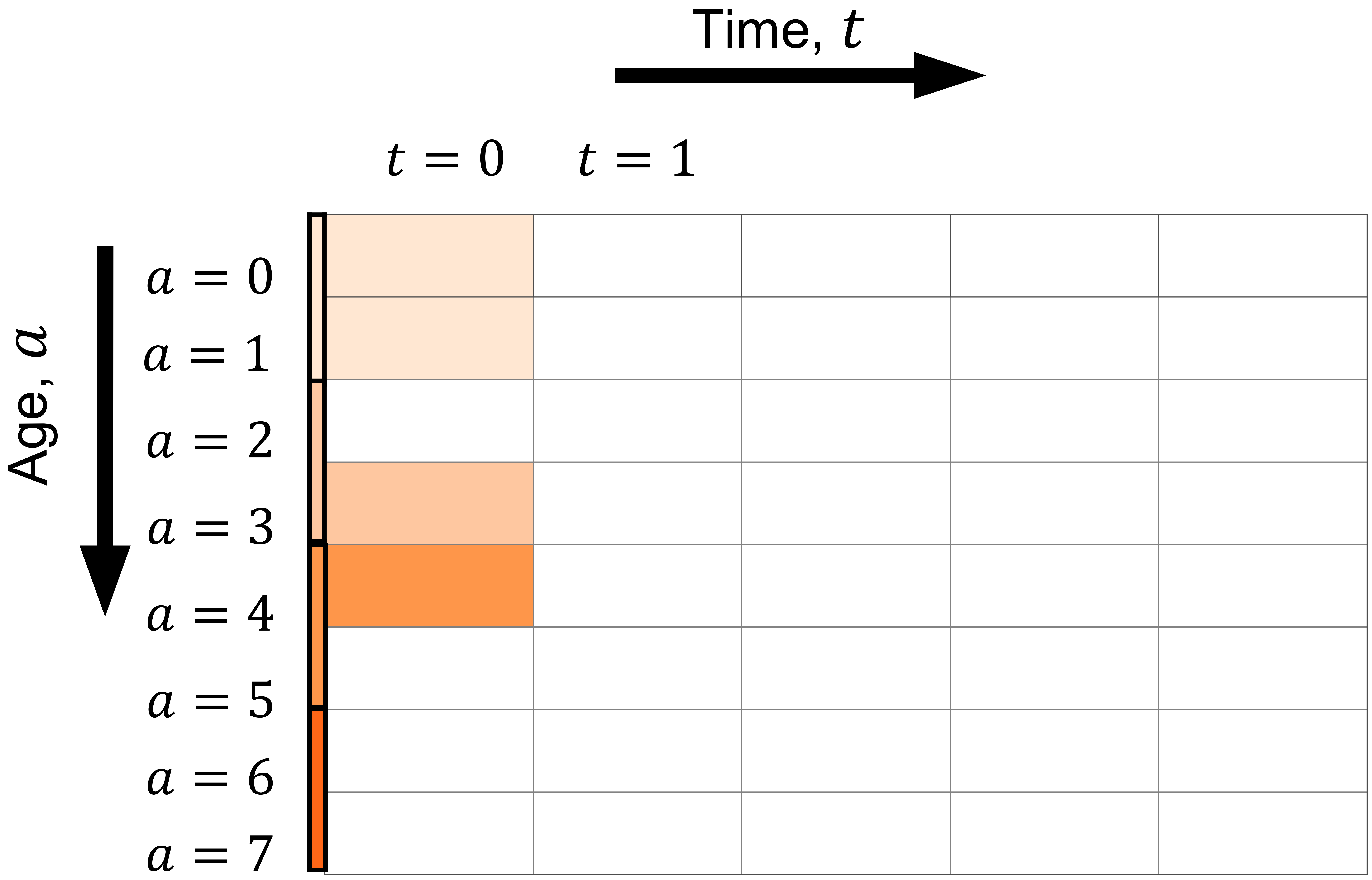
Our Model - Patch Dynamics

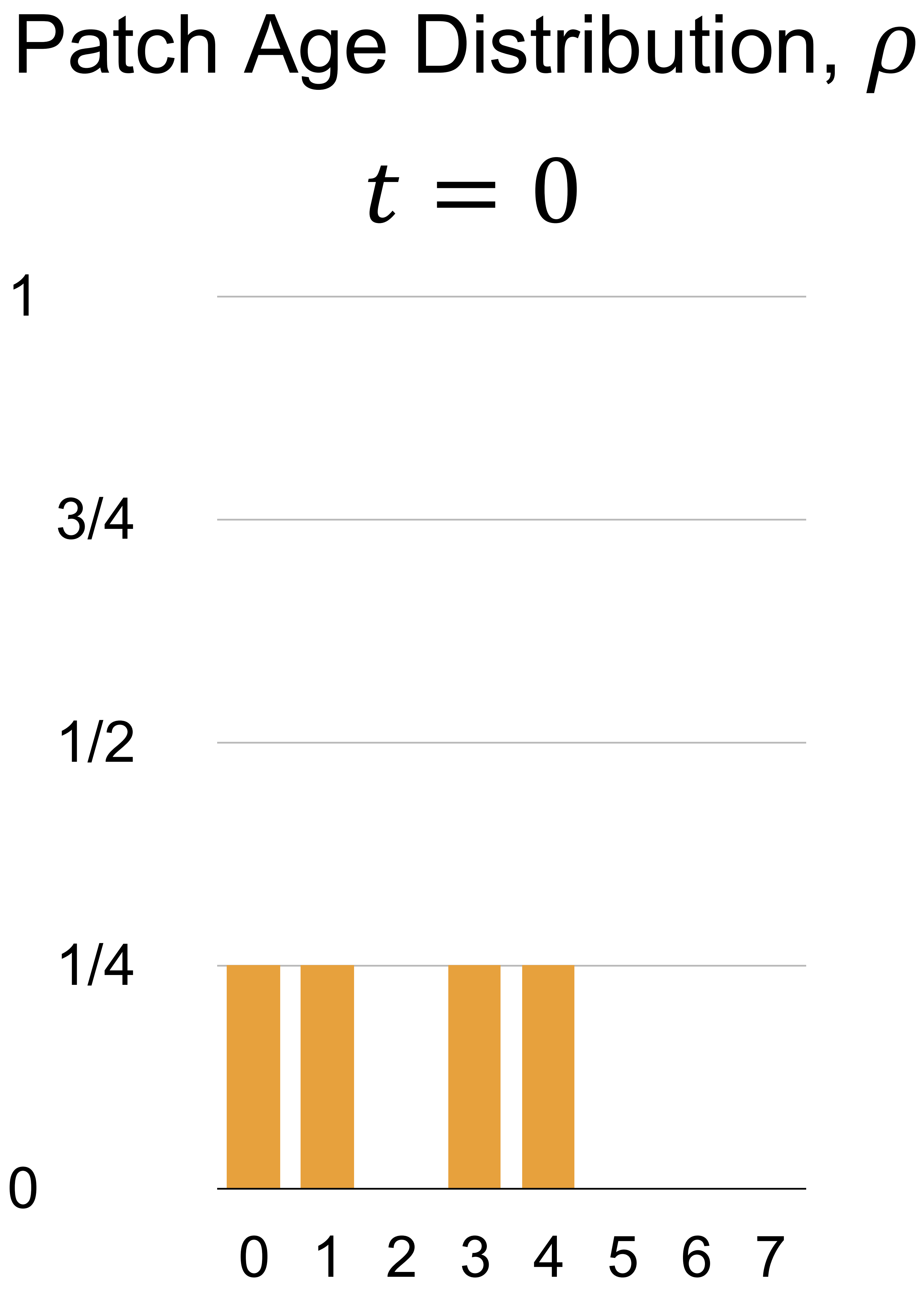


Patch Age Distribution, ρ

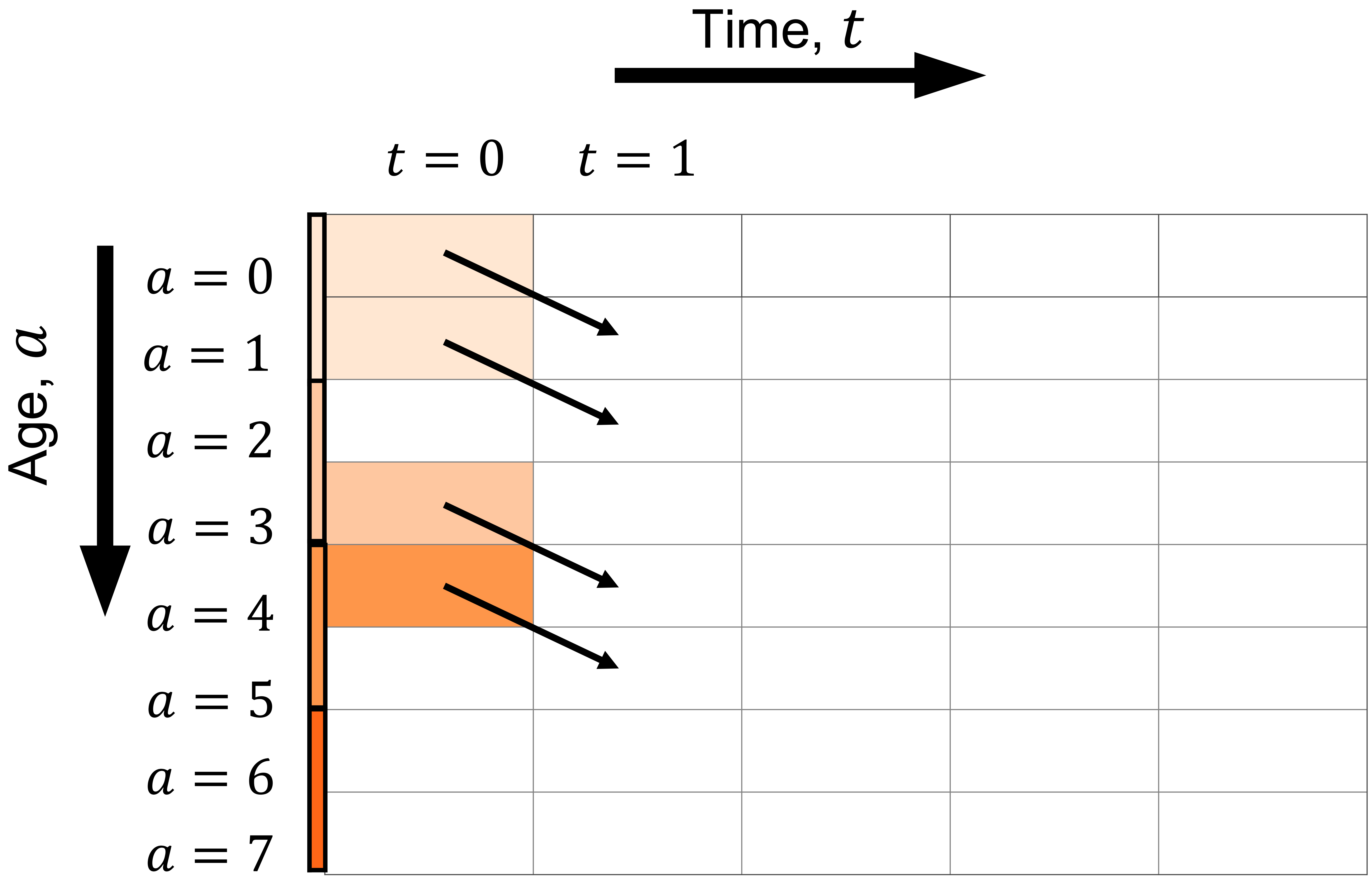


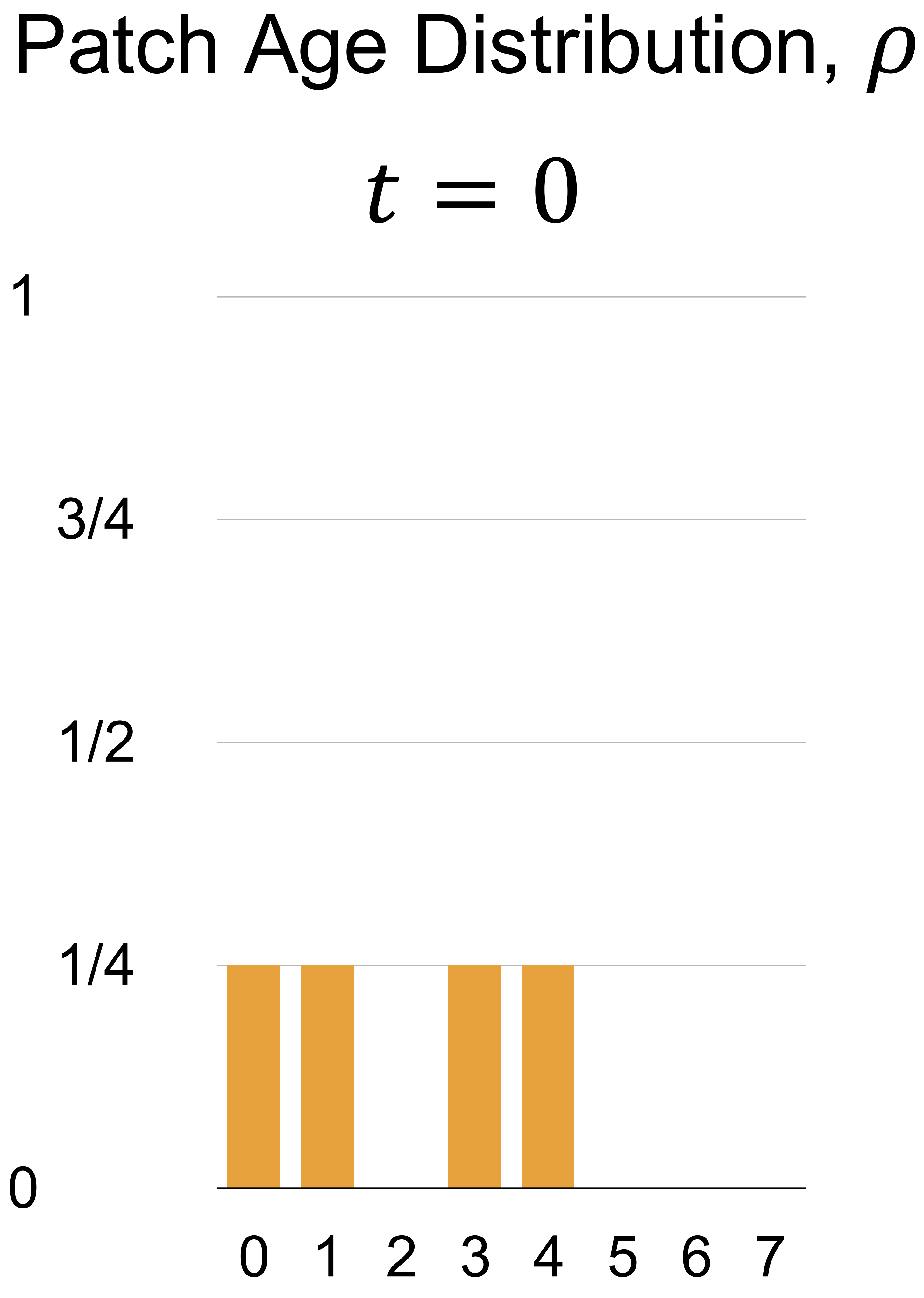
Our Model - Patch Dynamics



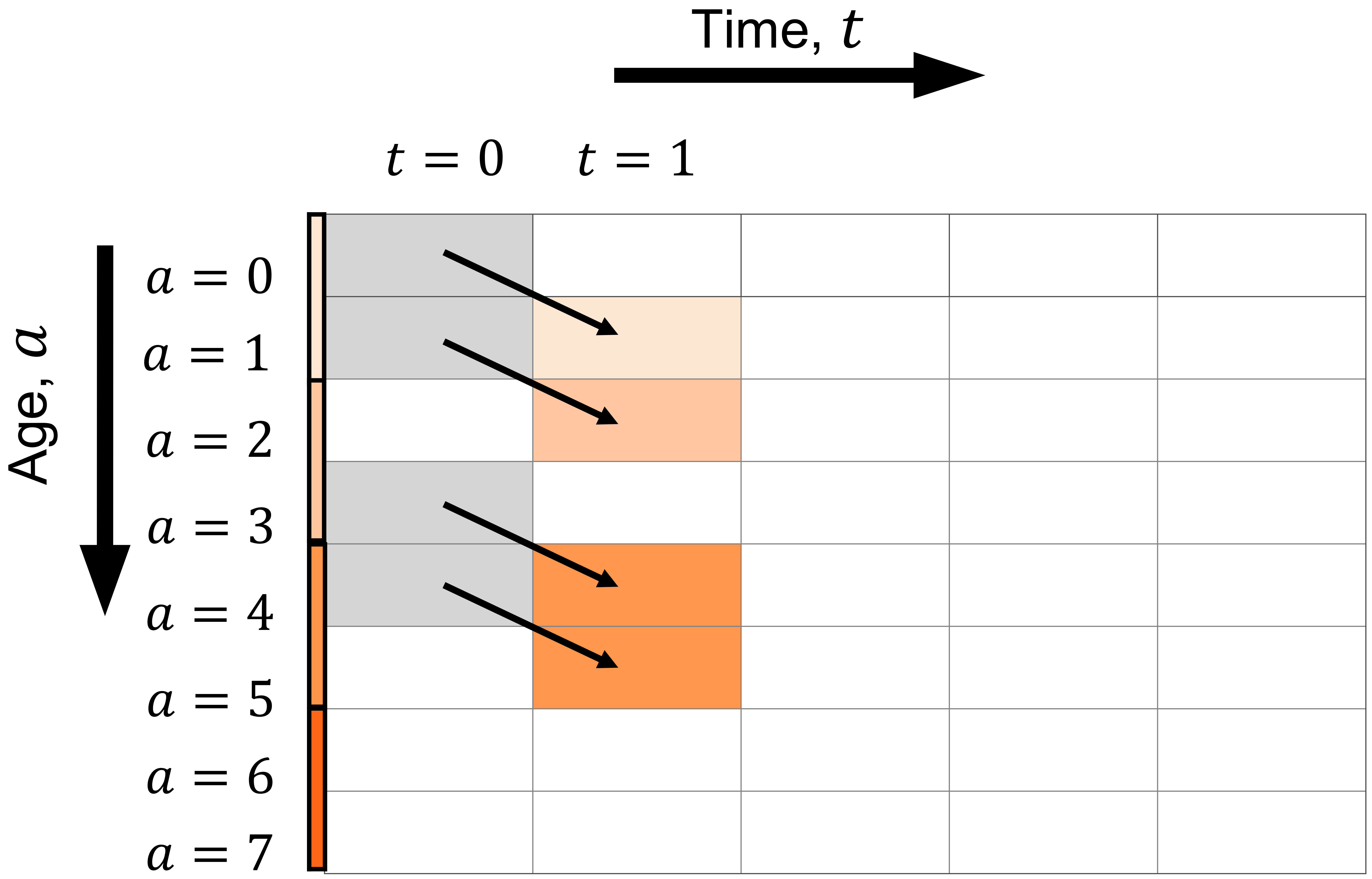


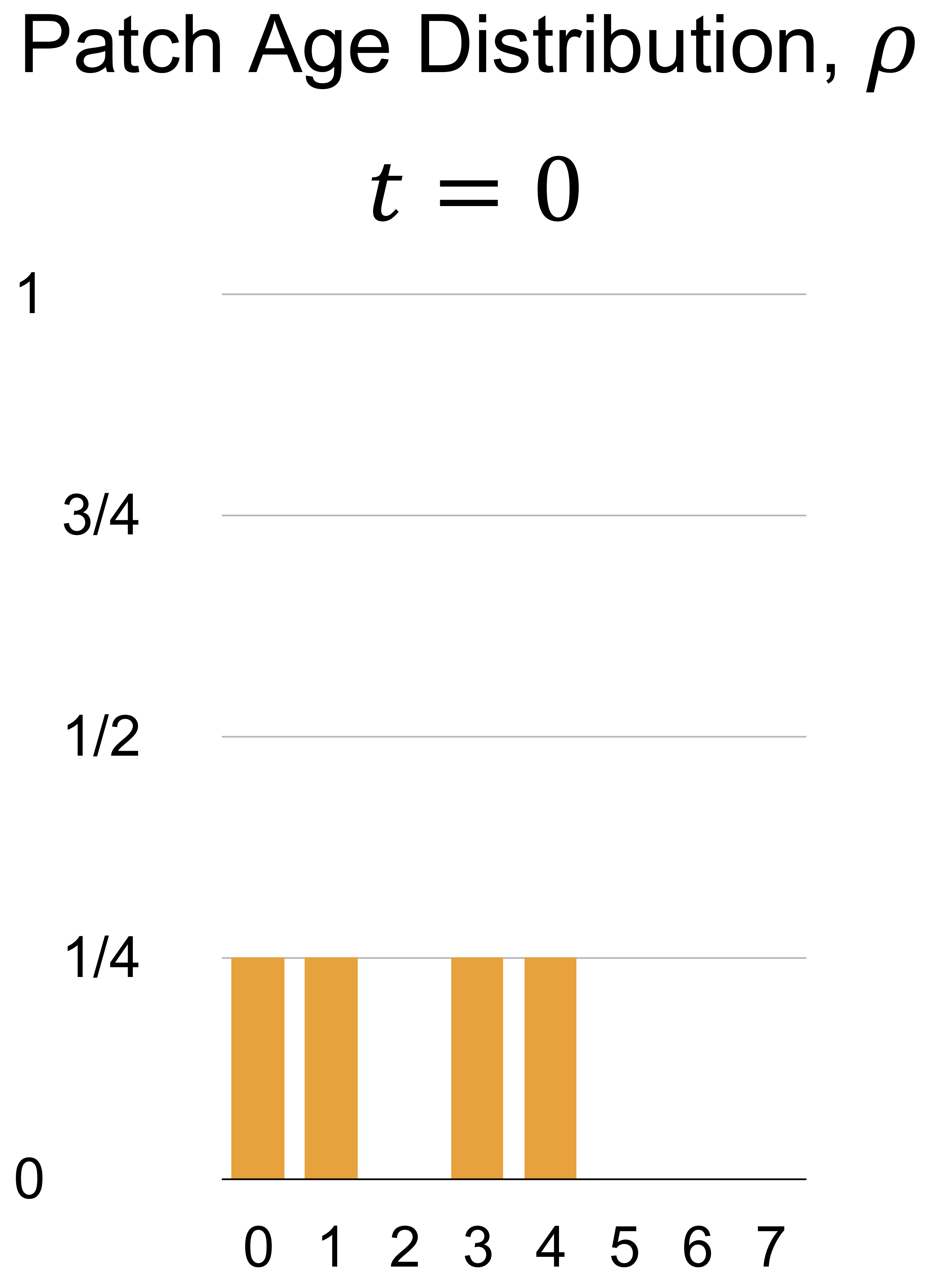
Our Model - Patch Dynamics



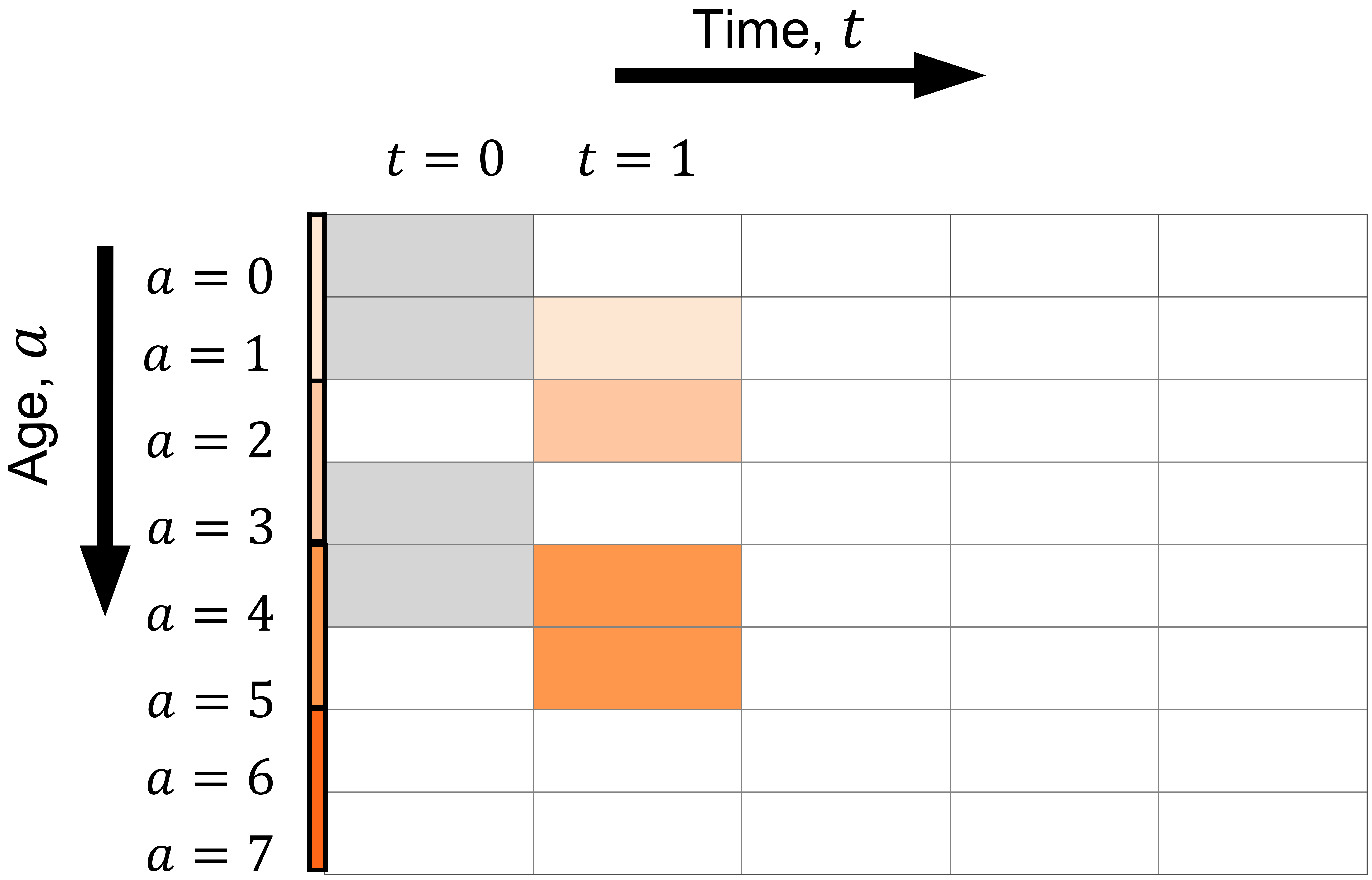


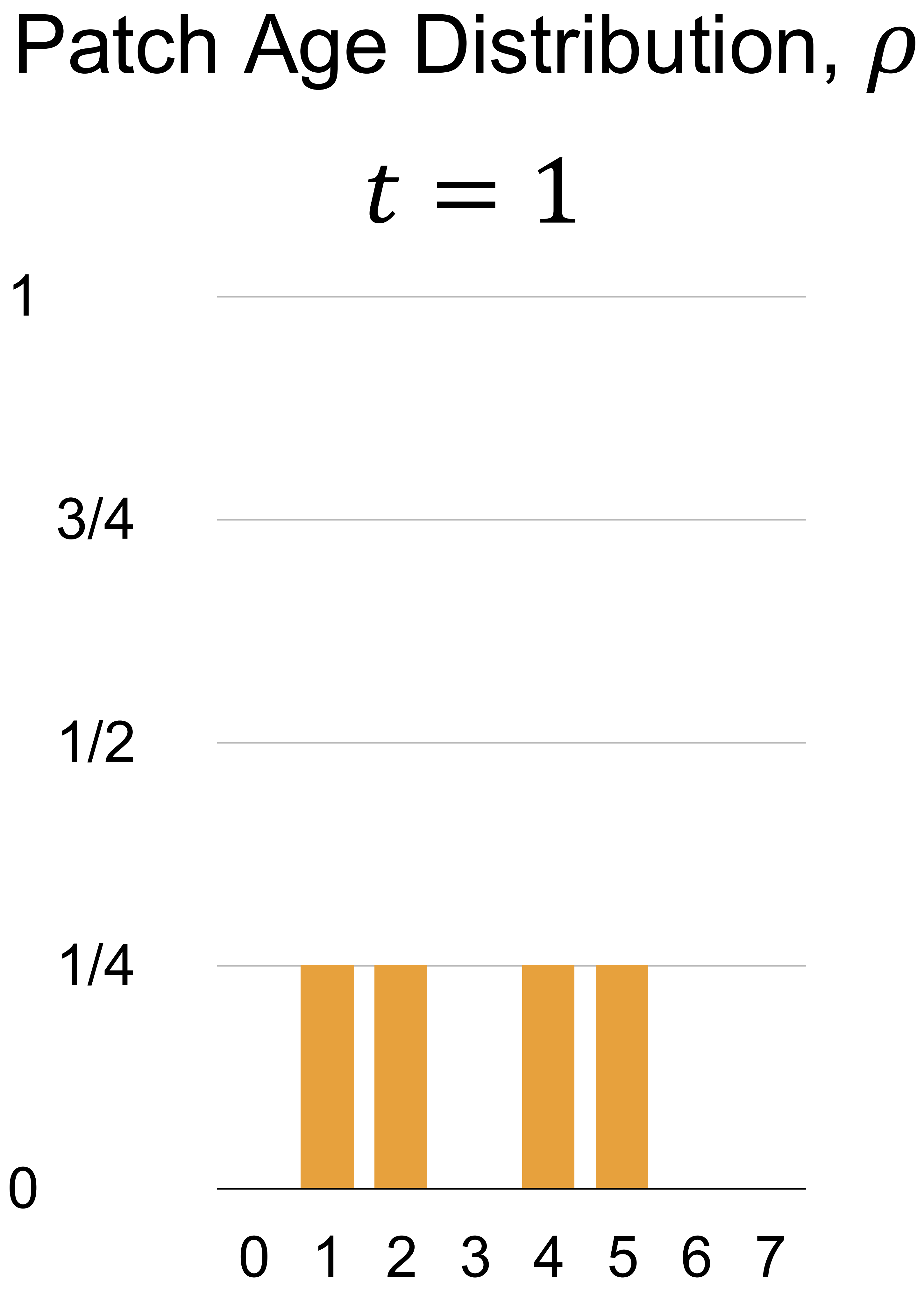
Our Model - Patch Dynamics



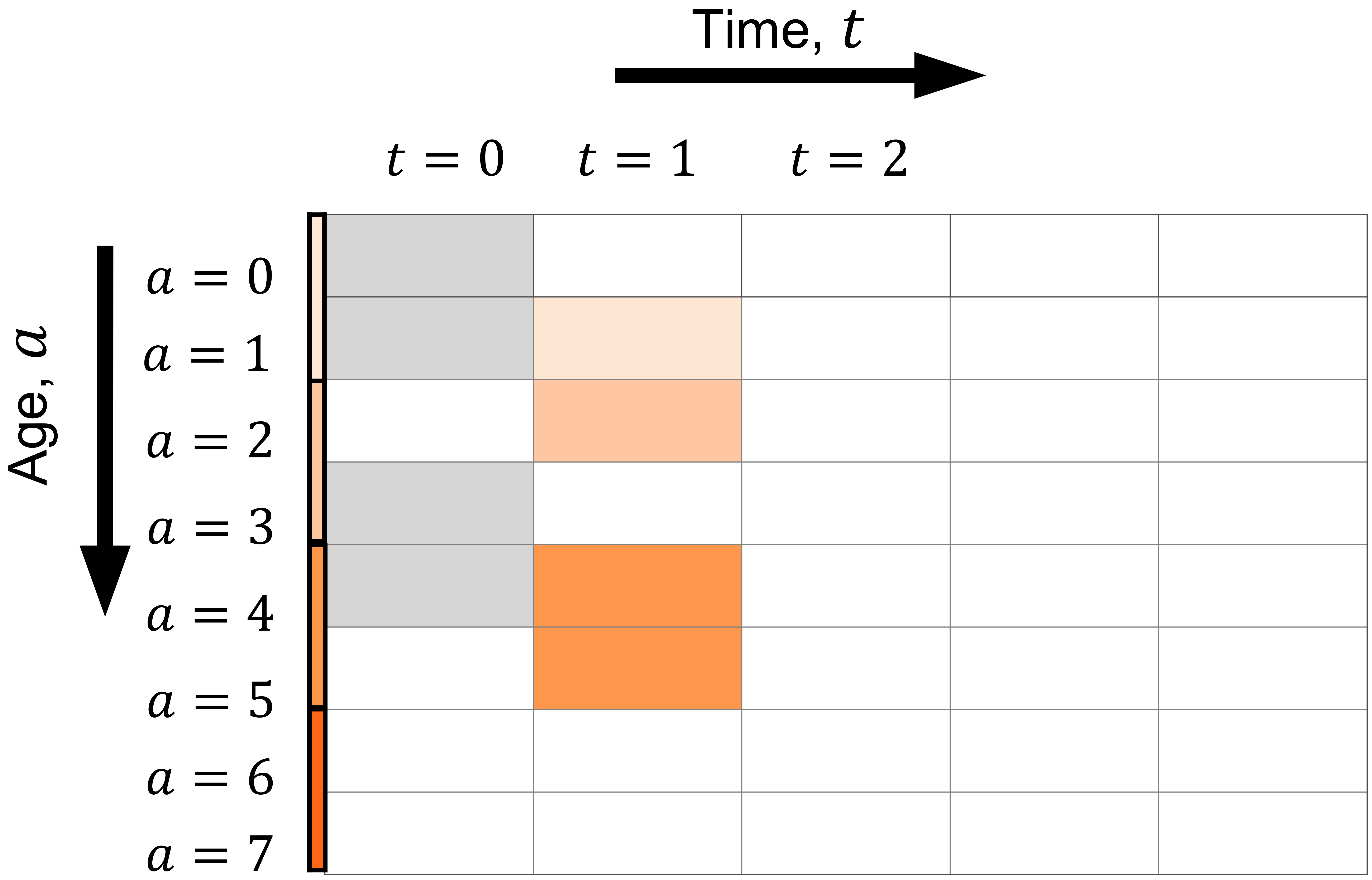


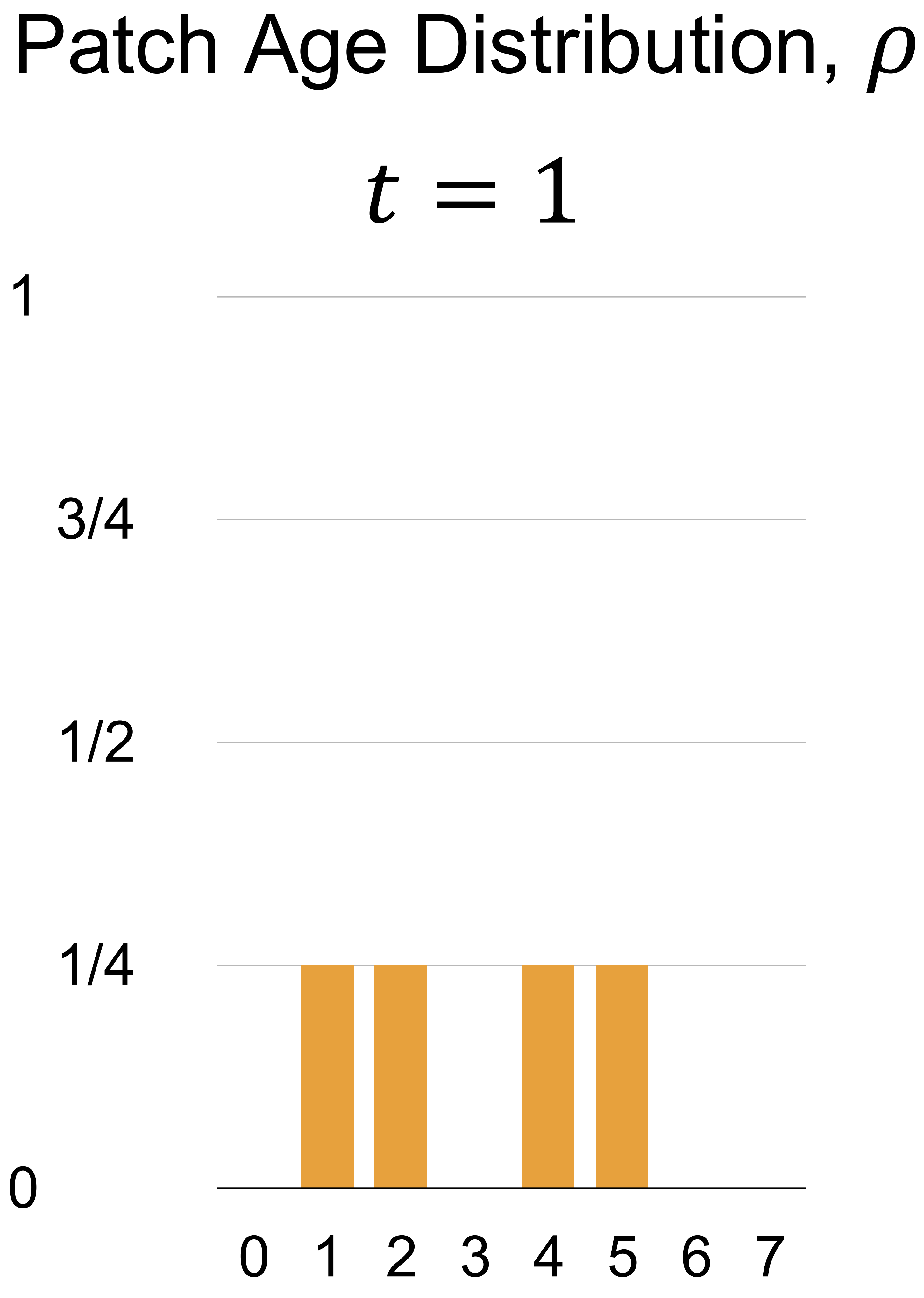
Our Model - Patch Dynamics



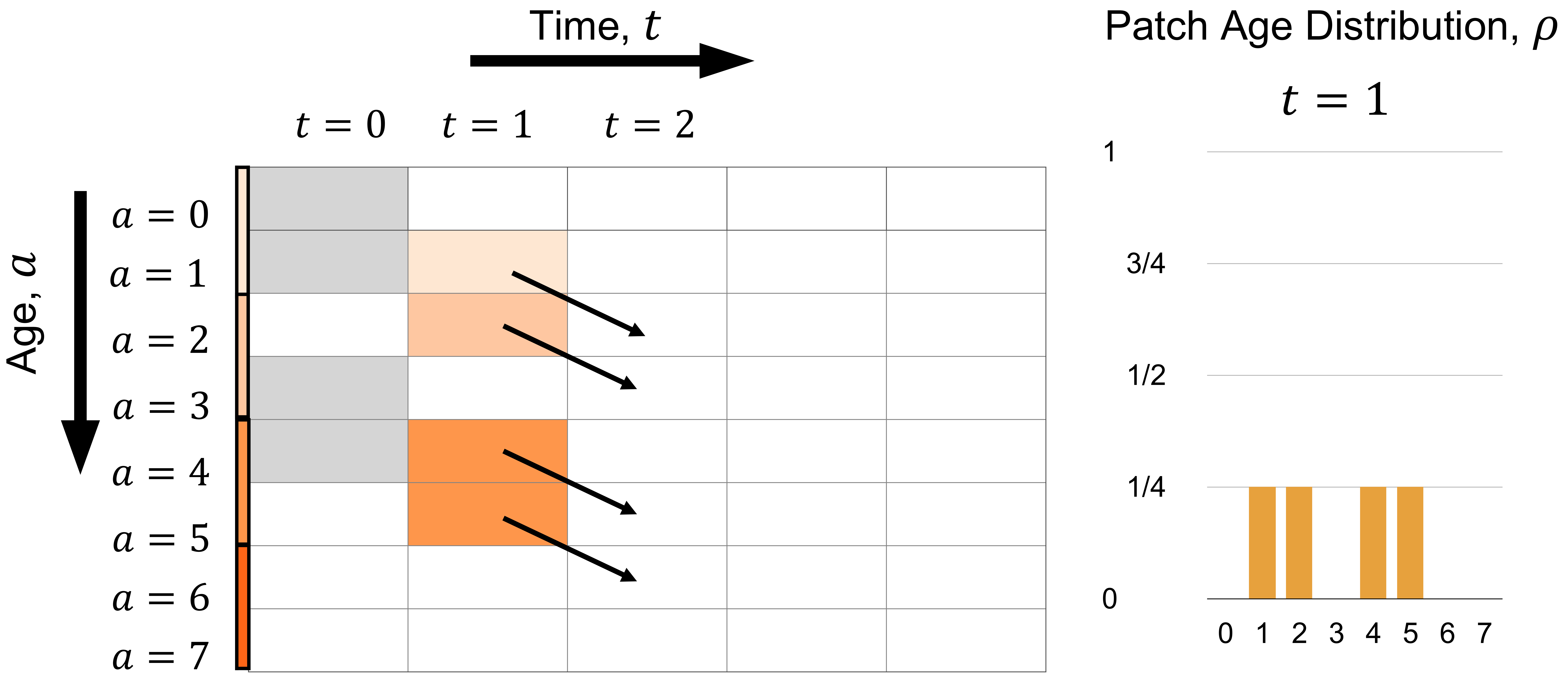


Our Model - Patch Dynamics

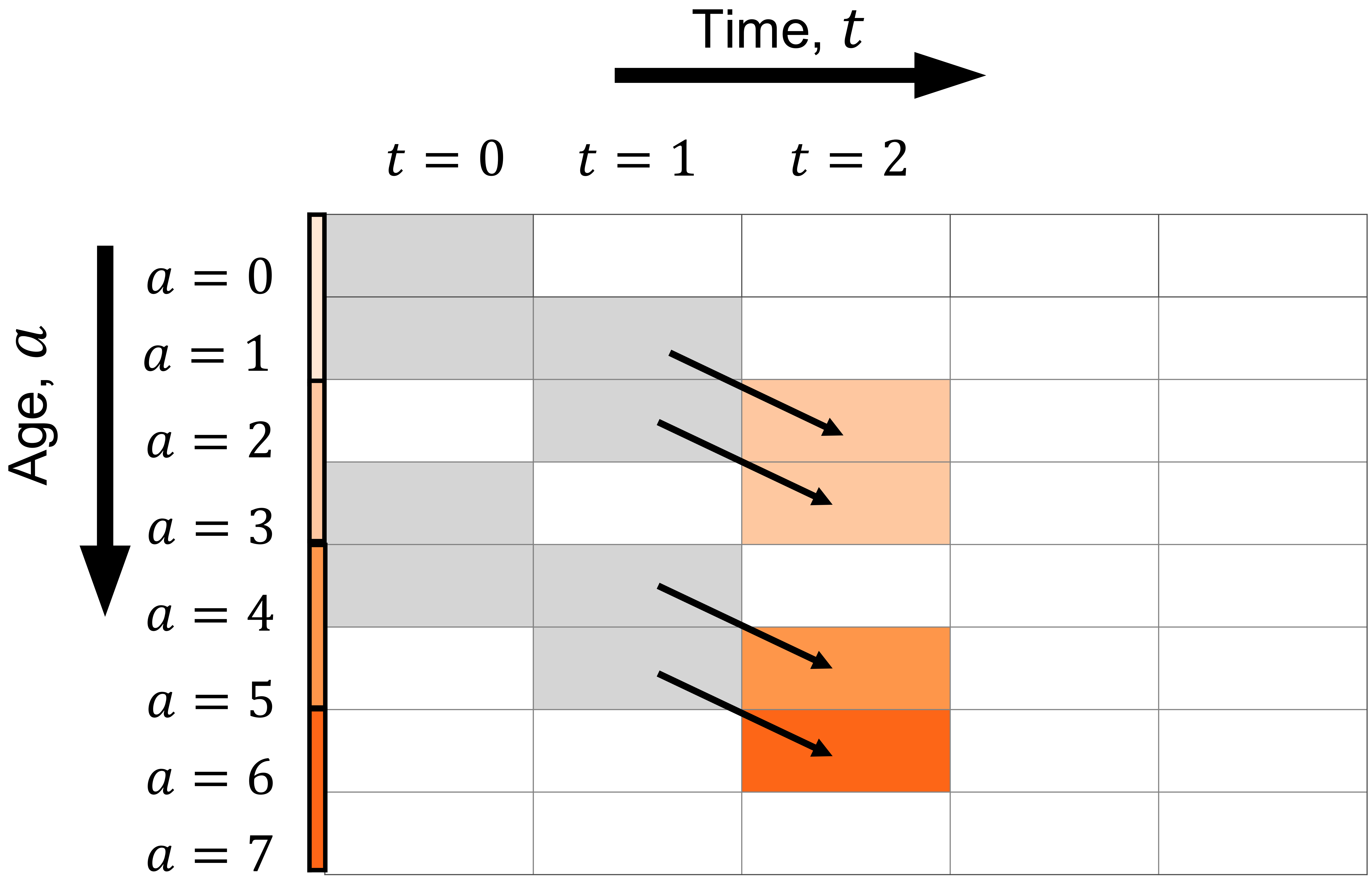




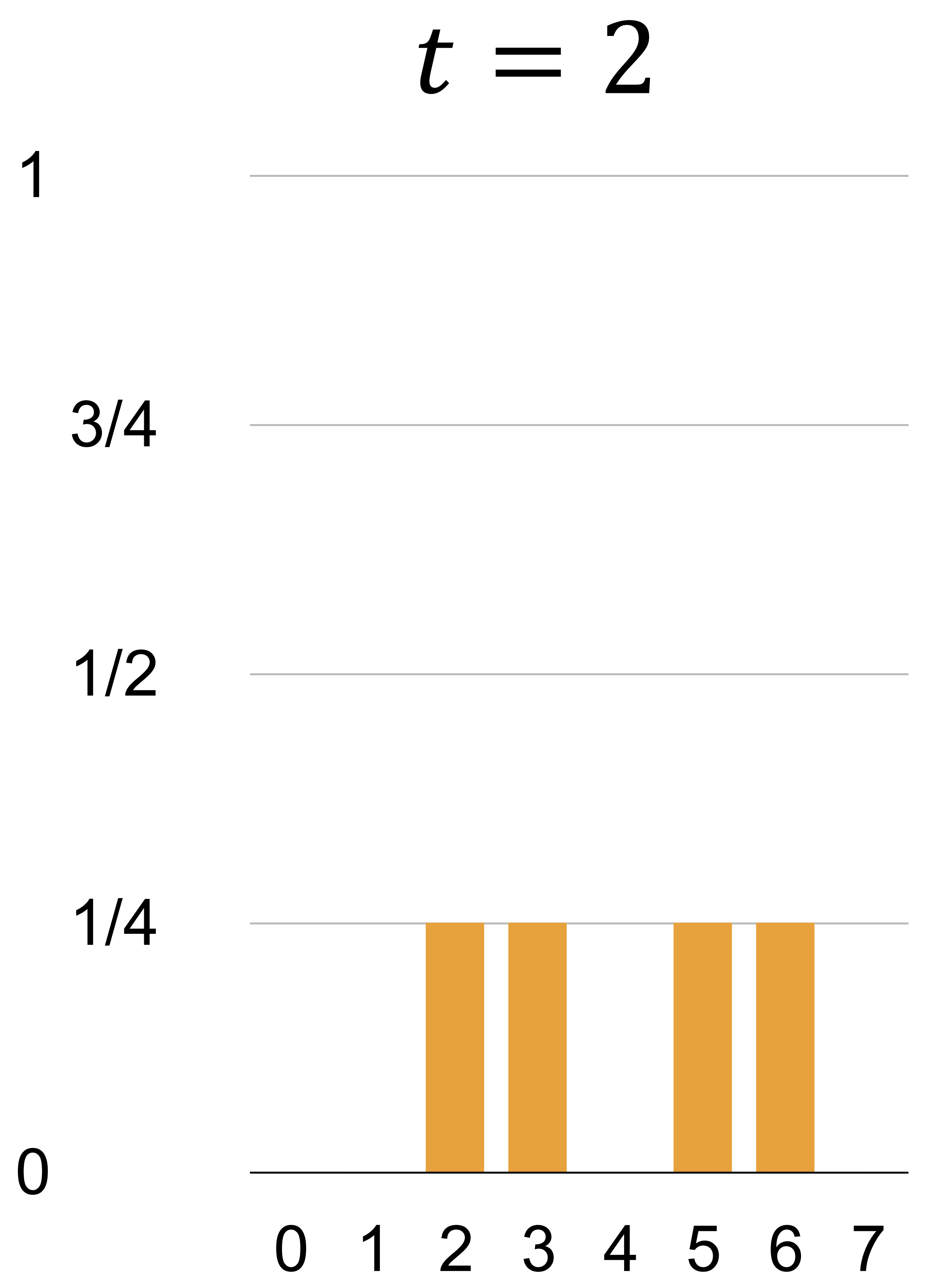
Our Model - Patch Dynamics



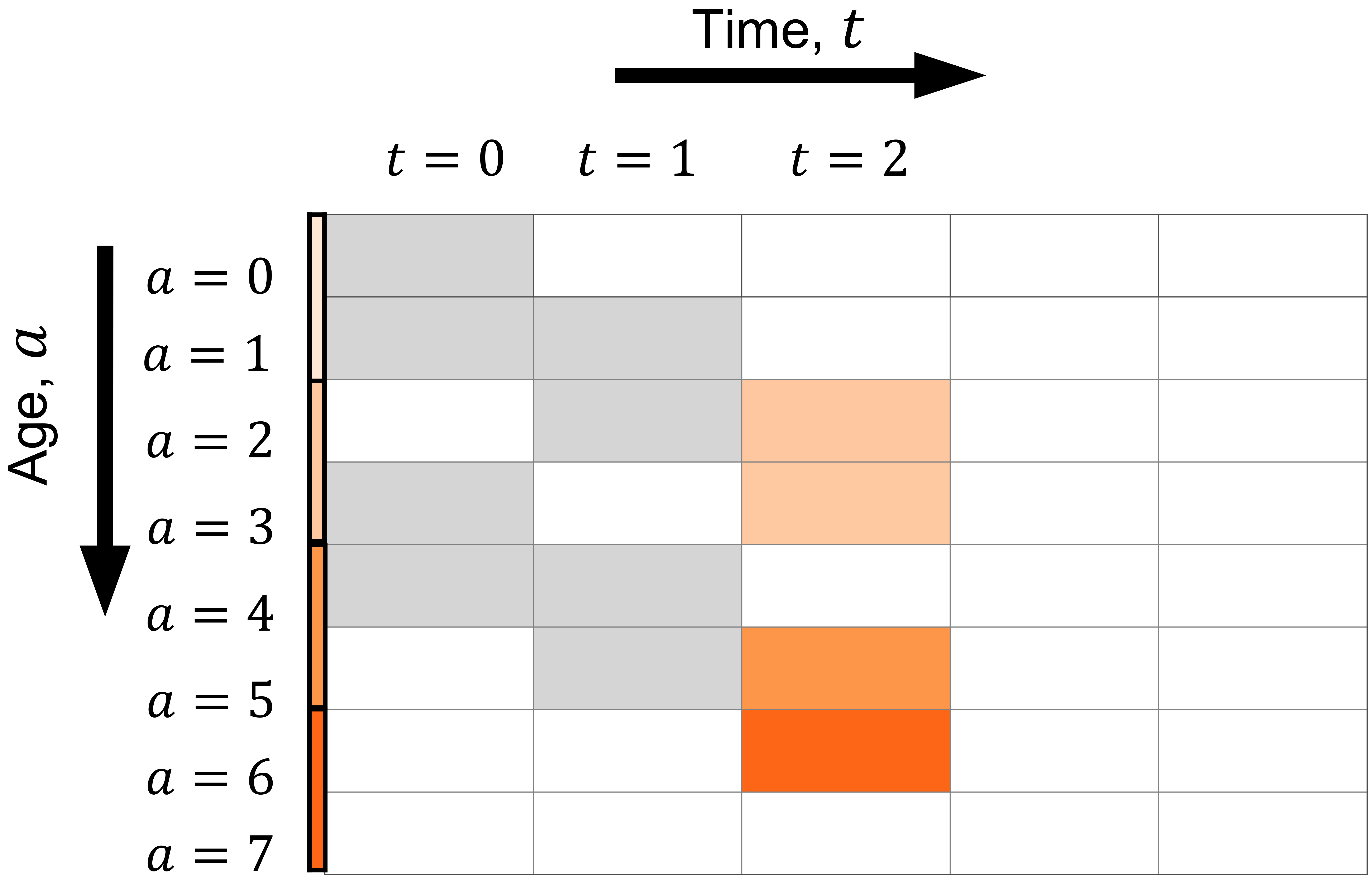
Our Model - Patch Dynamics

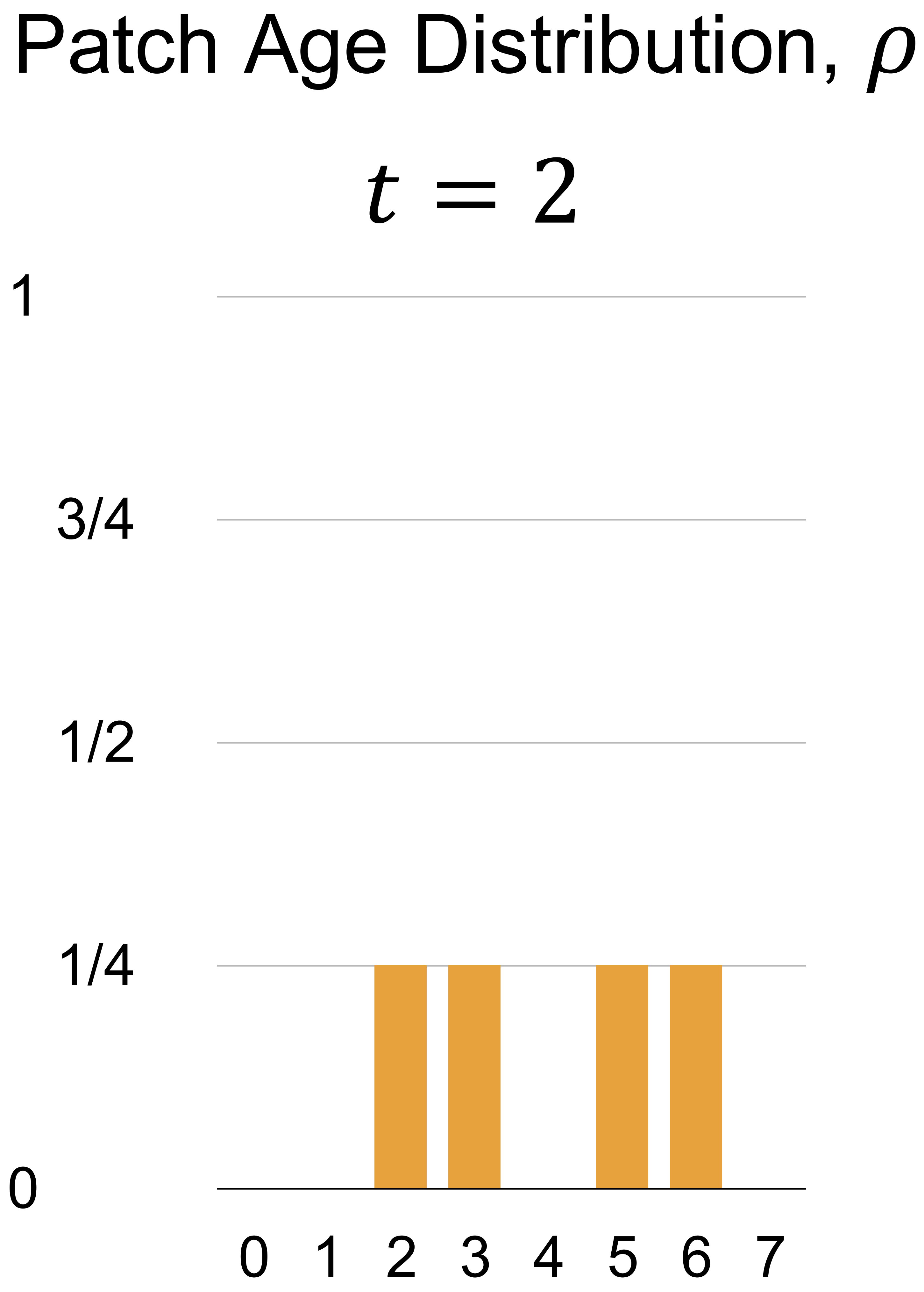


Patch Age Distribution, ρ

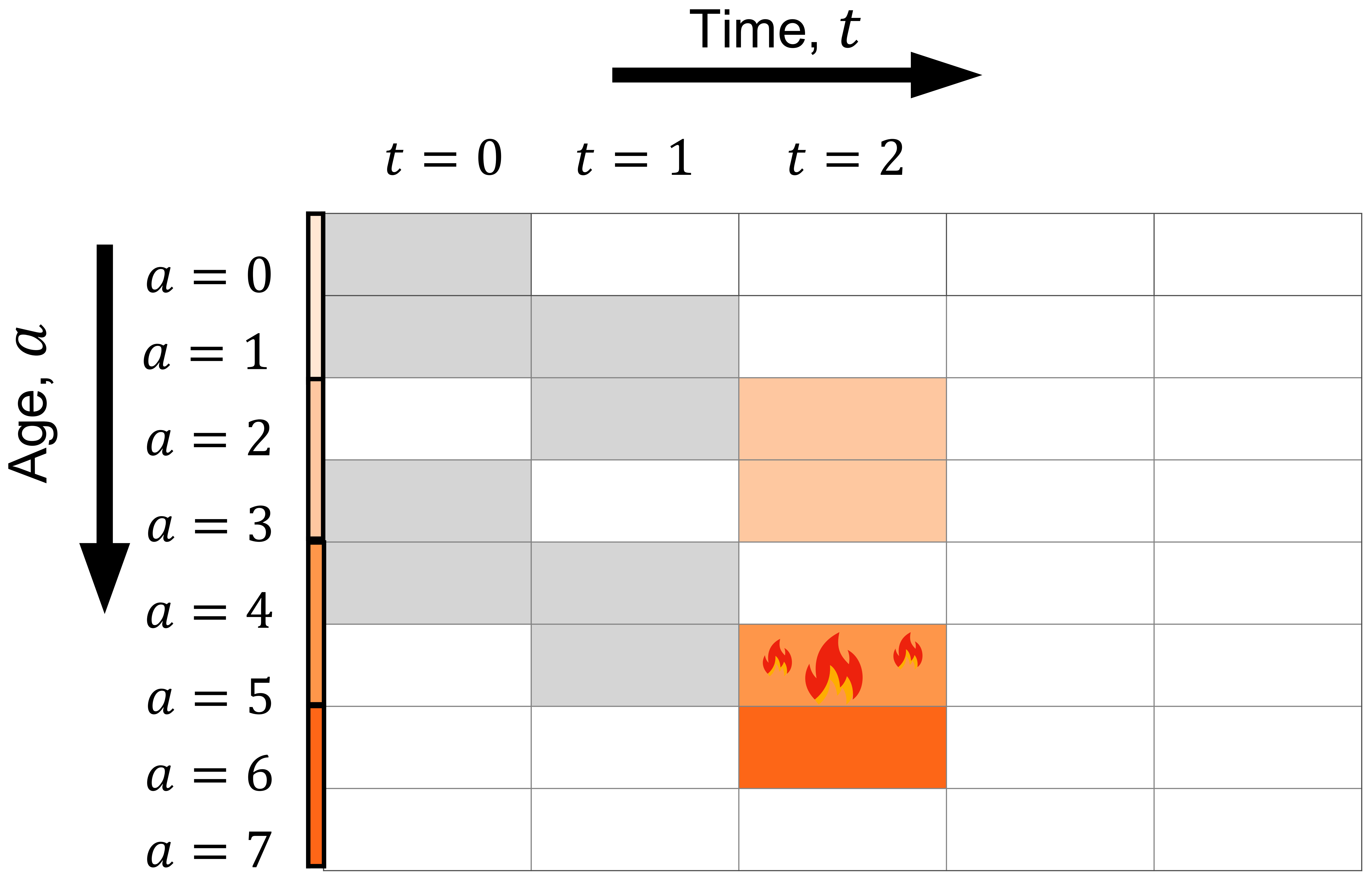


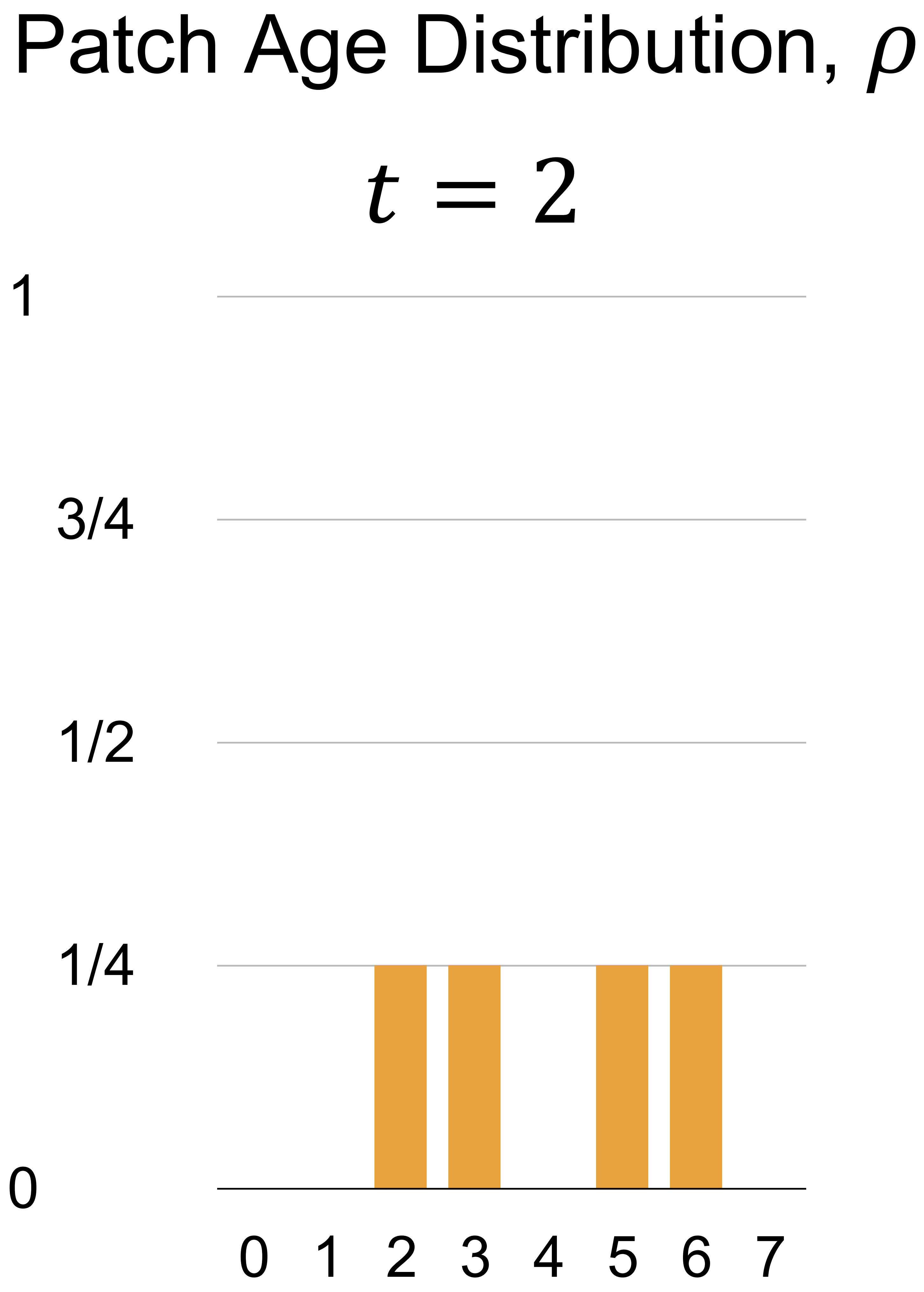
Our Model - Patch Dynamics



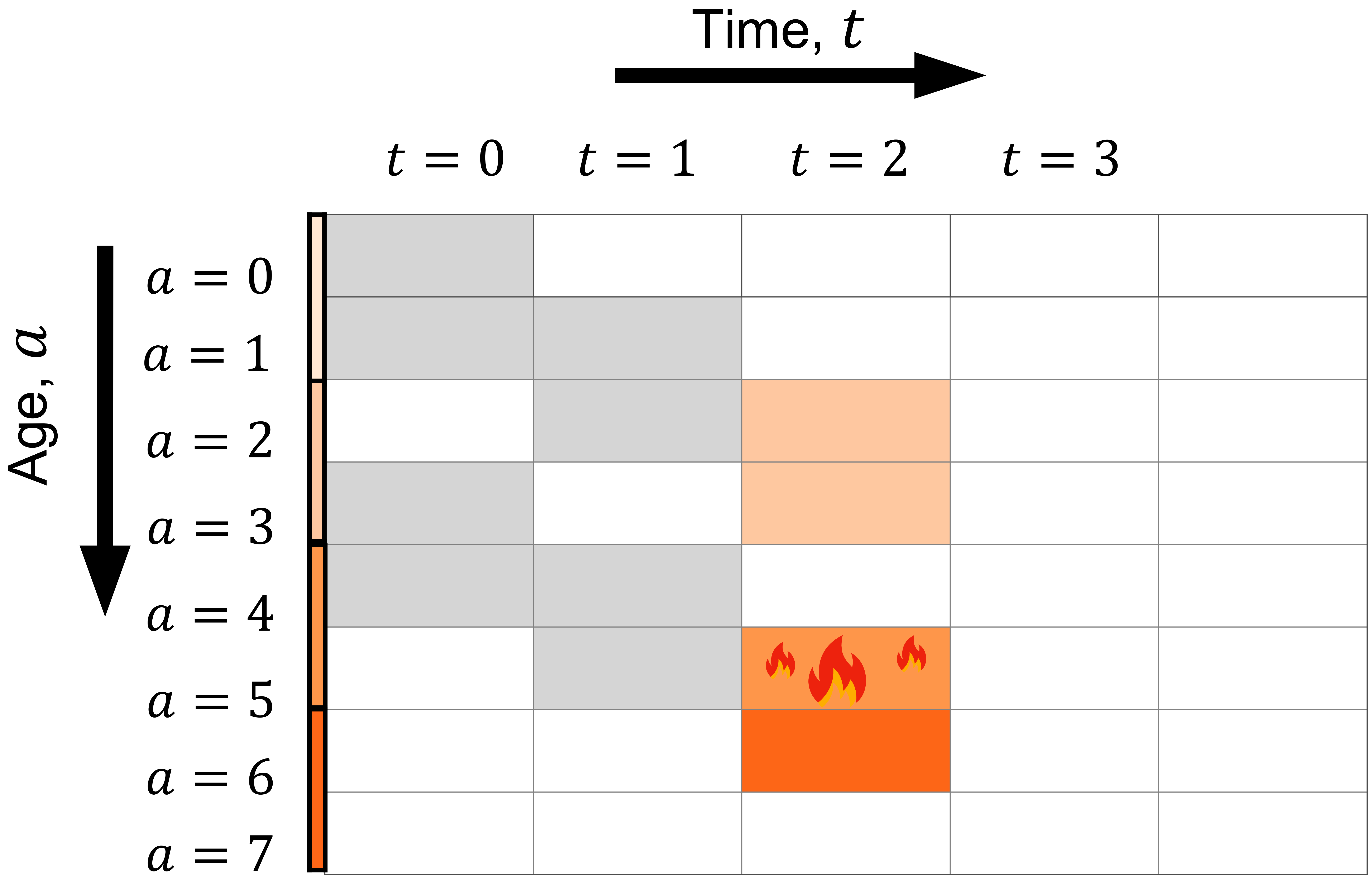


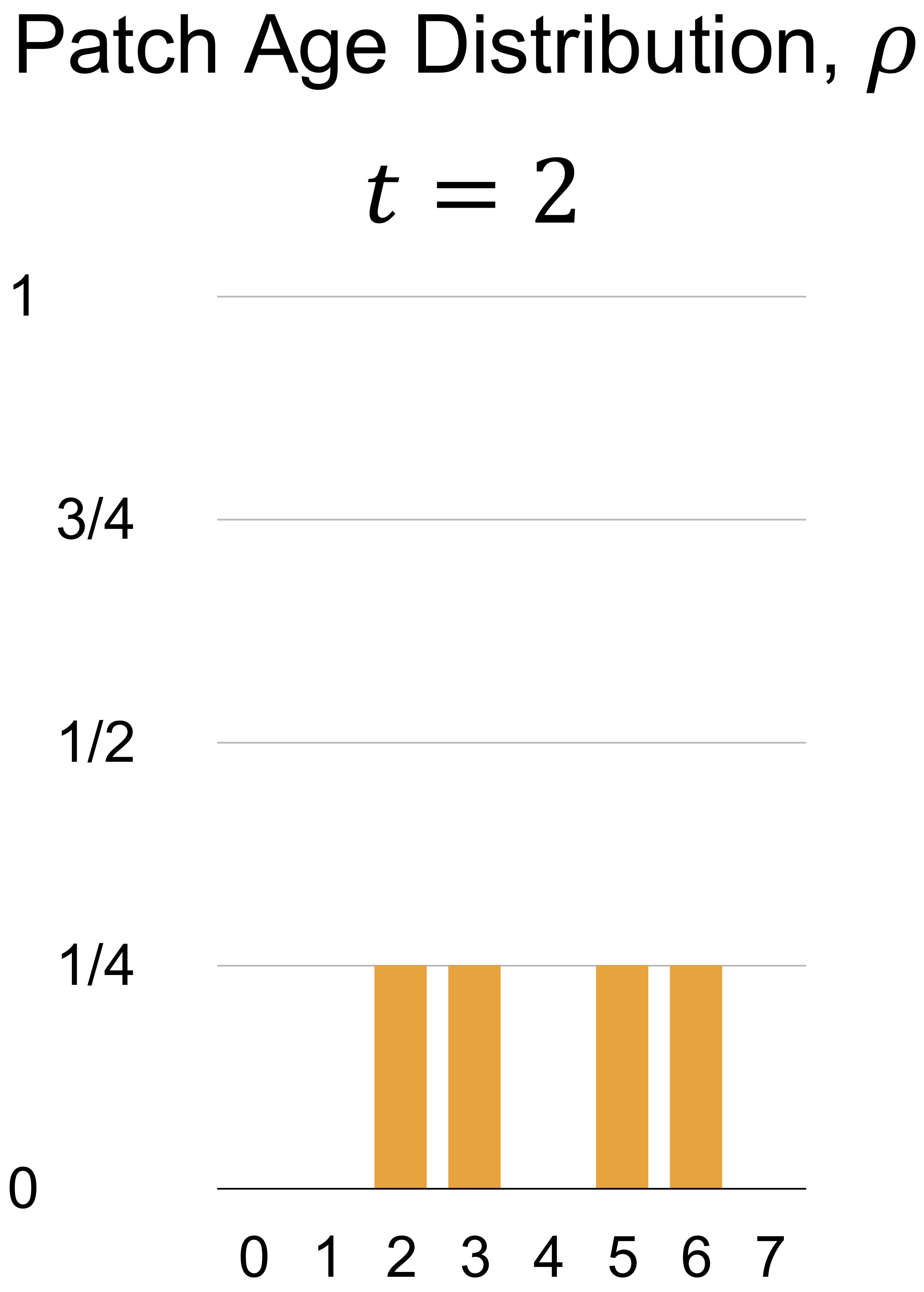
Our Model - Patch Dynamics



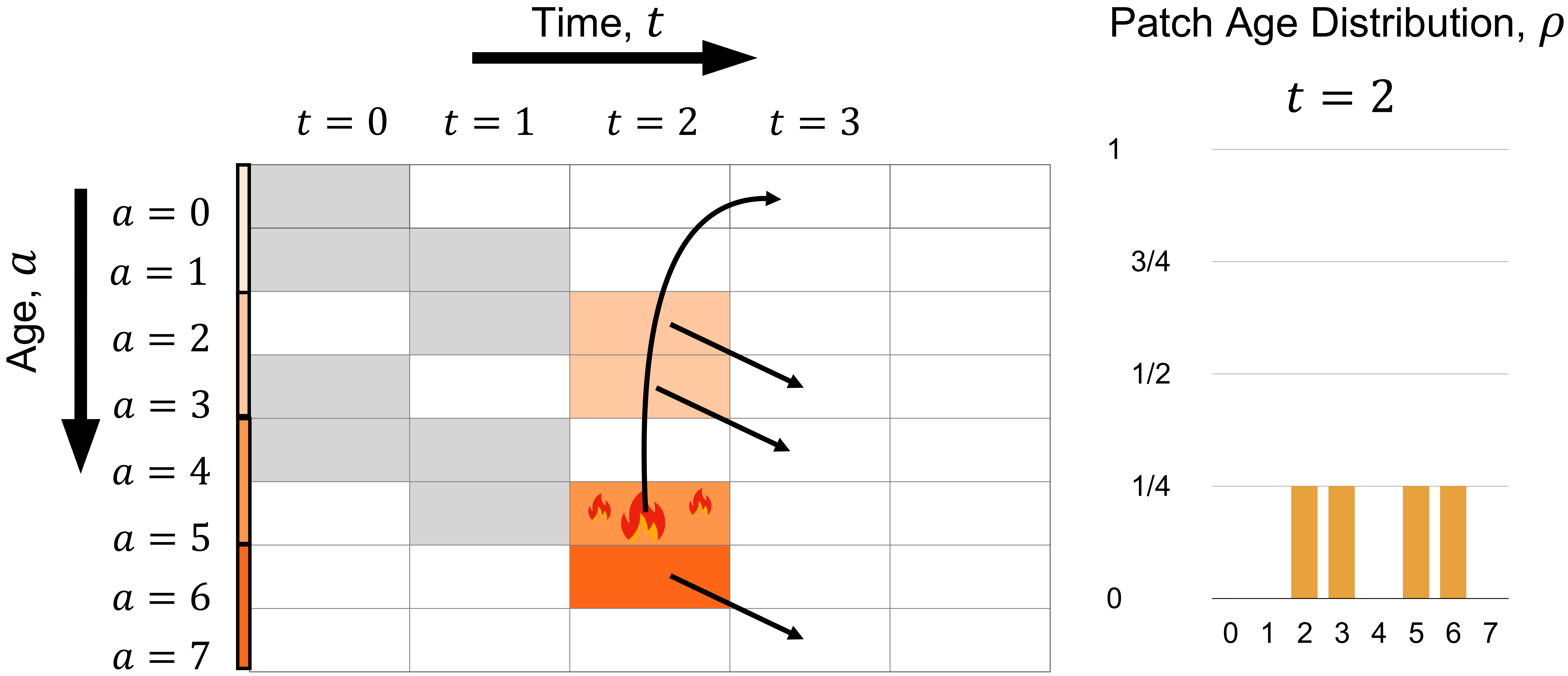


Our Model - Patch Dynamics

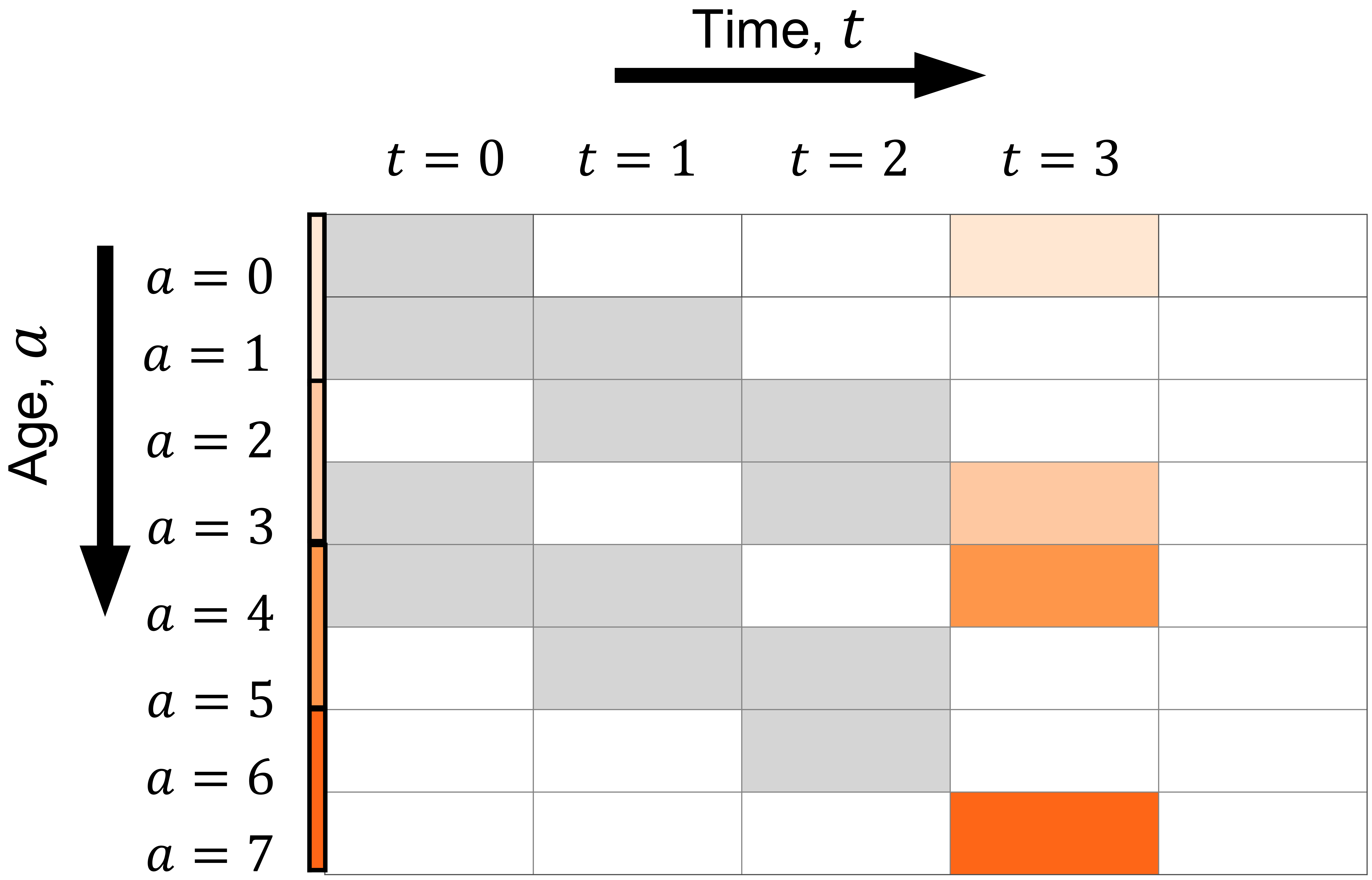


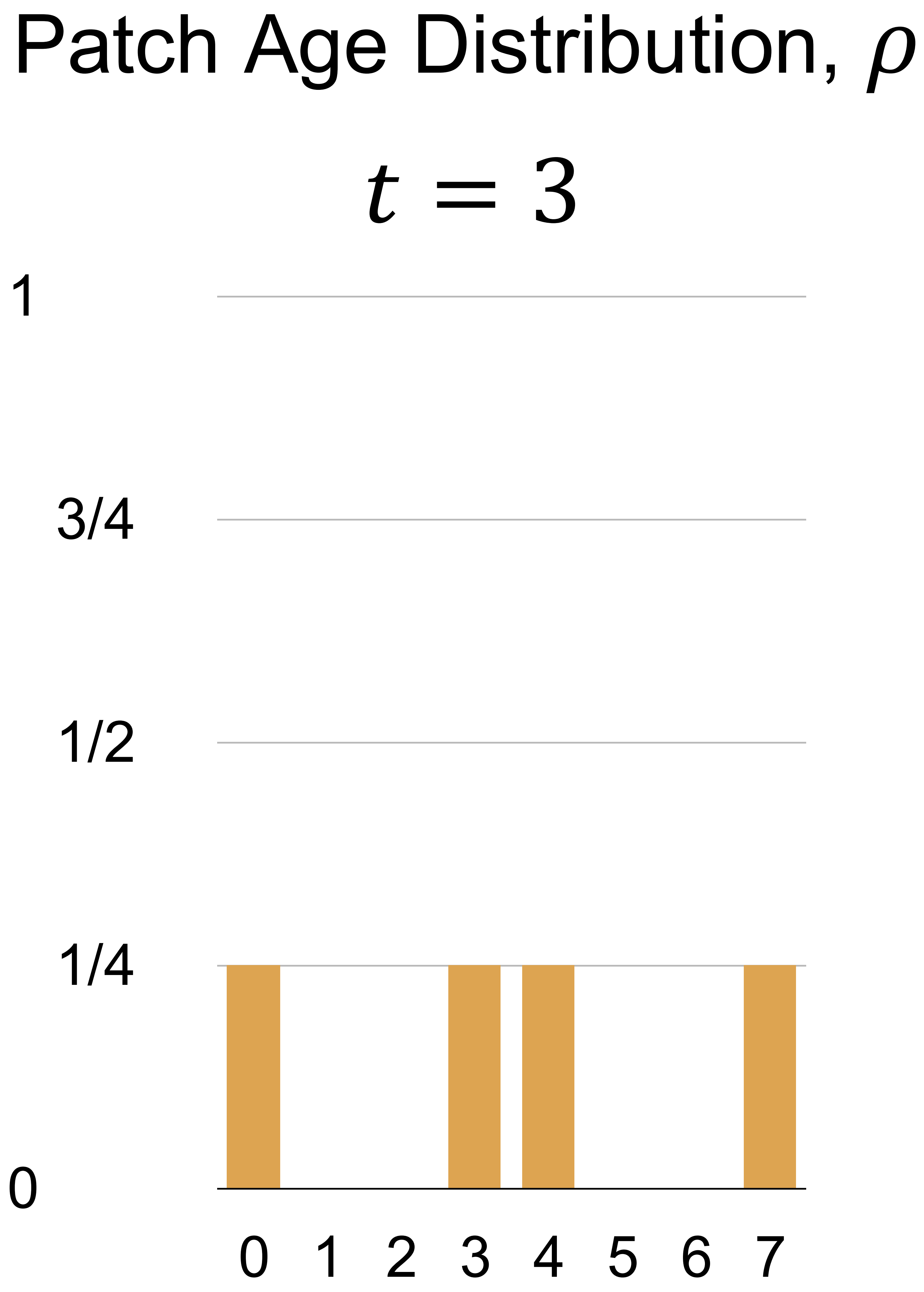


Our Model - Patch Dynamics

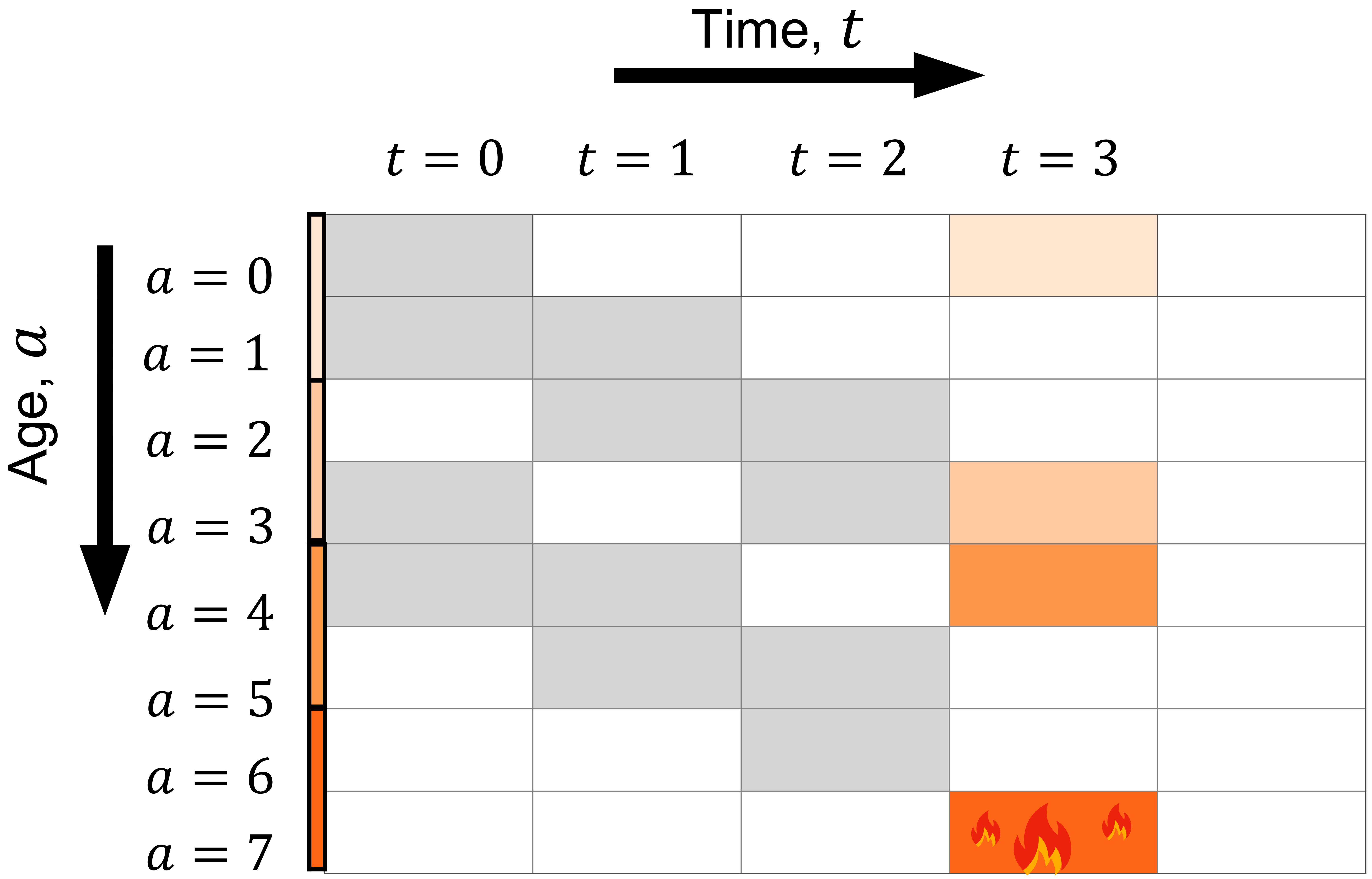


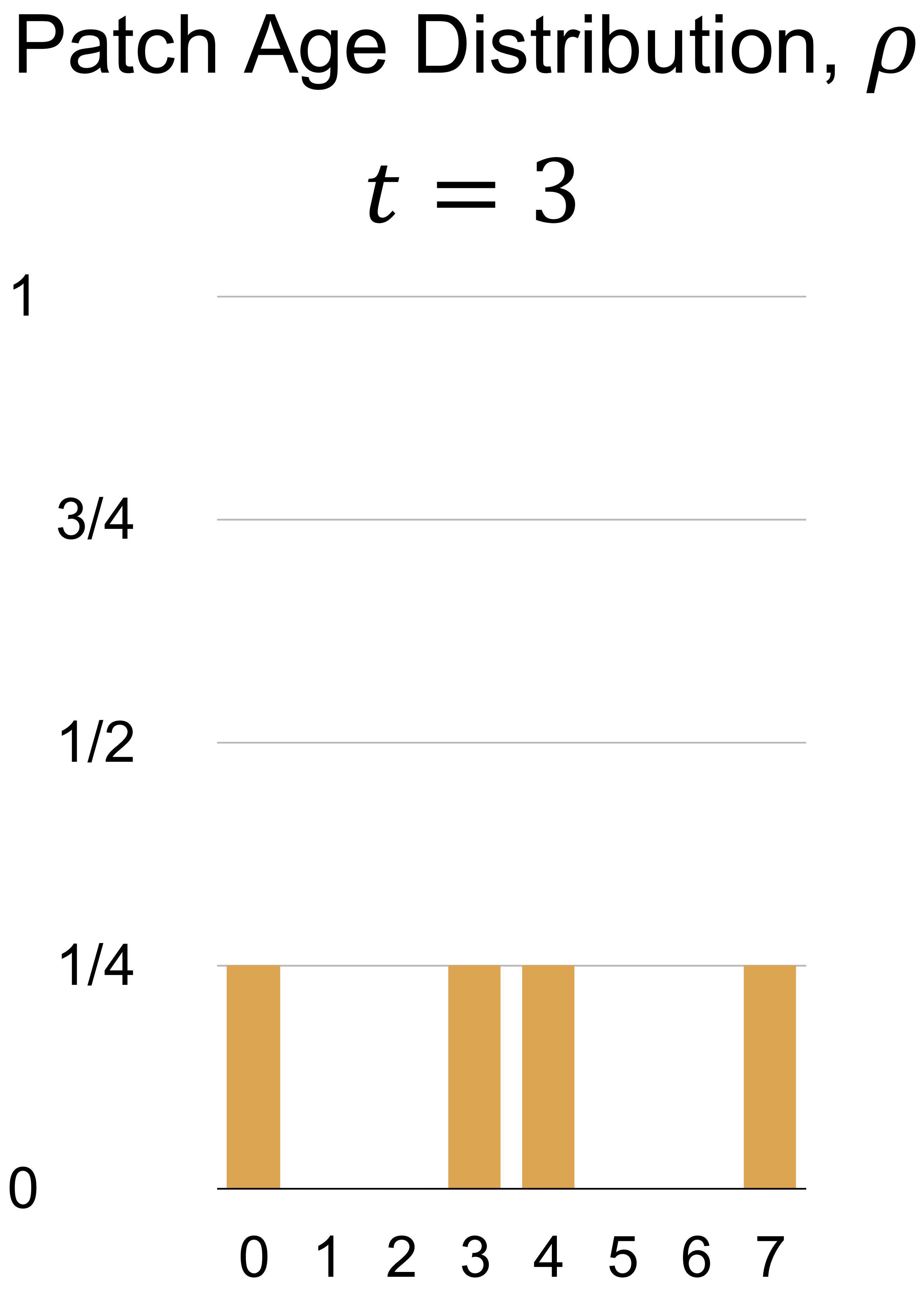
Our Model - Patch Dynamics



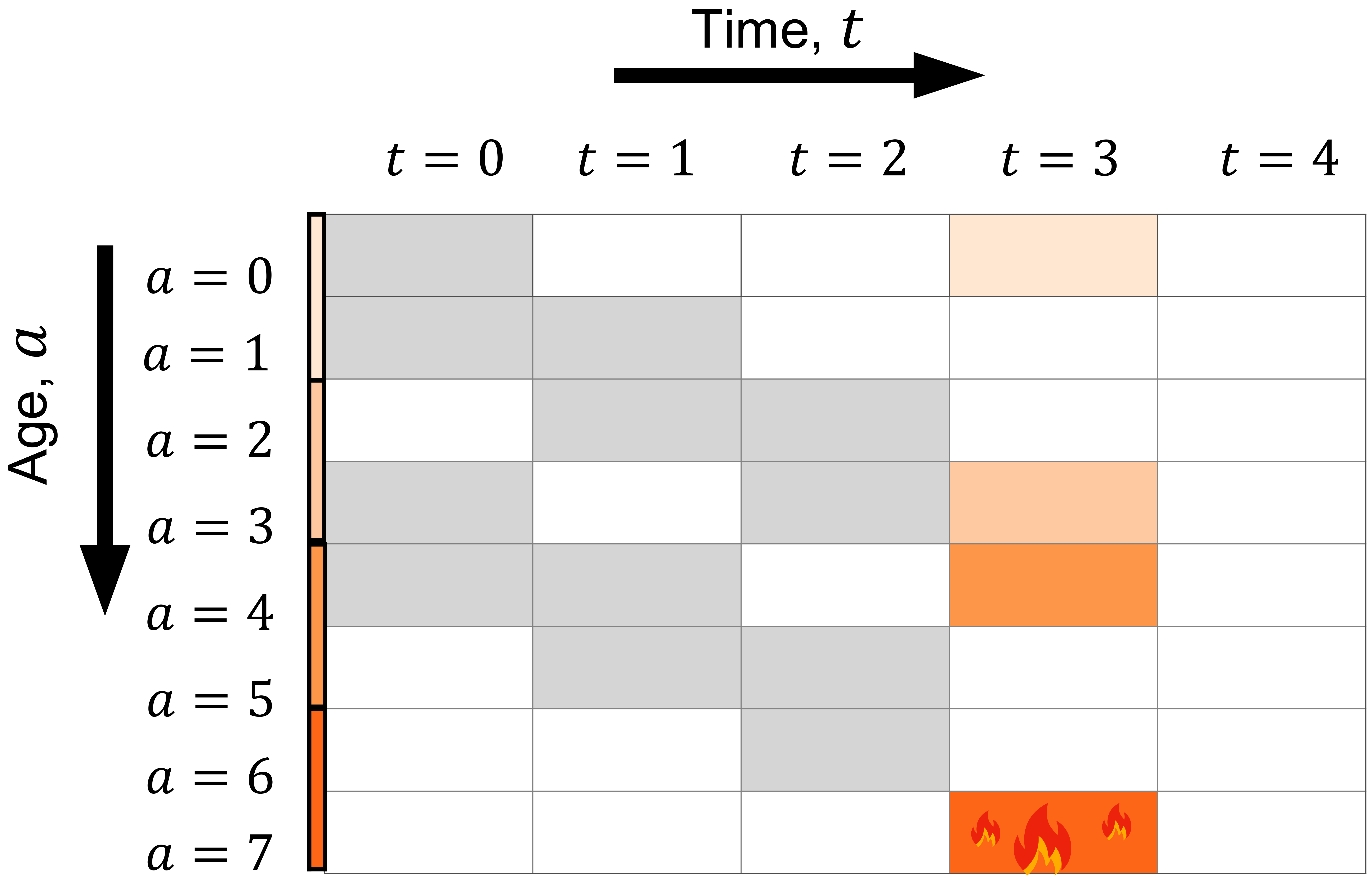


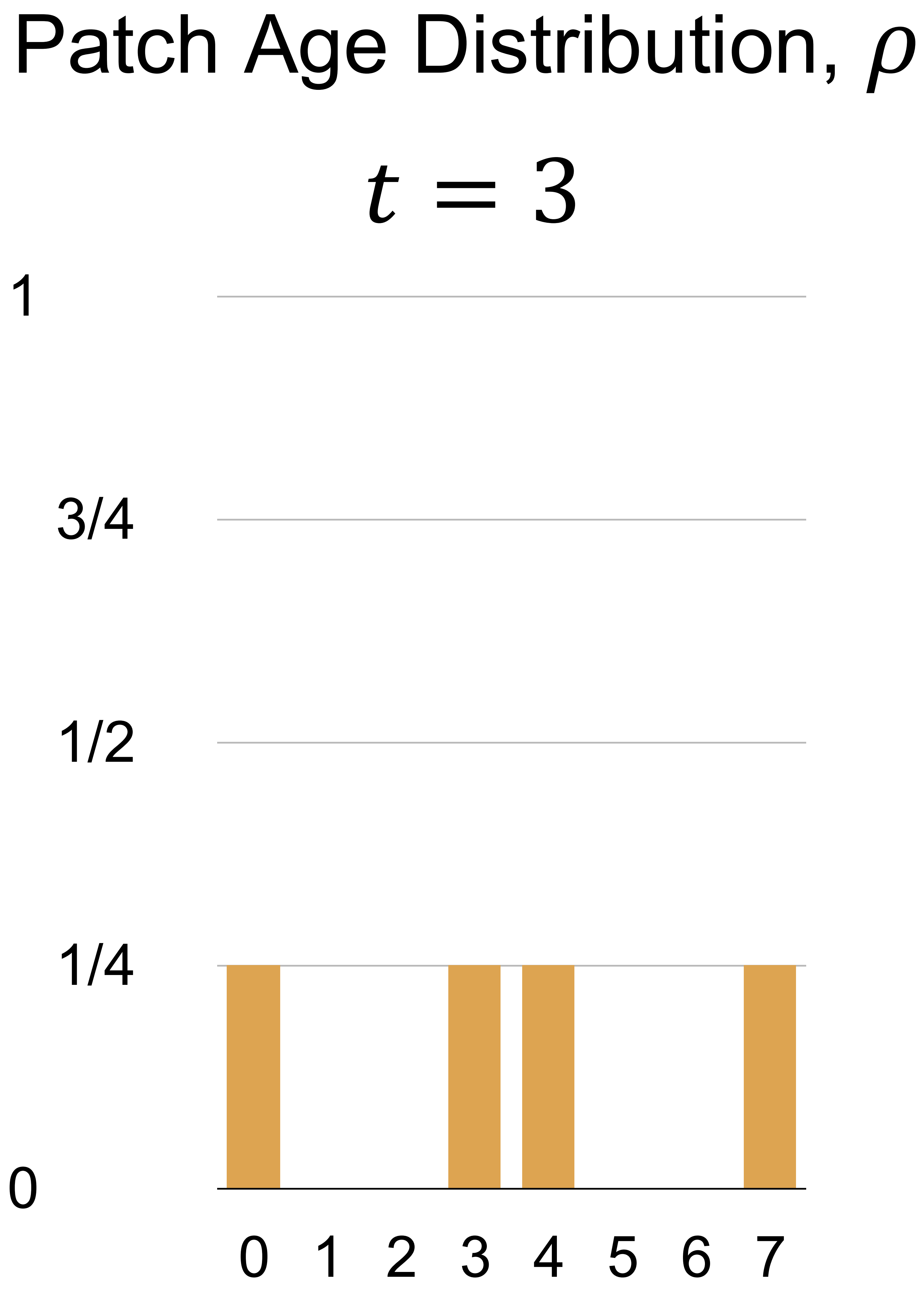
Our Model - Patch Dynamics



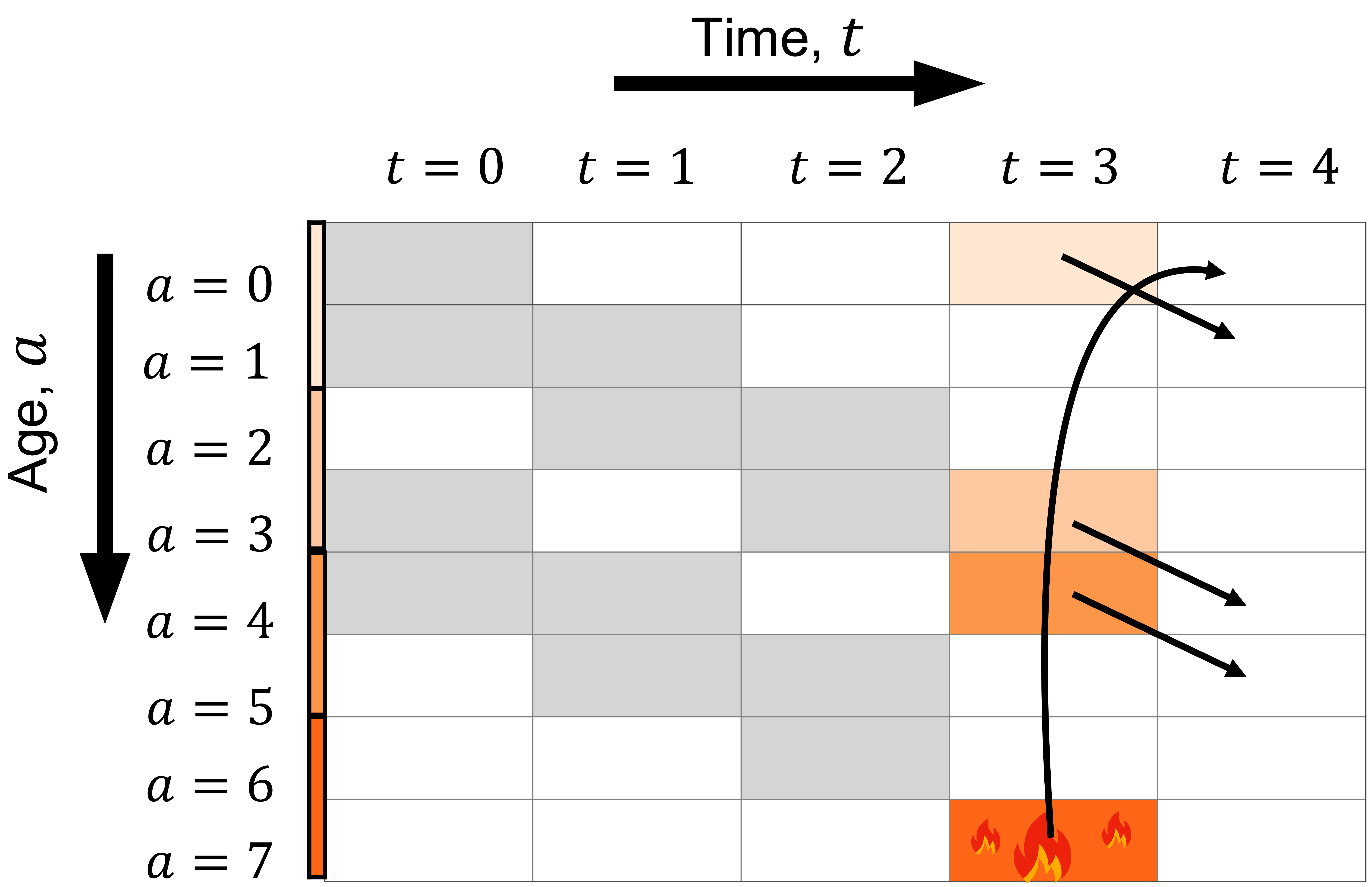


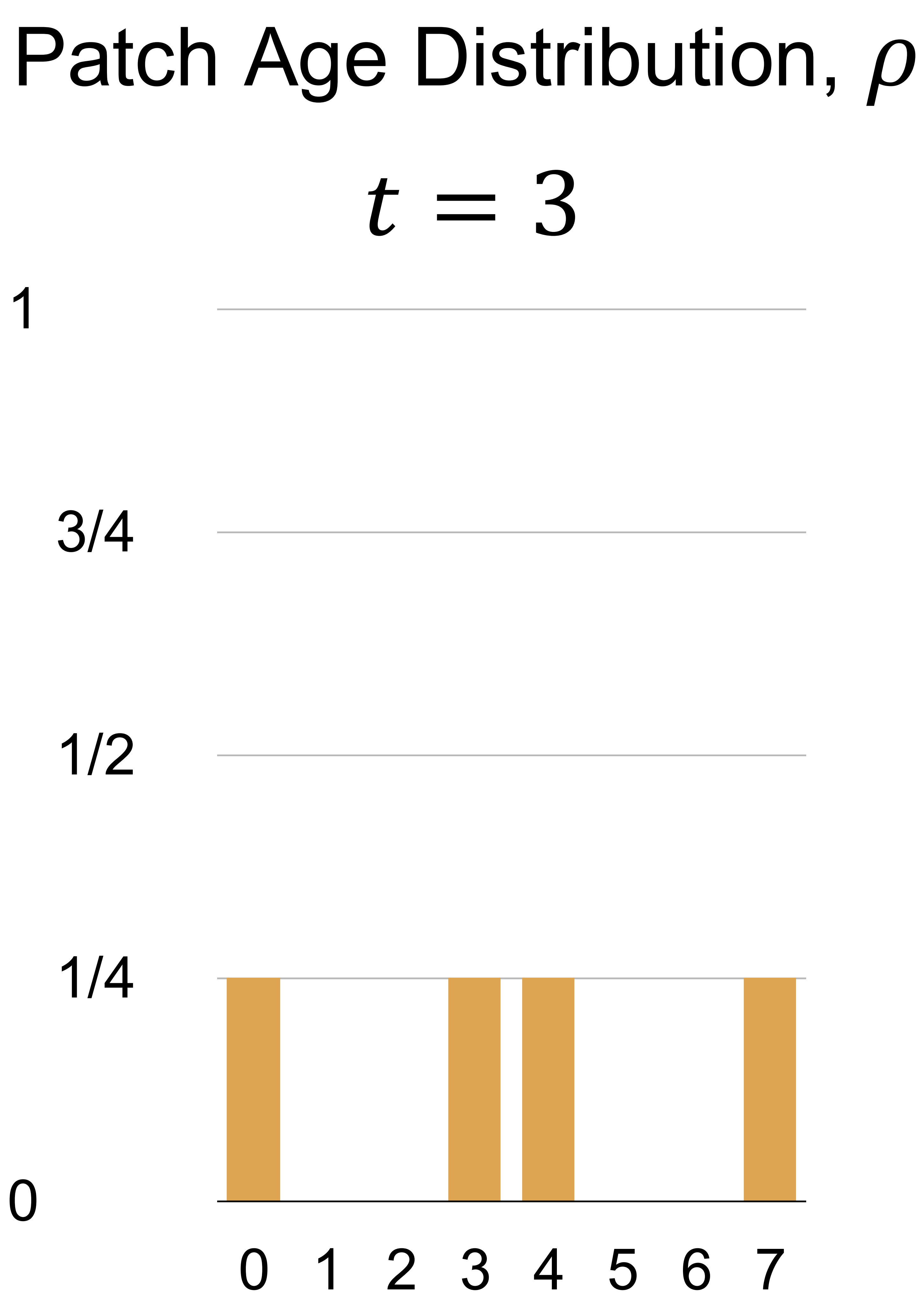
Our Model - Patch Dynamics



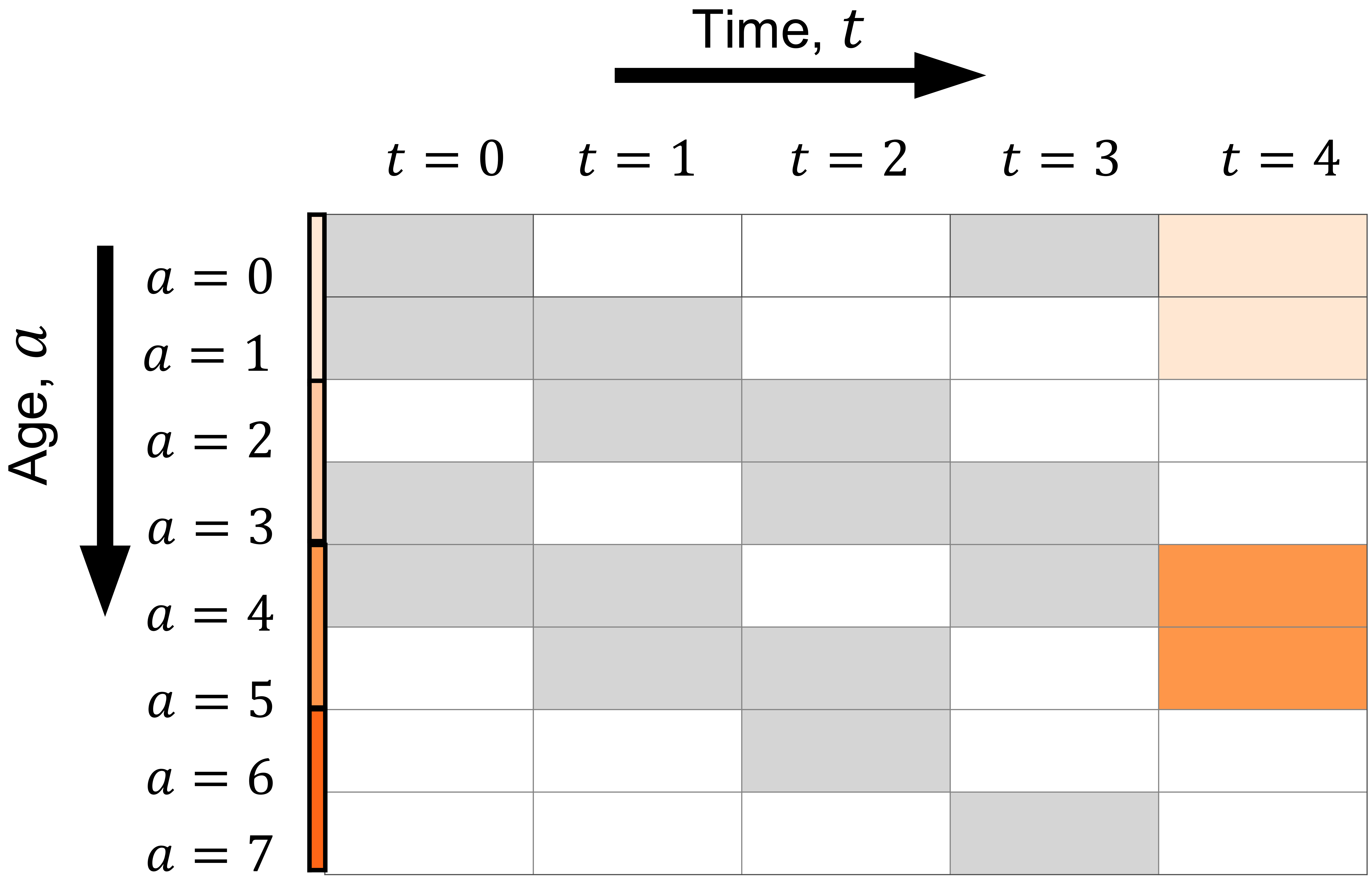


Our Model - Patch Dynamics

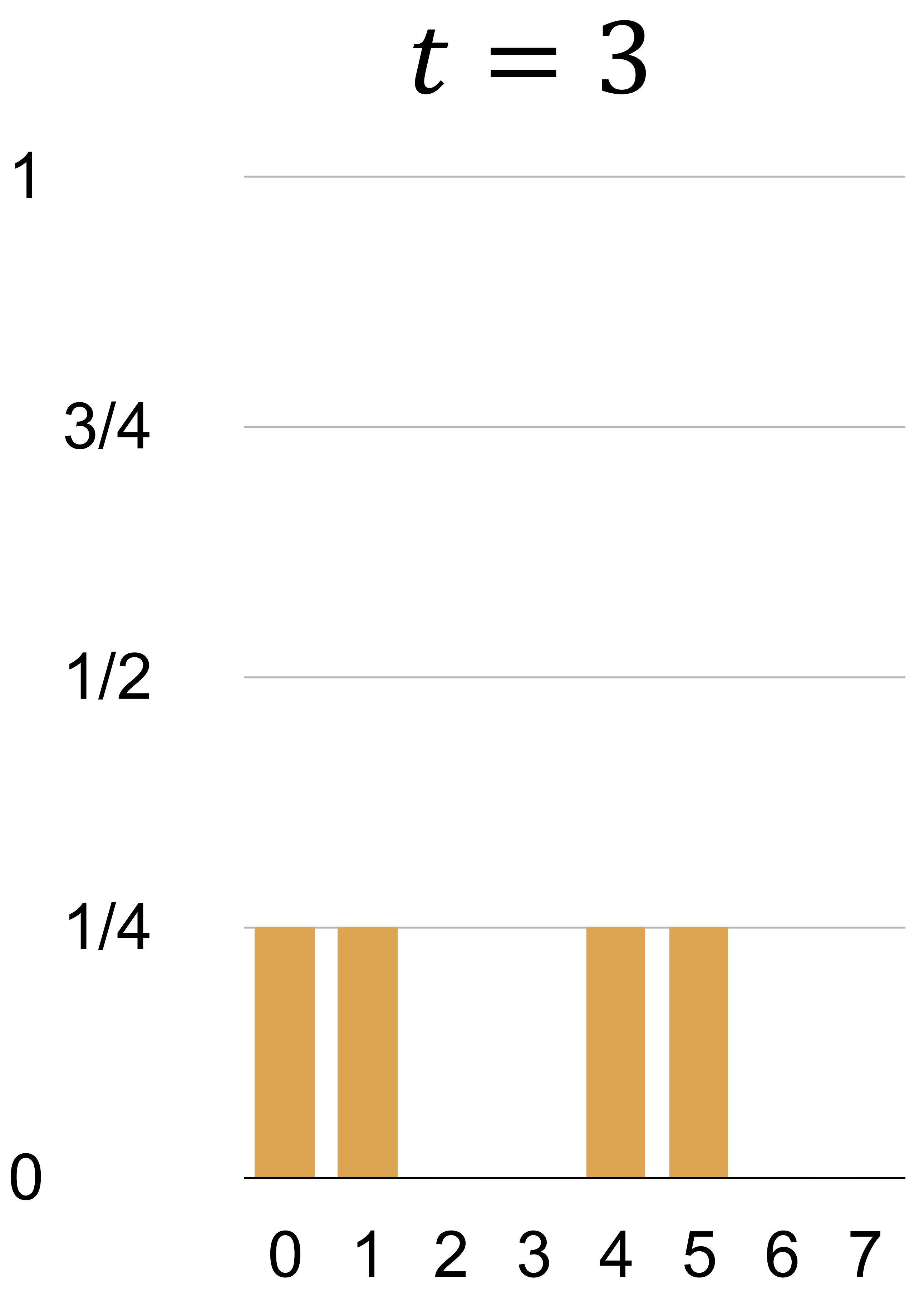




Our Model - Patch Dynamics



Patch Age Distribution, ρ



Our Model - Population Dynamics (1 species)

Now, we put competitive/population dynamics on top of our patches

Our Model - Population Dynamics (1 species)

Now, we put competitive/population dynamics on top of our patches

Let $n = n(a, t)$ be the number of mature individuals on patches of age a at time t

Our Model - Population Dynamics (1 species)

Now, we put competitive/population dynamics on top of our patches

Let $n = n(a, t)$ be the number of mature individuals on patches of age a at time t

$$\frac{\partial}{\partial t} n = -\frac{\partial}{\partial a} n + H(a - \tau)[R(\rho, n; t - \tau) - \mu n]$$
$$n(a, 0) = n_0(a)$$
$$n(s, t) = 0 for s \leq \tau$$

Our Model - Population Dynamics (1 species)

Now, we put competitive/population dynamics on top of our patches

Let $n = n(a, t)$ be the number of mature individuals on patches of age a at time t

Patches younger than τ have no reproductive individuals

aging

Change in number of adults now depends on how many individuals were produced τ time units ago

$$\frac{\partial}{\partial t} n = -\frac{\partial}{\partial a} n + H(a-\tau)[R(\rho, n; t-\tau) - \mu n]$$

mortality

$$n(a, 0) = n_0(a)$$ Initial condition

$$n(s, t) = 0 \quad s \leq \tau$$ Boundary condition

Our Model - Population Dynamics (1 species)

We couple patch dynamics with population dynamics through the reproduction term. Each patch older than τ can contribute to reproduction. Maturation time is accounted for with the time delay.

$$\frac{\partial}{\partial t}n_i = -\frac{\partial}{\partial a}n_i + H(a-\tau_i)[R(\rho, n; t-\tau_i) - \mu_i n]$$

$$n_i(a,0) = n_{i,0}(a)$$

$$n_i(s,t) = 0 \quad s \le \tau_i$$

$$b\int_{\tau}^{\infty}\rho(s)n(s,t-\tau)(1-\alpha n(s,t-\tau))\mathrm{ds}$$

Our Model - Population Dynamics (k species)

Each species has the following dynamics:

$$\frac{\partial}{\partial t} n_i = -\frac{\partial}{\partial a} n_i + H(a-\tau_i)[R(\rho, n; t-\tau_i) - \mu_i n]$$

$$n_i(a, 0) = n_{i,0}(a)$$

$$n_i(s, t) = 0 \mathit{for} s \leq \tau_i$$

Coupled via competition

$$b_i \int_{\tau}^{\infty} \rho(s) n_i(s, t-\tau_i)\left(1 - \alpha_i \sum_{j}^{k} n_j(s, t-\tau_i)\right) \mathrm{ds}$$

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (1 Species)

Our Model - Pop. Dynamics (2 Species)

Theoretical Results

Theoretical Results

Analytical results are derived from an *invasion analysis*

- Assume a resident species j is at equilibrium and insert a small density of species i. We then derive conditions for species i positive per capita growth rate

Theoretical Results

Analytical results are derived from an *invasion analysis*

- Assume a resident species j is at equilibrium and insert a small density of species i. We then derive conditions for species i positive per capita growth rate

We establish analytical criteria for **mutual invasion** and ***stable coexistence*** when age of first reproduction, τ, is traded off against:

b - per capita recruitment rate to adulthood

μ - per capita (intrinsic) adult morality rate

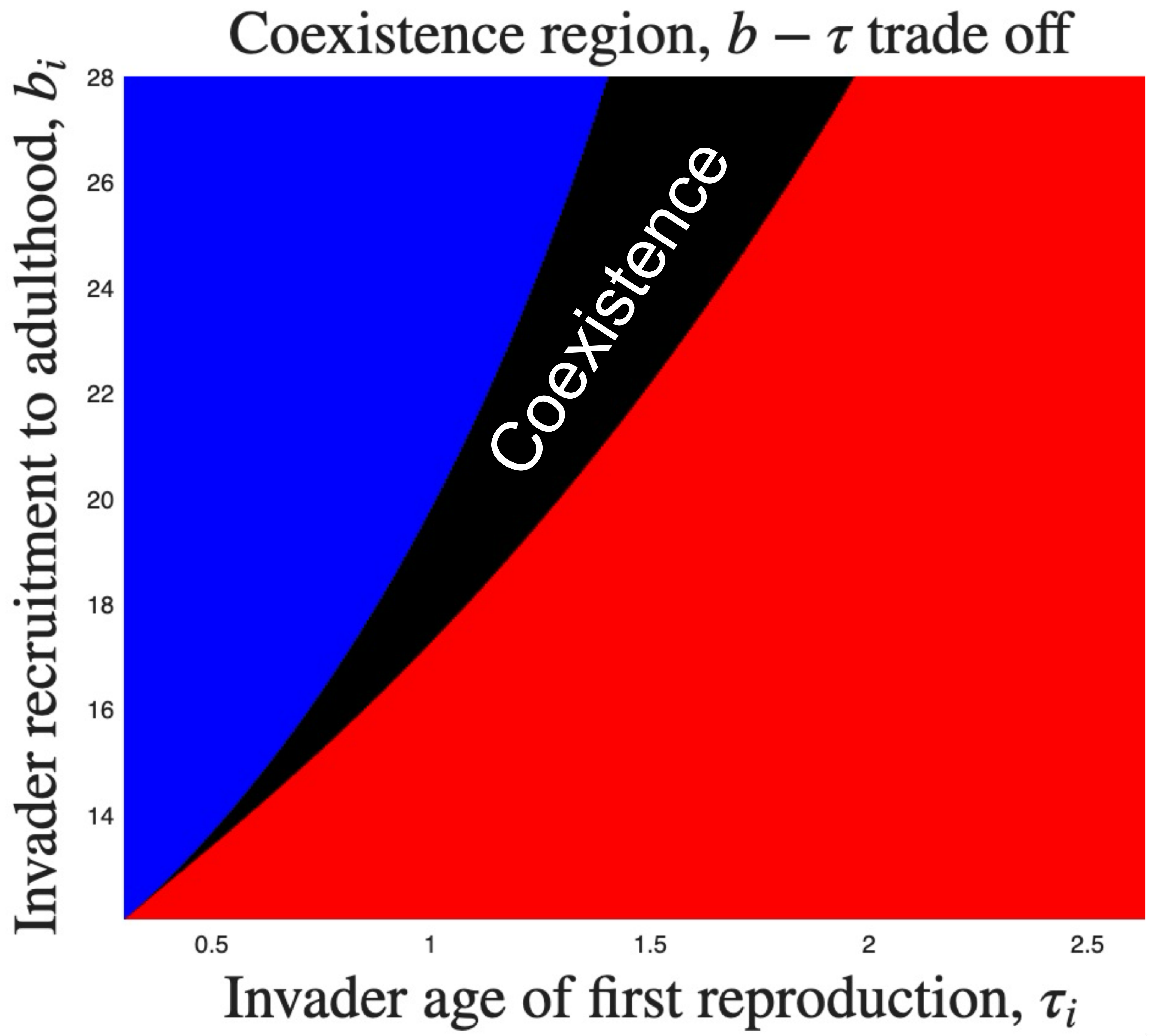
Theoretical Results

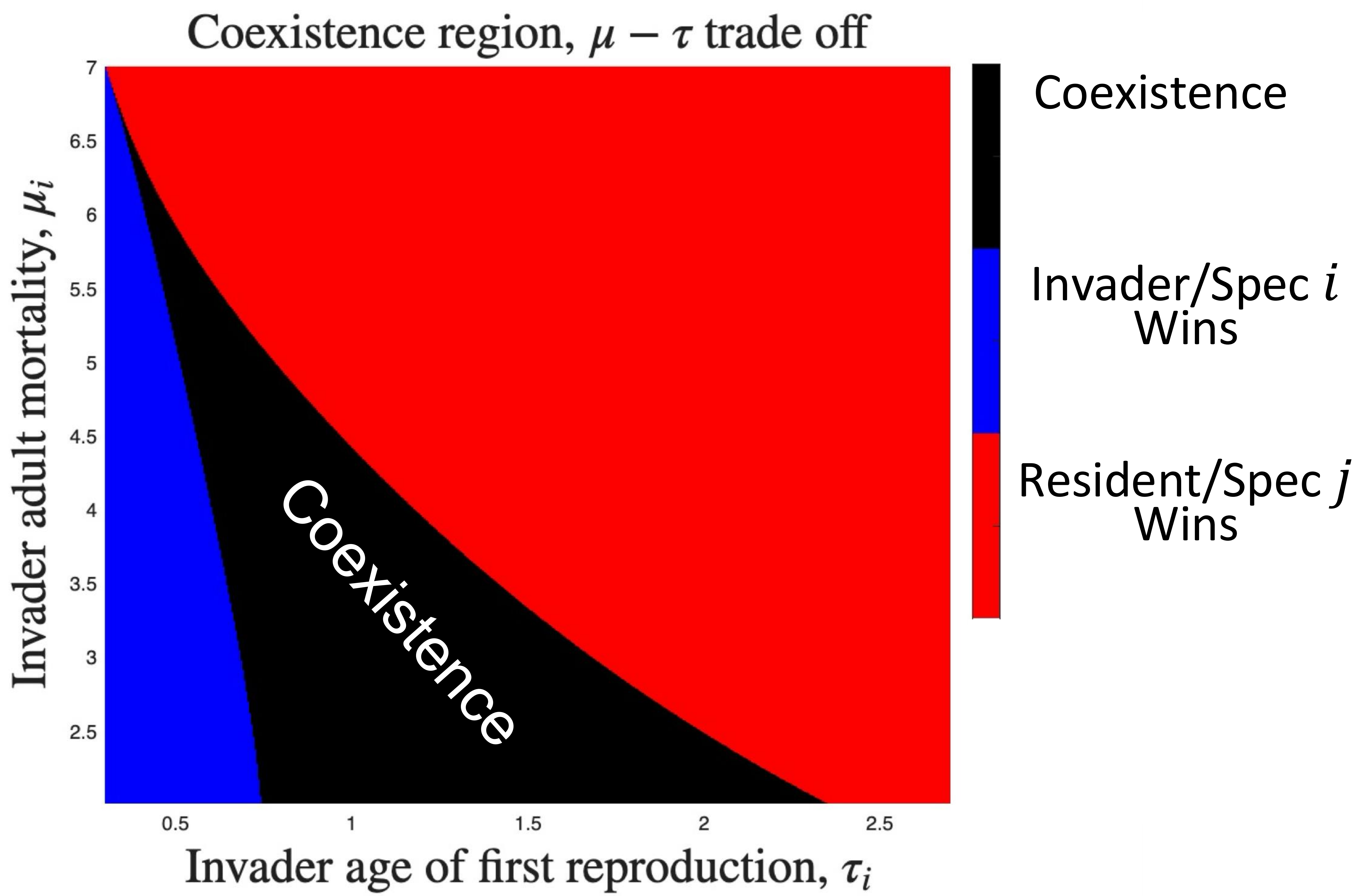
We can take this mutual invasibility criteria and parameterize our model with BCI data and generate theoretical coexistence regions.

Theoretical Results

axis are scaled*

We can take this mutual invasibility criteria and parameterize our model with BCI data and generate theoretical coexistence regions.

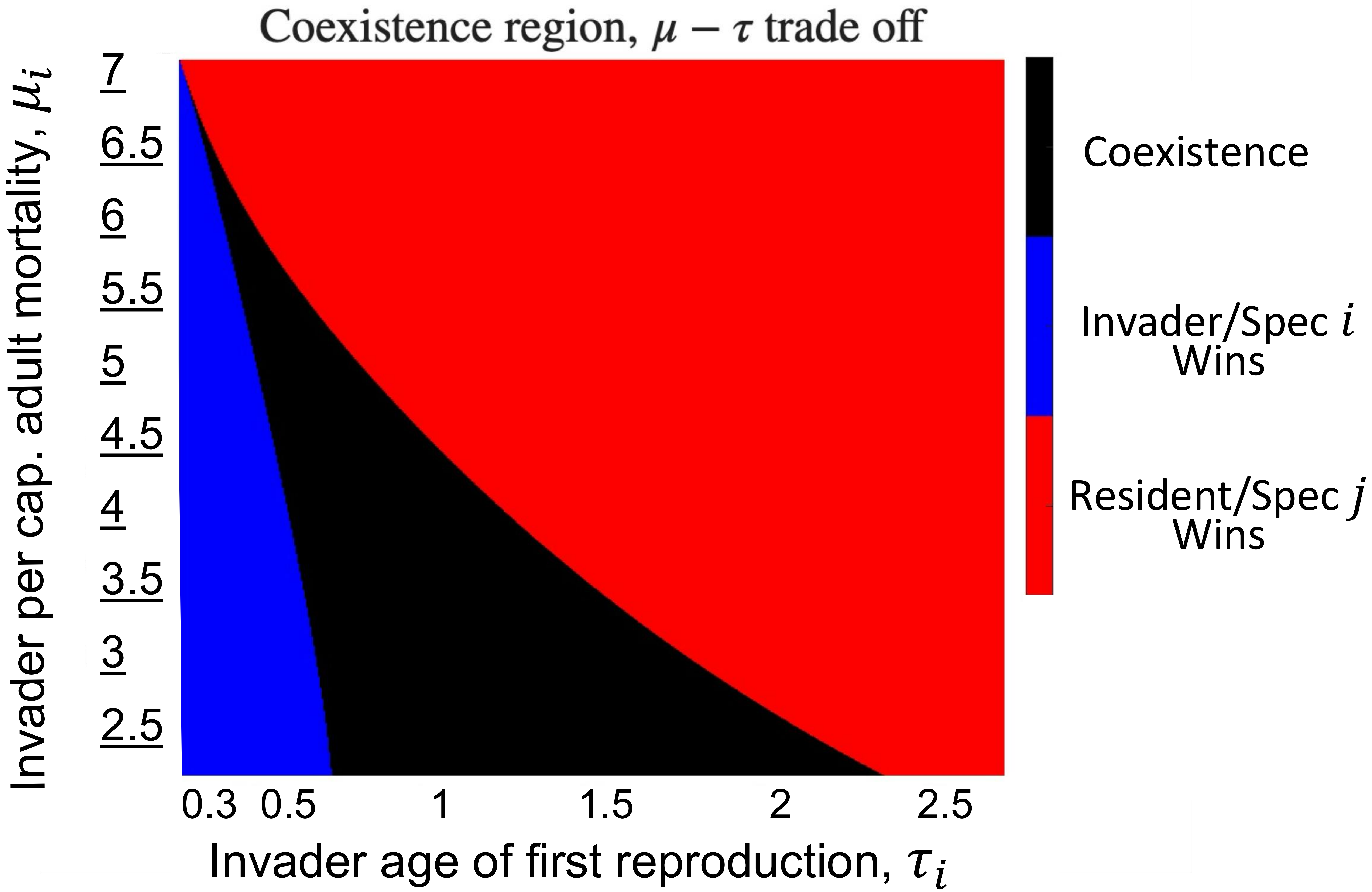




Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

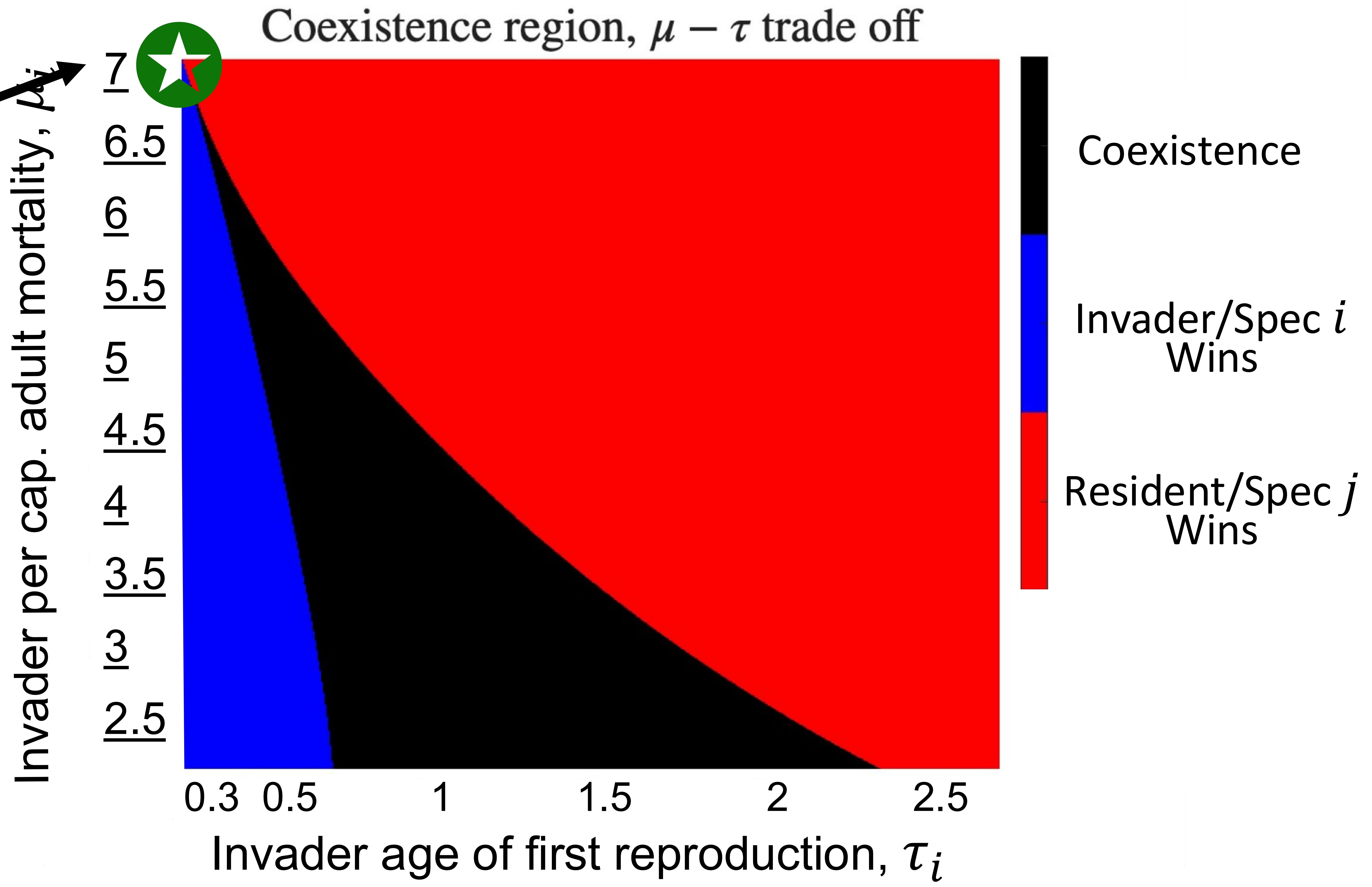


Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

Take a species j with
per cap. adult mortality, $\mu_j = 7$,

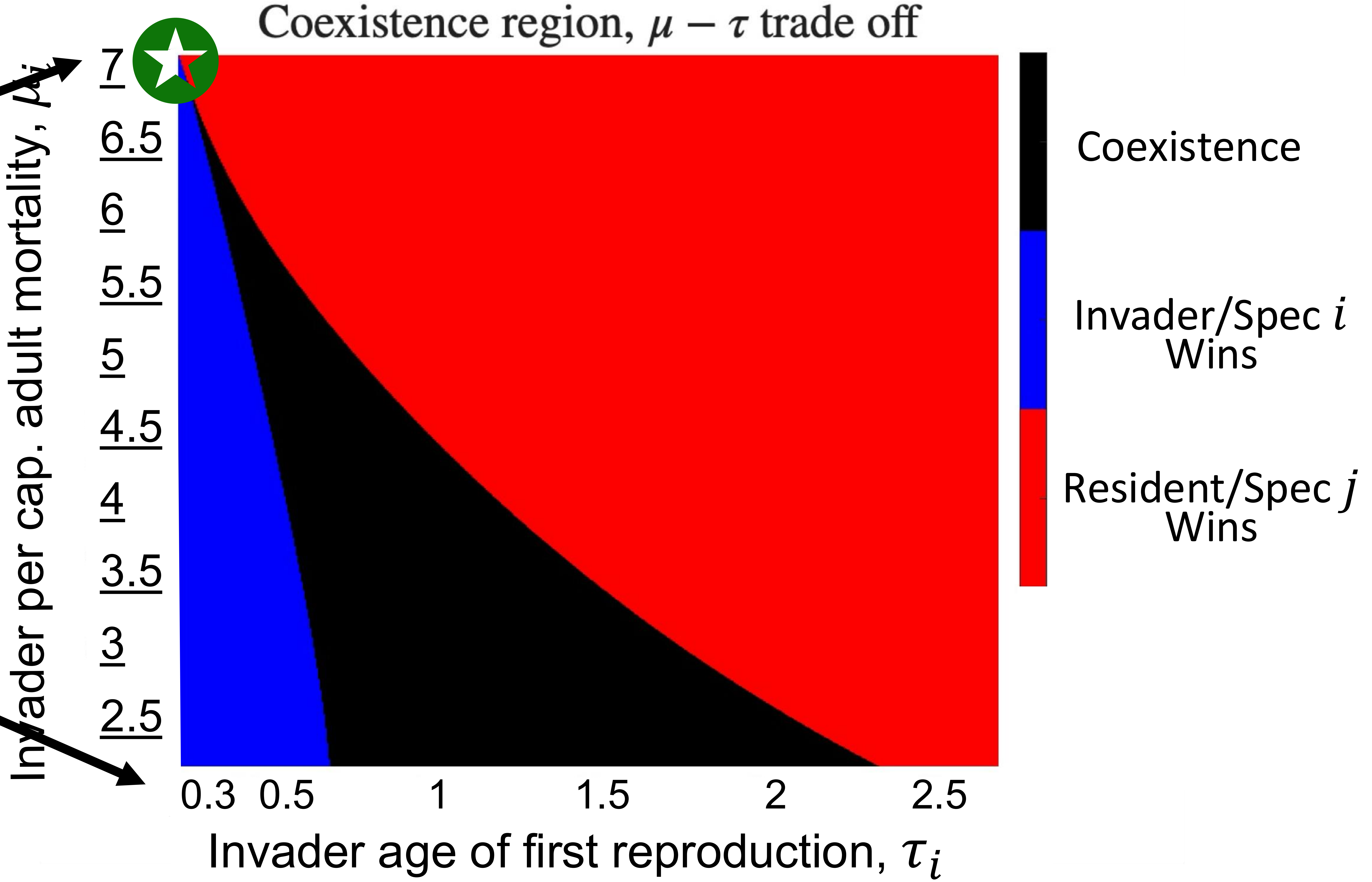


Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

Take a species j with per cap. adult mortality, $\mu_j = 7$, and age of first reproduction $\tau_j = .3$



axis are scaled*

$\tau = .3$ means 30 years

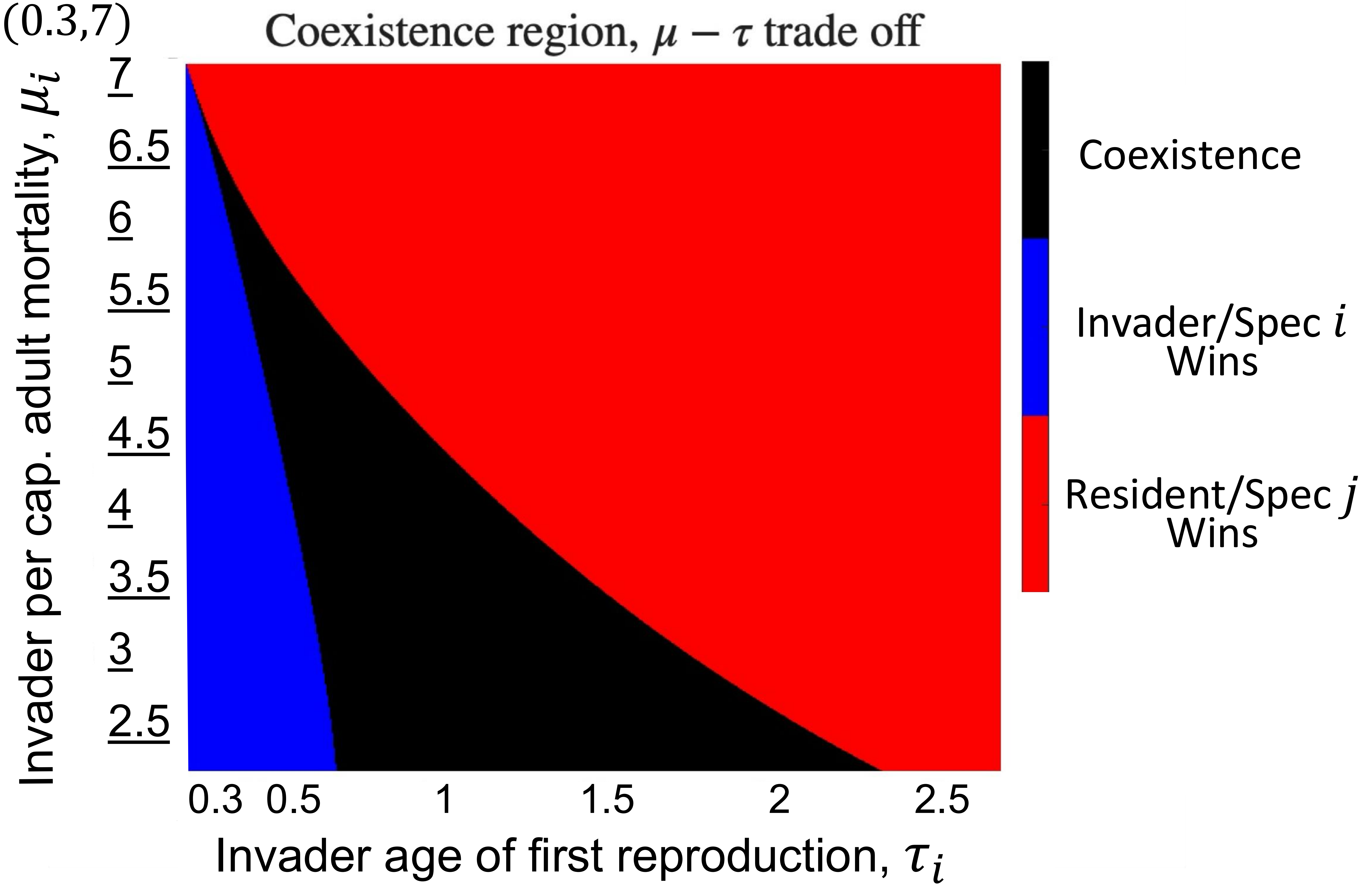
Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

$(\tau_j, \mu_j) = (0.3, 7)$

Take another species i



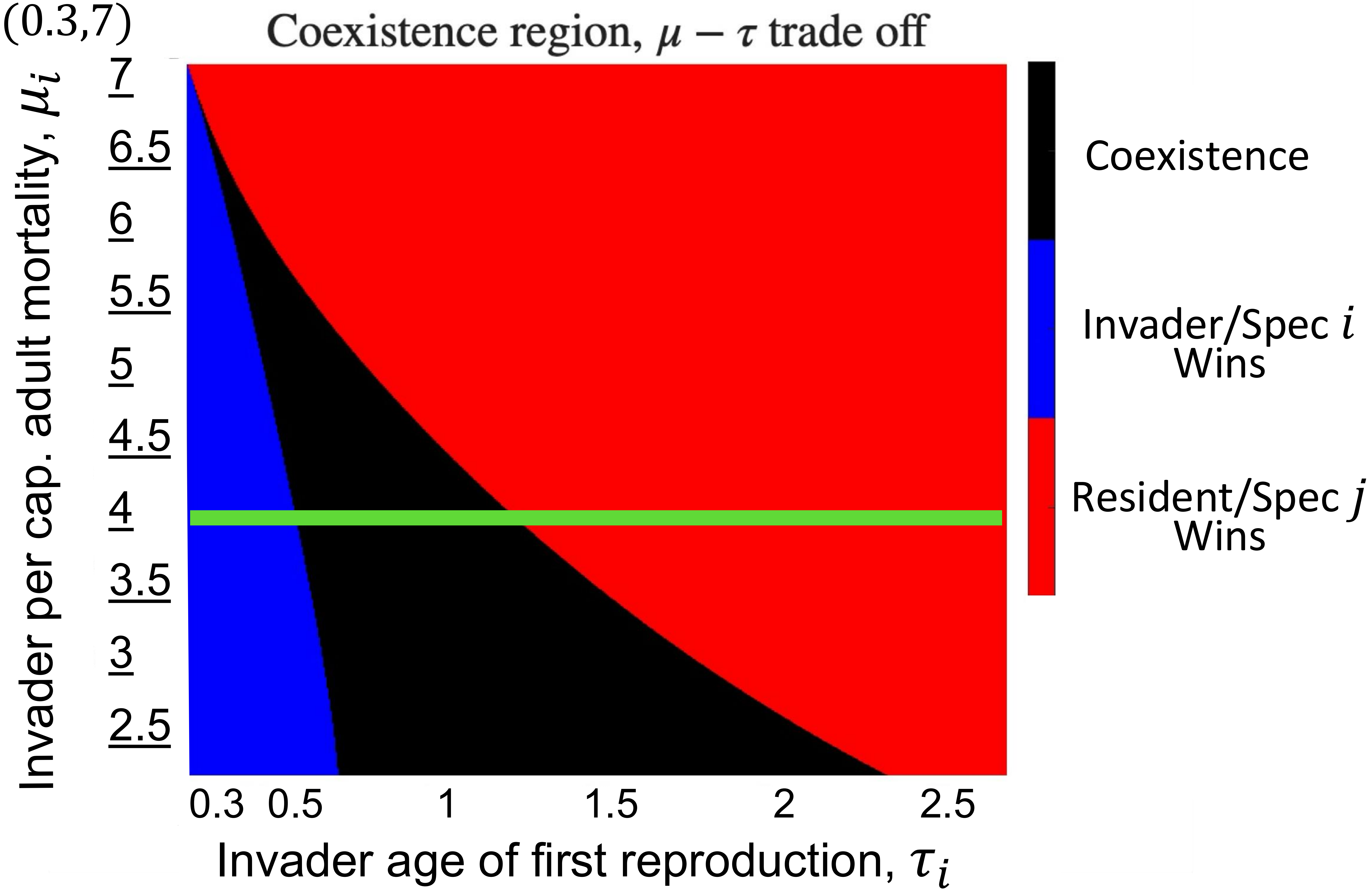
Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

$(\tau_j, \mu_j) = (0.3, 7)$

Take another species i
per cap. adult mortality, $\mu_i = 4$,



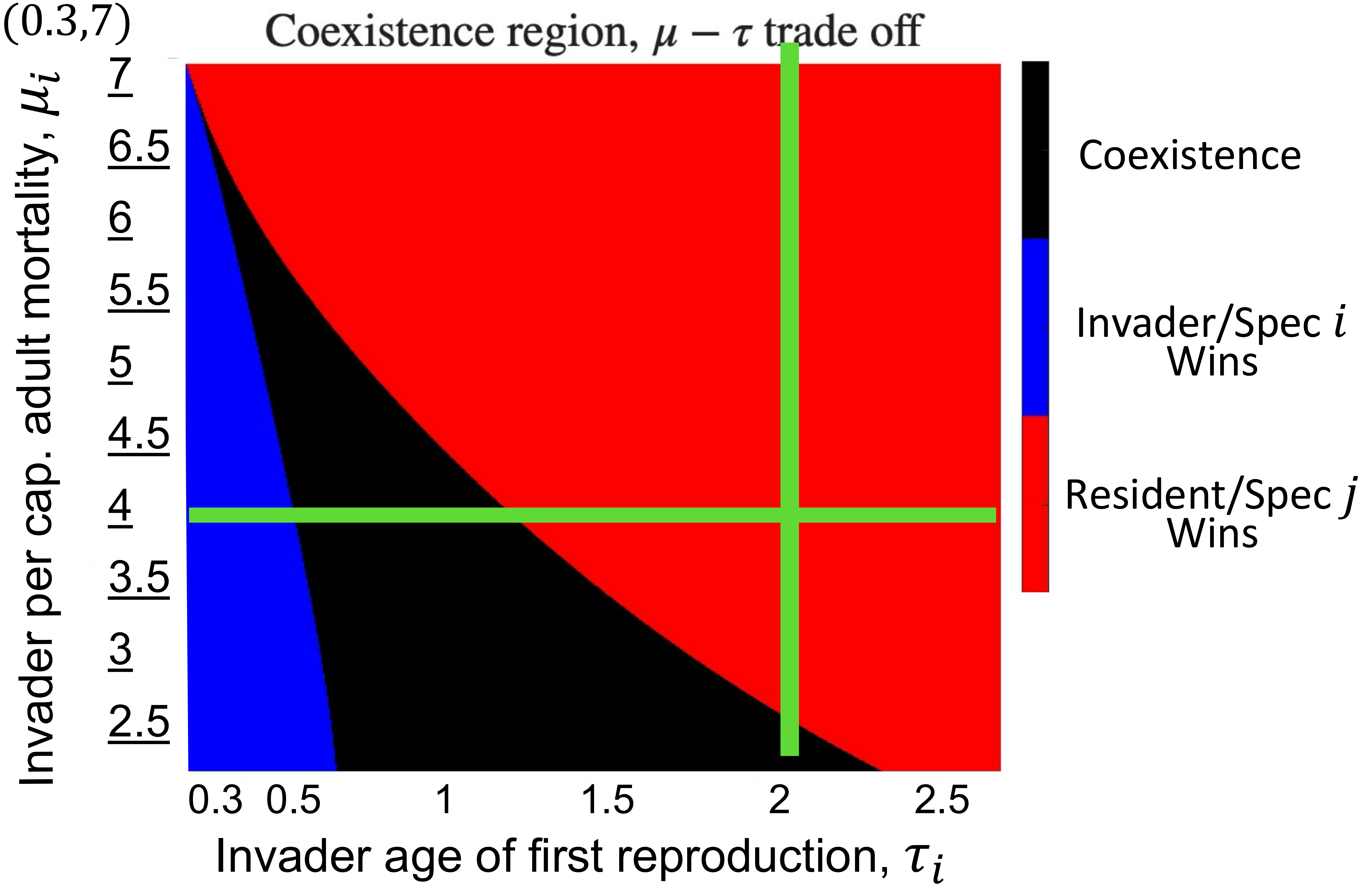
Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

$(\tau_j, \mu_j) = (0.3, 7)$

Take another species i
per cap. adult mortality, $\mu_i = 4$,
and age of first reproduction
$\tau_j = 2$



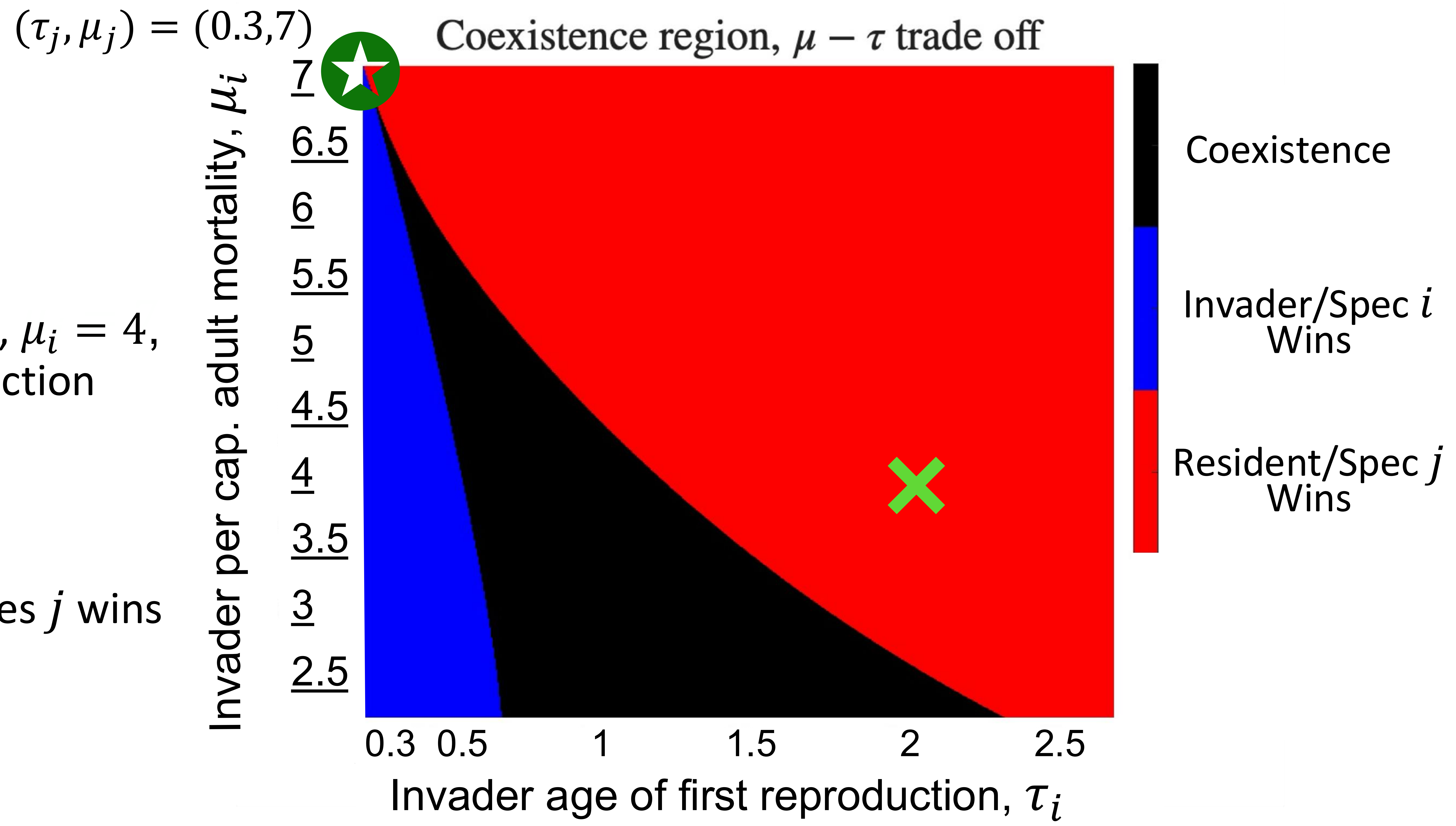
Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.

Take another species i
per cap. adult mortality, $\mu_i = 4$,
and age of first reproduction
$\tau_j = 2$

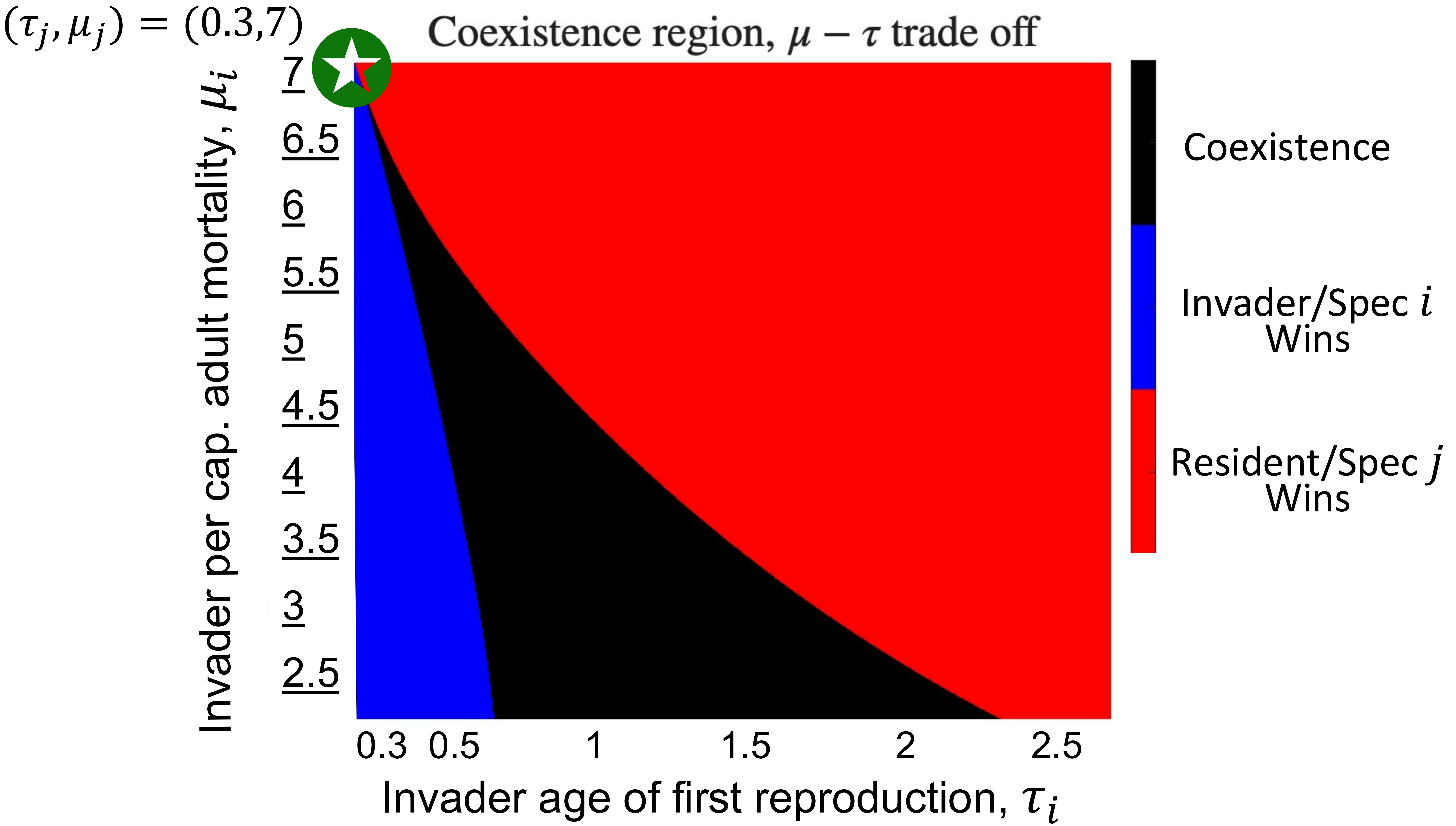
Then the resident species j wins



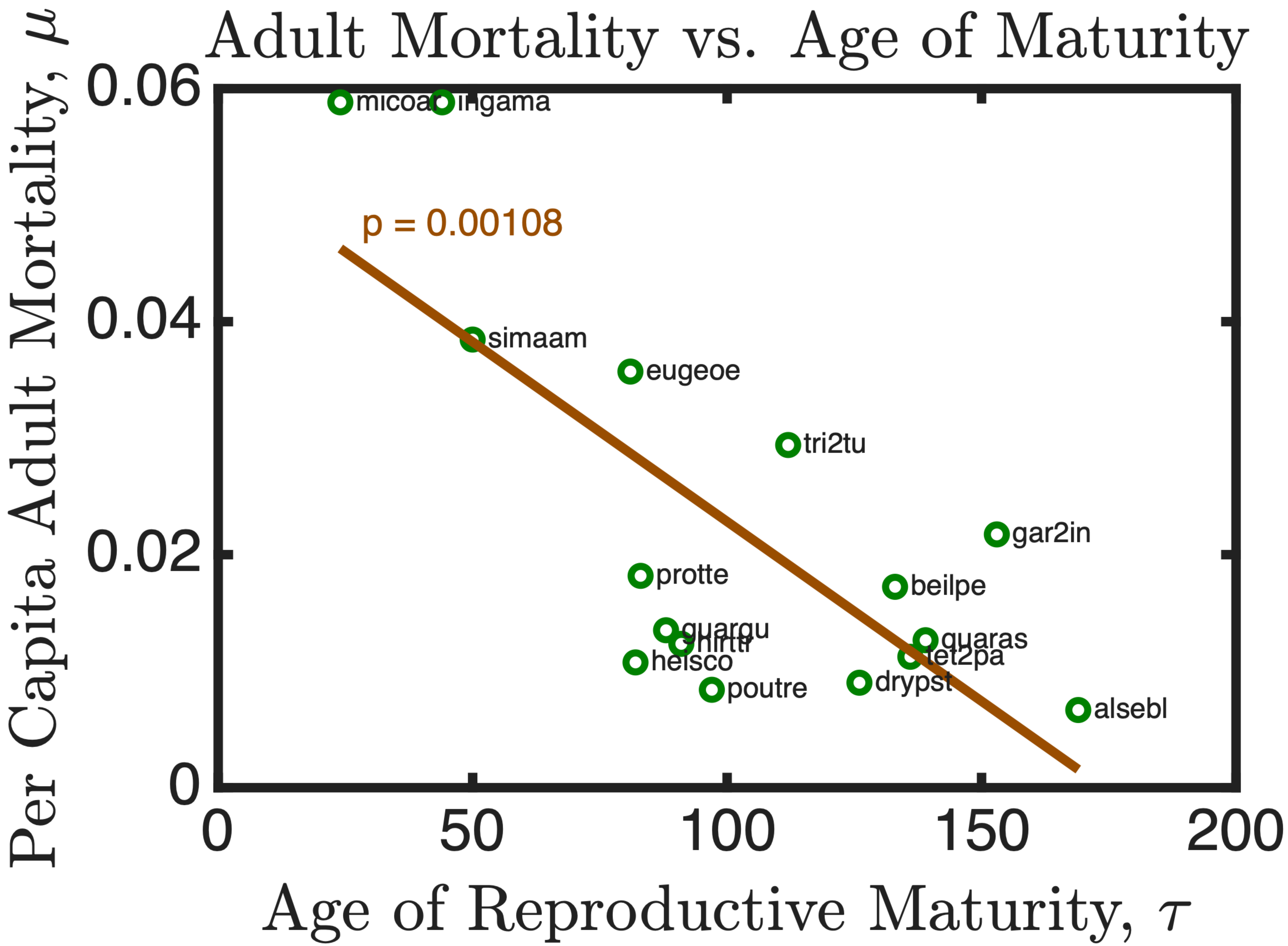
Theoretical Results

axis are scaled*

Trade-off between per cap. adult mortality rate, μ, and age of first reproduction, τ.



Data from BCI (ForestGeo Plot)



Labels are species shorthand.

Key Takeaways

Key Takeaways

- Age of first reproduction is a key trait axis which species vary along

Key Takeaways

- Age of first reproduction is a key trait axis which species vary along

- Age of first reproduction can trade off against several other demographic components to theoretically generate coexistence

Key Takeaways

- Age of first reproduction is a key trait axis which species vary along

- Age of first reproduction can trade off against several other demographic components to theoretically generate coexistence

- Empirical evidence trade offs against age of first reproduction is operating a tropical forest

Advertisement

Preprint will be out imminently so keep an eye out on BioRxiv!

Presentation and code available on github:

https://github.com/Jrostaggs97/age_of_reproduction_patch_dynamics

Acknowledgements and Questions

Thank you to my collaborators, coauthors, and Ostling lab

Acknowledgements and Questions

Thank you to my collaborators, coauthors, and Ostling lab

Thank you to Rick Condit for helpful discussions

Acknowledgements and Questions

Thank you to my collaborators, coauthors, and Ostling lab

Thank you to Rick Condit for helpful discussions

BCI Acknowledgement:

The BCI forest dynamics research project was made possible by National Science Foundation grants to Stephen P. Hubbell, support from ForestGEO, STRI, the John D. and Catherine T. MacArthur Foundation, the Mellon Foundation, the Small World Institute Fund, and numerous private individuals, and through the hard work of over 100 people from 10 countries over the past three decades.

Acknowledgements and Questions

Thank you to my collaborators, coauthors, and Ostling lab

Thank you to Rick Condit for helpful discussions

BCI Acknowledgement:

The BCI forest dynamics research project was made possible by National Science Foundation grants to Stephen P. Hubbell, support from ForestGEO, STRI, the John D. and Catherine T. MacArthur Foundation, the Mellon Foundation, the Small World Institute Fund, and numerous private individuals, and through the hard work of over 100 people from 10 countries over the past three decades.

Thank you to ESA conference organizers, admin, and volunteers

Acknowledgements and Questions

Thank you for listening!

Questions?

Email: jon.staggs@utexas.edu

https://github.com/Jrostaggs97/age_of_reproduction_patch_dynamics