Steady States in Population Dynamics

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Overview

Models of population dynamics

- That reach steady state—i.e., neither grow without limit nor die out
- From classical (nineteenth century) to quite recent
- We consider first, mean field models, then, models with spatial dynamics

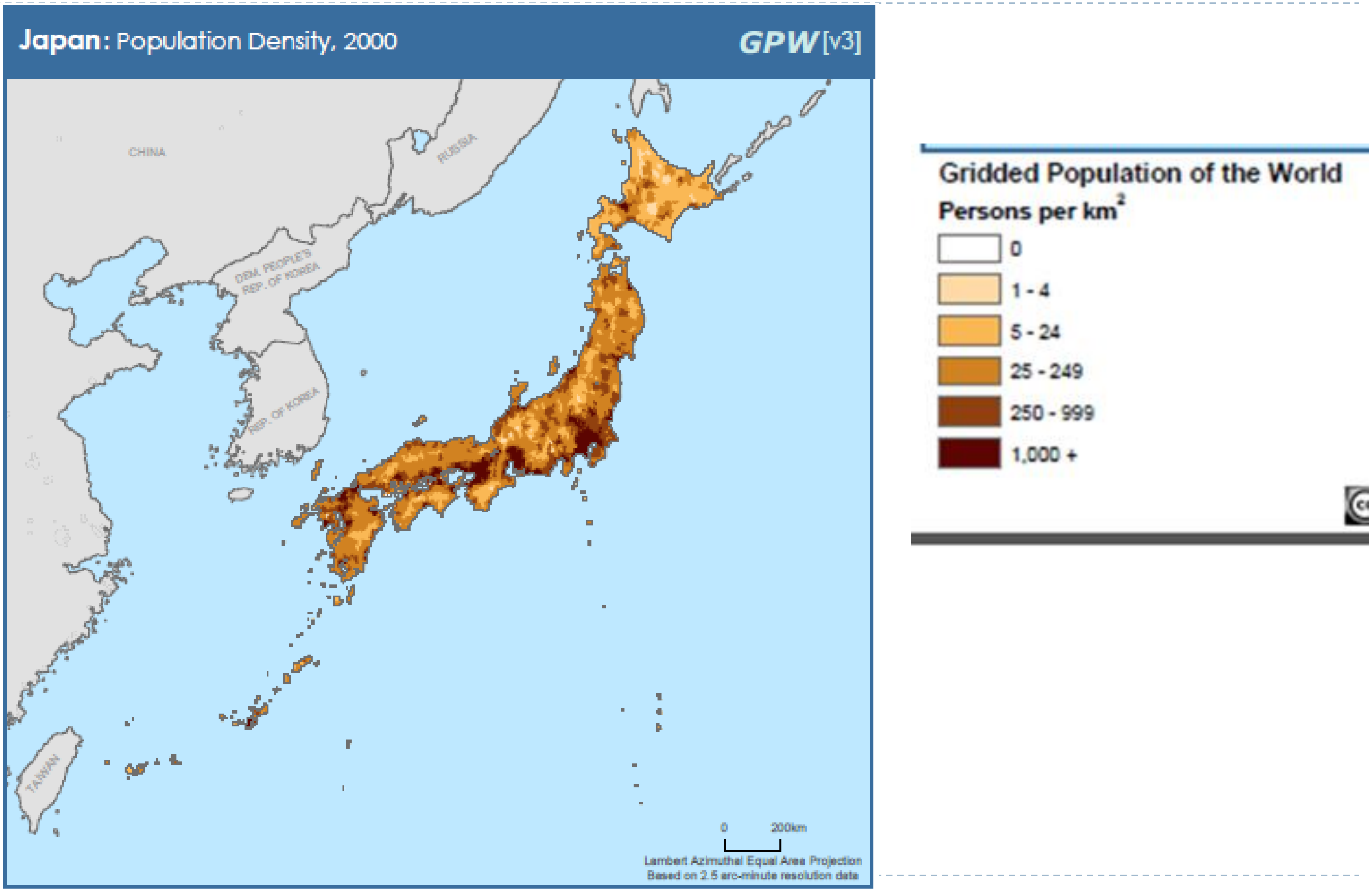
Related qualitative effects in steady state populations

- Clusterization: tendency of population to form clusters of increasing size separated by nearly empty space of increasing size (see satellite photographs)

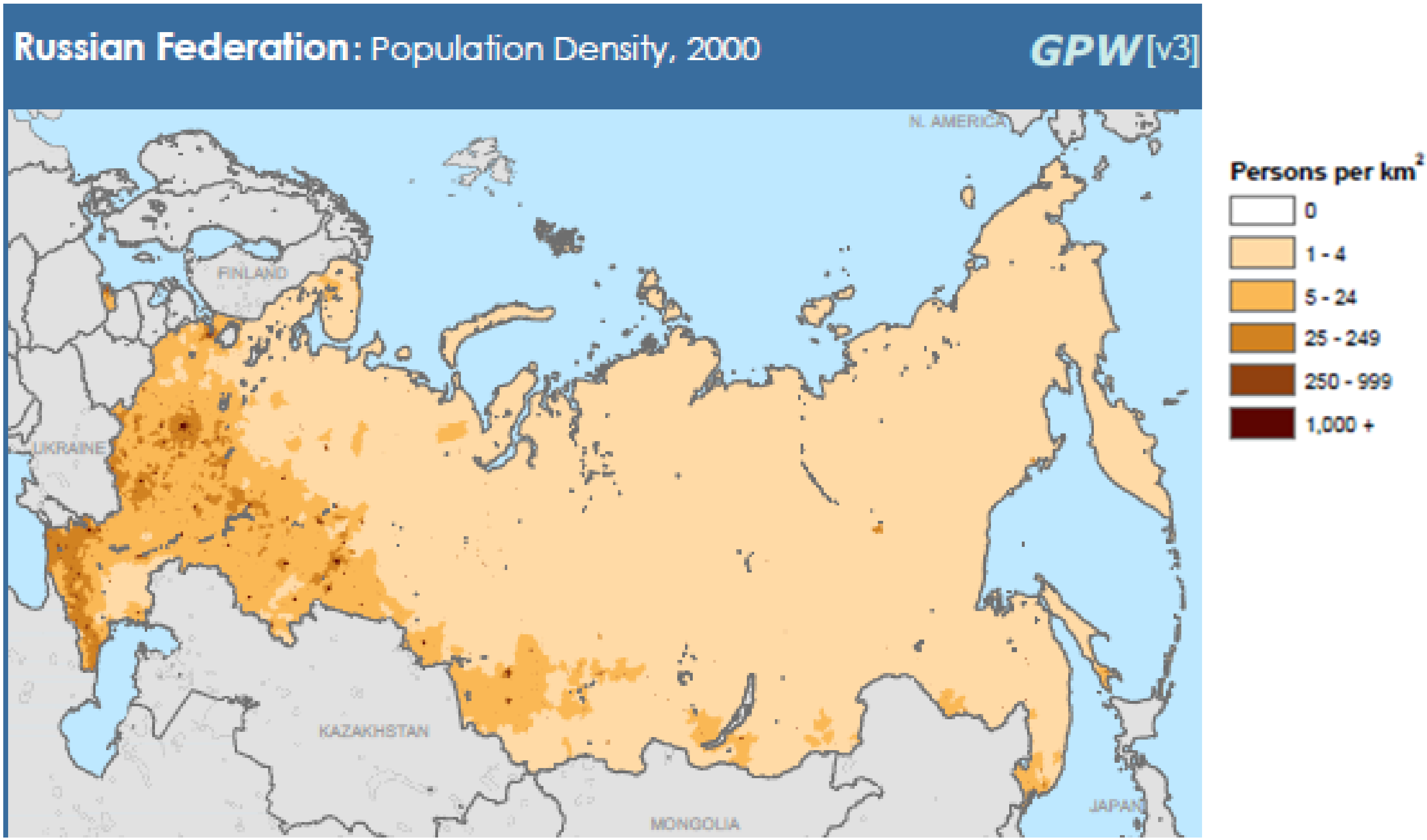
- Intermittency: identified mathematically by $\dfrac{m_2}{m_1^2} \xrightarrow[t\to\infty]{} \infty$
  where m_1 and m_2 are first and second moments
  closely related to clusterization

- Globalization: a network effect
  the vast majority of the nodes in a network become indirectly linked
  a manifestation of the Erdös-Renyi Theorem for random graphs
  i.e., a giant component emerges above a critical value of expected degree

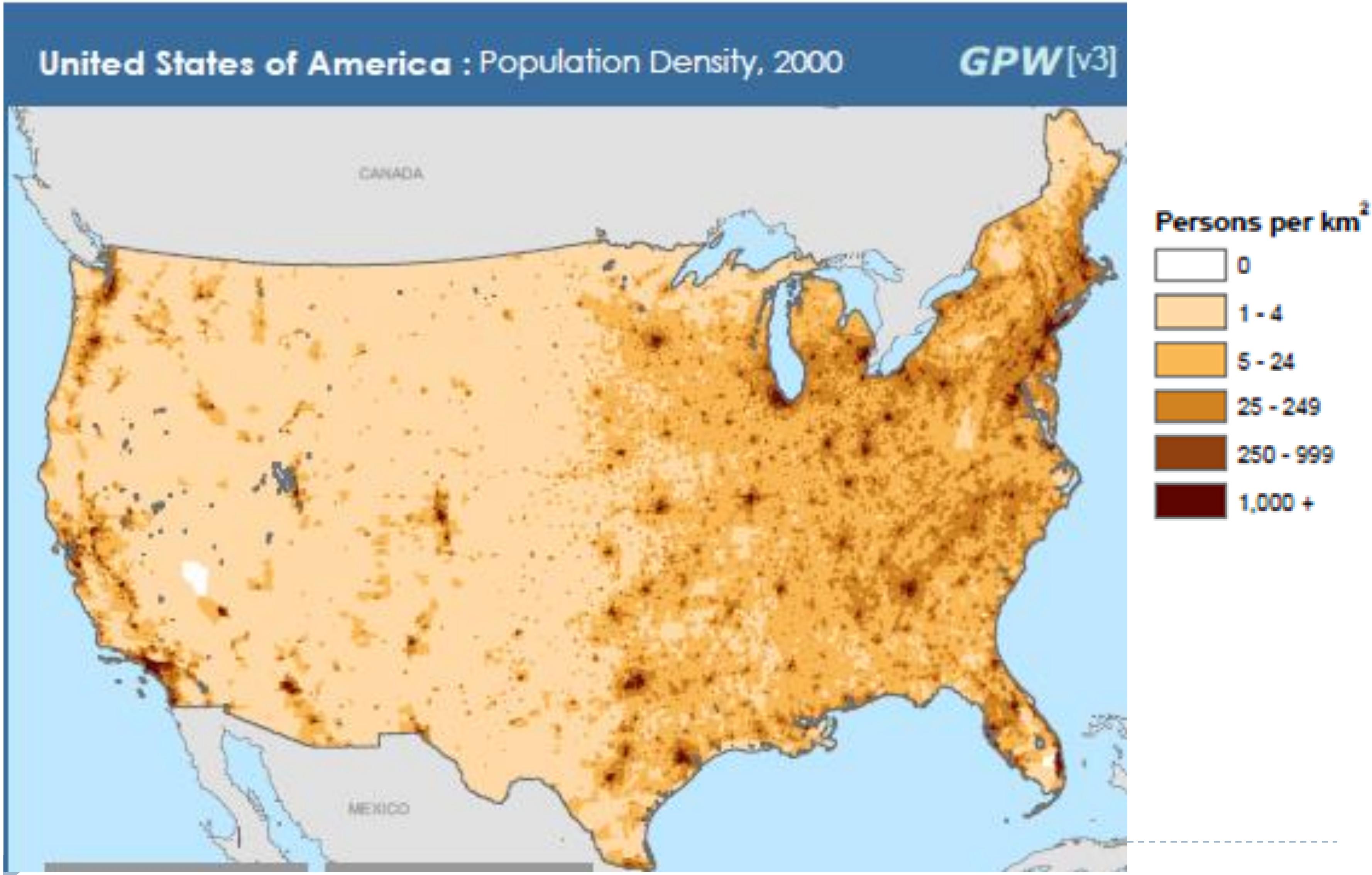
Population Clusterization in Japan (Data from OECD.Stat)



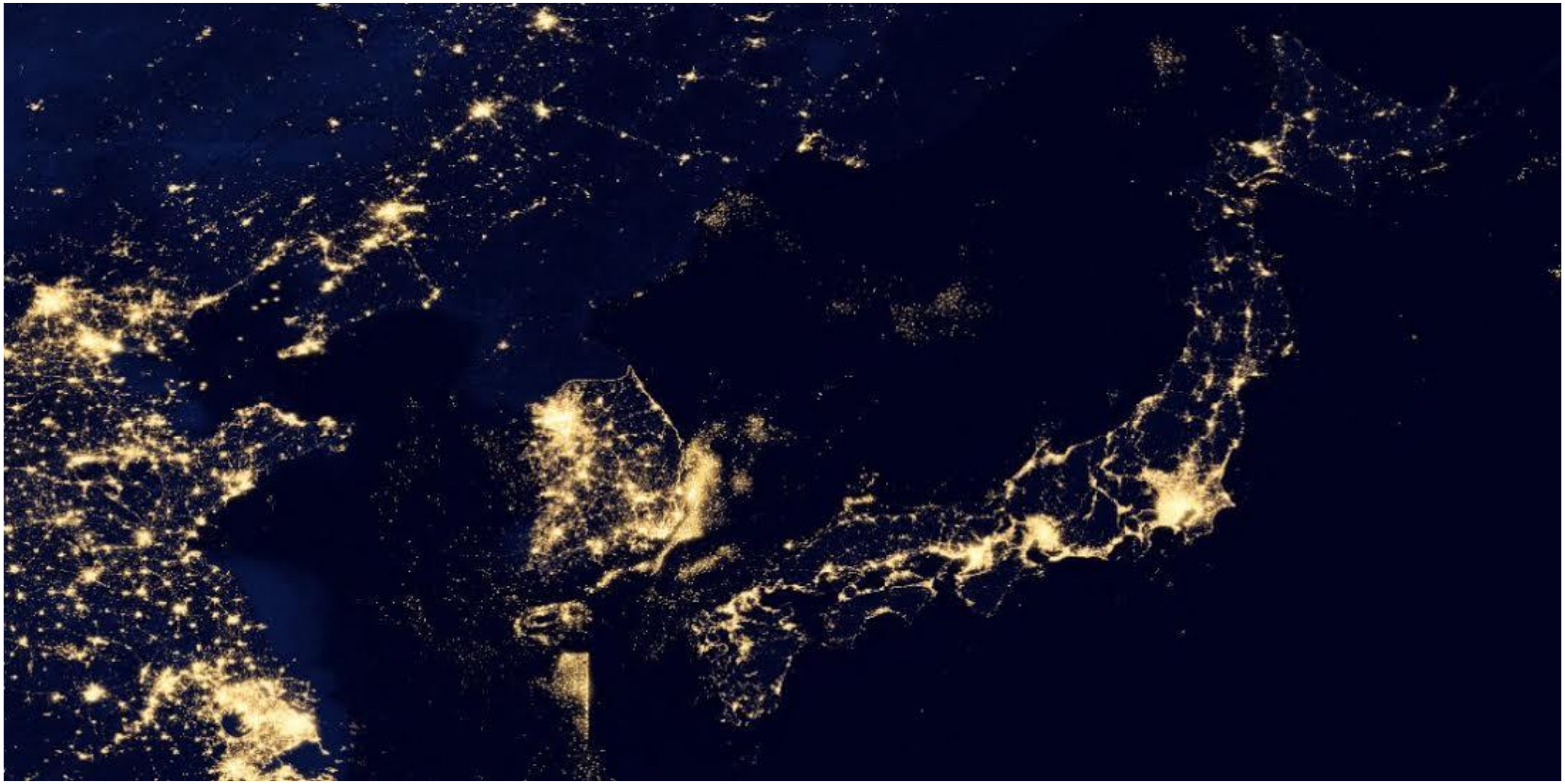
Population Clusterization in Russian Federation (Data from OECD.Stat)



Population Clusterization in USA (Data from OECD.Stat)



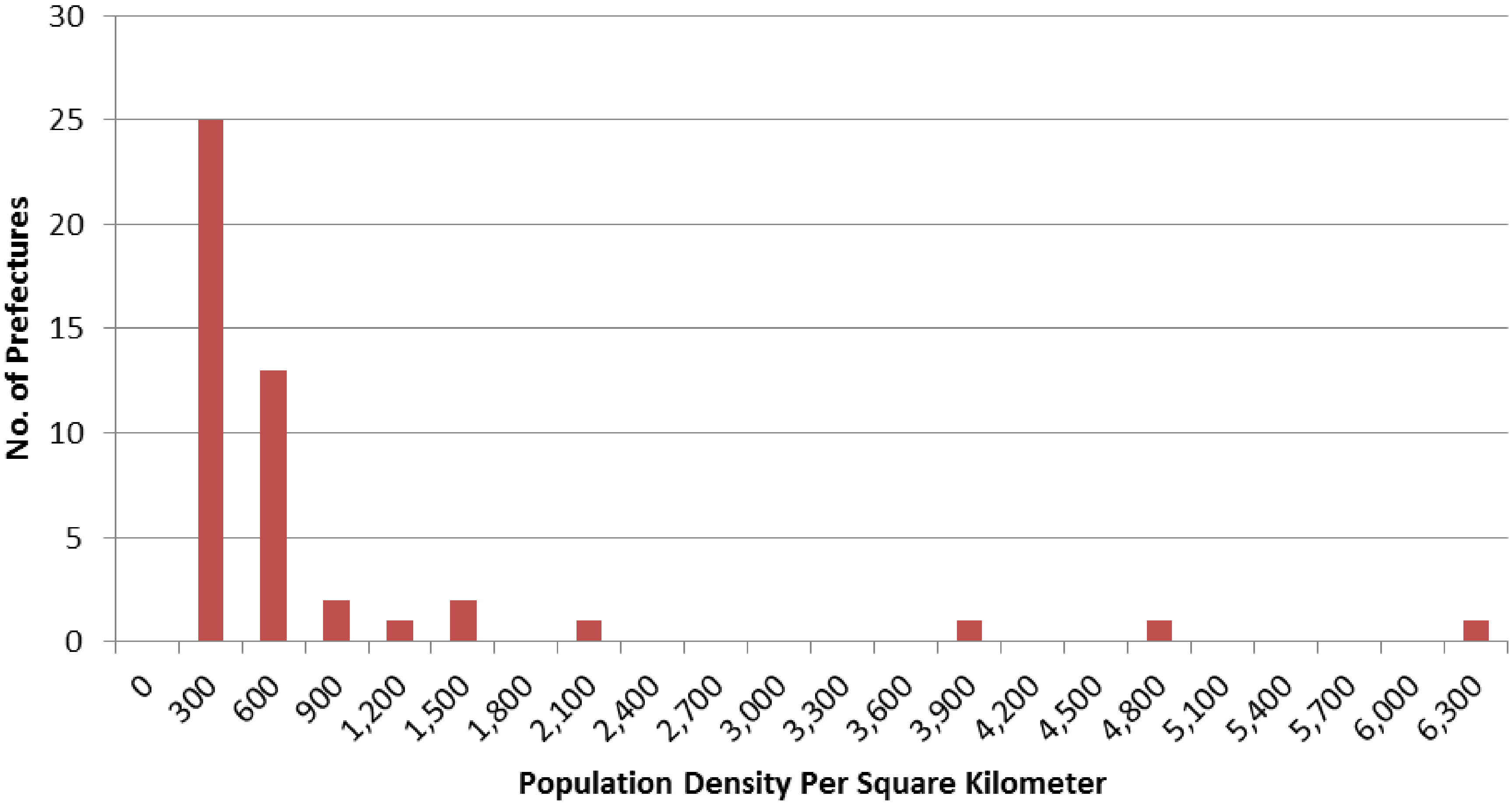
Satellite photo of nighttime lights in Japan, S. Korea, China



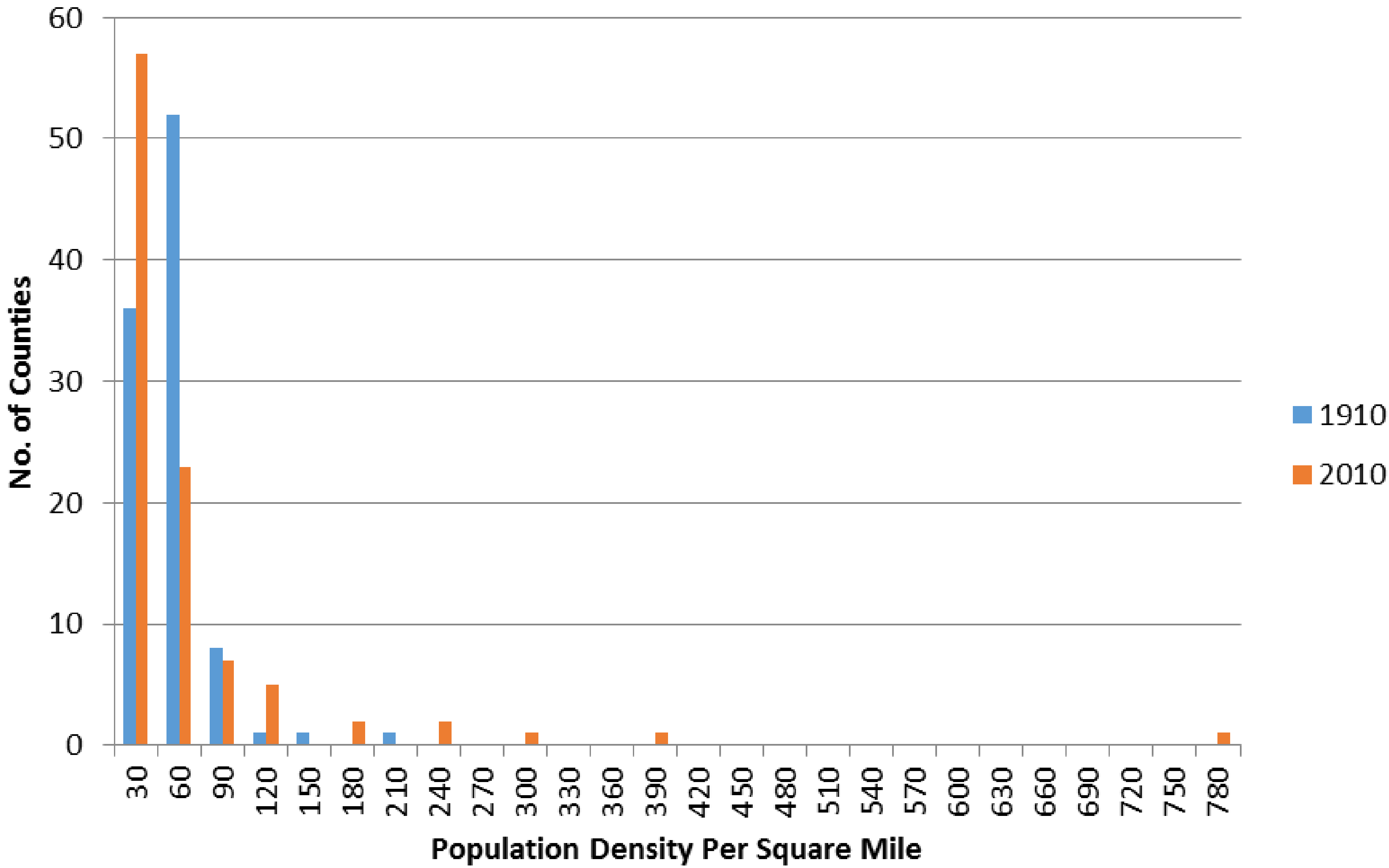
Satellite photo of nighttime lights in Europe

Satellite photo of nighttime lights in USA

Distribution of Population Density in Japan



Distribution of Pop. Density in Iowa



Introduction

Population dynamics theory:

Study of random integer valued measures $n(t,\Gamma)$, $\Gamma \subset \mathbb{R}^d$ (or $\mathbb{Z}^d$).

$n(t,\Gamma)$ is number of particles in set Γ at moment $t \geq 0$.

Use neutral language of "particles," as models too simple even for biological applications.

Particle field must be, for fixed $t \geq 0$, homogeneous and ergodic in space.

Its evolution in time should include:

random motion in space (migration), birth and death processes, immigration, and, in some cases, interaction between particles.

Central problem: convergence in law of $n(t,\Gamma)$, $t \to \infty$, to steady state $n(\infty,\Gamma)$.

I.e., ergodicity of Markov process $n(t,\cdot)$ in space of infinite configurations of particles

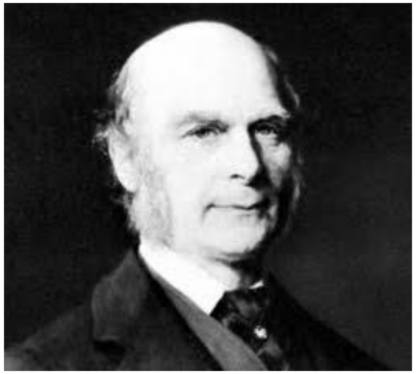
In ergodic situation obtain population process that is homogeneous in time and space.

All models based on branching random processes, reaction-diffusion equations, and so forth.

Historically, starting point of theory was FKPP (Fischer-Kolmogorov-Petrovskii-Piskunov) non-linear equation describing diffusion of new (superior) gene in supercritical regime.

I. Galton-Watson (continuous time)

Sir Francis Galton

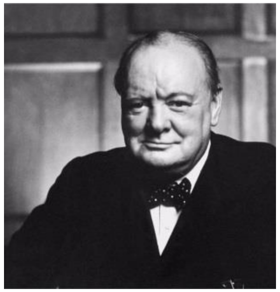


Inspiration for Galton's model: disappearance of noble families in England

Name passed on only through males

Extinction rate: About 50 % per century from medieval through modern times

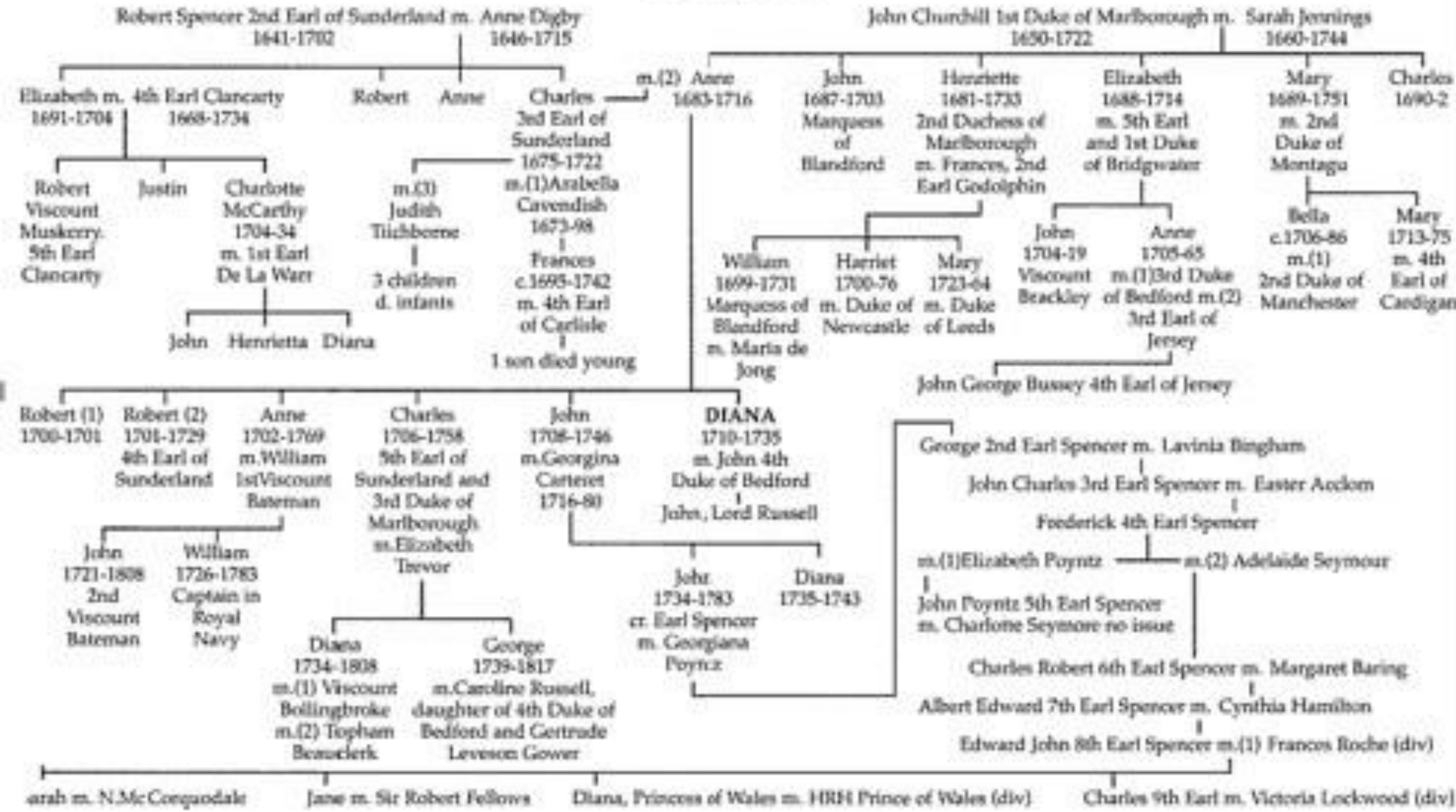
"Life expectancy" of family: No more than 3 generations



But a few of these families grow quite large, e.g., Spencer family

(including Sir Winston Churchill, Dukes of Marlborough, Princess Diana)

Spencer–Churchill Family Tree

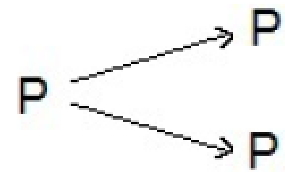


I. Galton-Watson (continuous time)

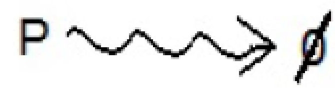
$n(t)$: number of particles at t, $n(0) = 1$.

During $(t, t + dt)$ each particle either

produces one offspring with probability βdt



or dies (annihilation) with probability μdt



$$\boxed{\beta = \mu \quad \text{critical case}}$$

For $u(t, z) = Ez^{n(t)}$, backward Kolmogorov equation: $\frac{\partial u}{\partial z} = \beta(u-1)^2, \quad u(0, z) = z$

Results:

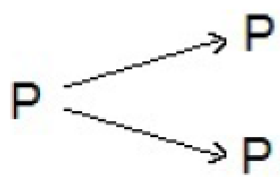
$$En(t) \equiv 1, \qquad En^2(t) = 1, \qquad P\{n(t) = 0\} = \frac{\beta t}{1+\beta t} \to 1, \; t \to \infty$$

but $[E[u(t)|u(t) > 0] = 1 + \beta t$ (the central observation by Galton)

II. Galton-Watson + immigration

Possible reactions during time interval $(t, t+dt)$:

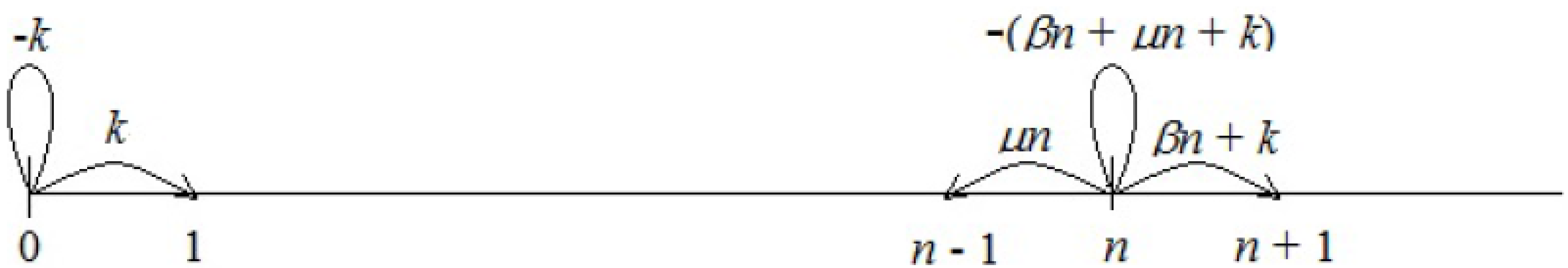
With probability βdt



With probability μdt

New particle appears from outside with probability kdt, k the immigration rate

Process $n(t)$, $t \geq 0$ is random walk on $\mathbb{Z}_+^1 = (0, 1, \ldots)$:



II. Galton-Watson + immigration (cont.)

Limit Theorem 2.1. If $\beta < \mu$, $k > 0$, then there exists the limiting distribution

$$\pi(m) = \lim_{t\to\infty} p(t, n_0, m) =$$

$$= \frac{k(\beta+k)\cdots((m-1)\beta+k)}{\mu^m m!}\left(1+\frac{k}{\mu}+\ldots+\frac{k(\beta+k)\cdots((n-1)\beta+k)}{\mu^n n!}+\ldots\right)^{-1}$$

In addition, $En(t) \to \dfrac{k}{\mu-\beta}$, $t \to \infty$. *If* $\beta \geq \mu$, $k > 0$ *then* $n(t) \to \infty$ *(P-a.s.).*

If the last parameter is large, then

$$n^*(t) = \frac{n(t) - \frac{k}{\mu-\beta}}{\sqrt{\frac{k\mu}{(\mu-\beta)^2}}} \xrightarrow[k\to\infty]{\text{law}} N(0,1).$$

In stationary regime, random variable $n(t)$ has Gaussian fluctuations of order $\sqrt{\frac{k\mu}{(\mu-\beta)^2}}$ around mean value $\dfrac{k}{\mu-\beta}$.

II. Galton-Watson + immigration (cont.)

Limit Theorem (Kurtz-type result) 2.2. *If* $\beta < \mu$, $k > 0$, *then*

$$\frac{n_k(t) - \frac{k}{\mu-\beta}}{\sqrt{k}} \xrightarrow{\text{law}} \zeta(t)$$

which is an Ornstein-Uhlenbeck process.

Model for some countries in contemporary Europe:

Below replacement fertility compensated by immigration

Central result: convergence to statistical equilibrium even in case where $\mu(x)$ and $\beta(x)$ are random and $\ln \frac{\mu(x)}{\beta(x)} > 0$

II. Galton-Watson + immigration (cont.)

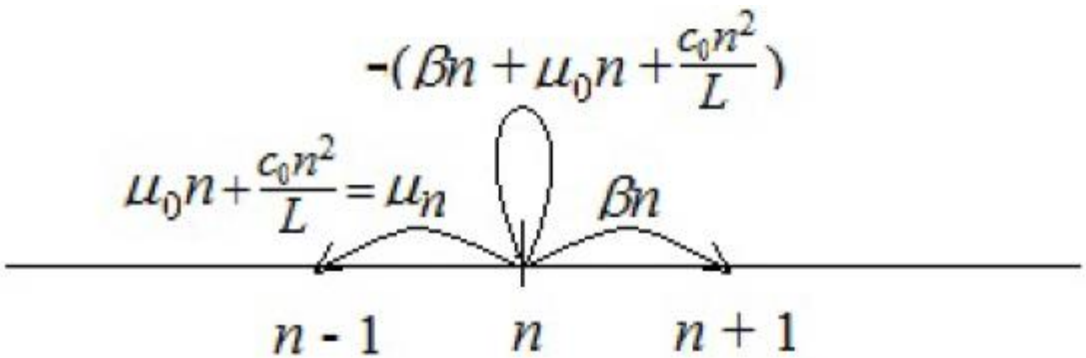
Country	Natural change rate (per thousand)			Immigration rate (per thousand)		
	2012	**2013**	**2014**	**2012**	**2013**	**2014**
Germany	-2.4	-2.6	-2.2	4.9	5.6	7.2
Italy	-1.3	-1.4	-1.6	6.2	19.7	1.8
Hungary	-3.9	-3.8	-3.3	1.6	0.5	0.5

III. Bolker-Pacala Model (mean field approximation)

In this model, $\beta > \mu_0$, but

Stability of population depends on additional *competition term* in mortality rate:

$\mu_n = \mu_0 n + c_0 \frac{n^2}{L}$, $L \gg 0$.



Equilibrium point n^* is given by equation

$$\mu_0 n + \frac{c_0 n^2}{L} = \beta n \quad \Rightarrow \quad n^* = \frac{(\beta - \mu_0)L}{c_0}$$

Gaussian fluctuations occur around this equilibrium.

IV. Branching random walk with immigration

Similar to critical FKPP-type model on lattice $\mathbb{Z}^d$

But includes immigration to any site $x \in \mathbb{Z}^d$

Initial configuration can be identically zero.

Backward approach of section I not applicable here:

Cannot split population $n(t,\Gamma)$ into sum of independent subpopulations $n(t,x,\Gamma)$.

Must use forward equations, therefore, for correlation functions

Generator of the underlying random walk: $\mathcal{L}\psi(x) := \sum_{z \neq 0} a(z)(\psi(x+z) - \psi(x))$

IV. Branching r.w. with immigration (cont.)

Simplest case is constant birth rate β, mortality rate μ and immigration at constant rate k.

Equation for $m_1(t,y) = E_x n(t,y)$:

$$\frac{\partial m_1(t,y)}{\partial t} = \mathcal{L} m_1(t,y) + (\beta - \mu) m_1(t,y) + k$$
$$m_1(0,y) = \rho_0$$

which yields: $m_1(t,y) \xrightarrow[t\to\infty]{} \frac{k}{\mu-\beta}$ (for $\mu > \beta$!)

Analysis of higher correlation functions is more difficult—
Not yet completed but we believe that limiting steady state exists.

This model is very stable.

IV. Branching r.w. with immigration (cont.)

Consider, next, case when $\beta(x,\omega), \mu(x,\omega)$, and $k(x,\omega)$ are random stationary fields on lattice $\mathbb{Z}^d$, and

a) $\mu(x,\omega) - \beta(x,\omega) \geq \delta > 0$

b) $k(x,\omega) \geq \delta_1 > 0$

Then, solution of equation

$$\frac{\partial m_1(t,y,\omega)}{\partial t} = \mathcal{L} m_1 + (\beta - \mu)(x,\omega) m_1 + k(x,\omega)$$
$$m_1(0,y) = \rho_0$$

tends, for $t \to \infty$, to limit: $\quad m_1(t,x,\omega) \to m_1(x,\omega)$.

IV. Branching r.w. with immigration (cont.)

Limiting density is solution of elliptic problem

$$\mathcal{L}m + (\beta - \mu)m = -k$$
$$m(t,x) = \sum_{y \in \mathbb{Z}^d} G(x,y)k(y,\omega)$$

where $G(x,y)$ is Green function for operator $H = \mathcal{L} + V$, $V \le -\delta < 0$.

$G(x,y)$ exists and is fast decreasing on $\mathbb{Z}^d$. $|G(x,y)| \le ce^{-\delta|x-y|}$, $c > 0$.

IV. Branching r.w. with immigration (cont.)

Consider, finally, case when β, μ, and k are stationary ergodic fields in space and time and, again

$$(\mu - \beta)(t, x, \omega) \geq \delta > 0$$
$$k(t, x, \omega) \geq \delta_1 > 0.$$

Even here, results on convergence to dynamics that are stationary in space and time are similar.

V. Backward approach to ergodic theorem. Lattice FKPP-type equation

Phase space: $\mathbb{Z}^d$; Uniform initial distribution: $n(0,x) \equiv 1$

Critical case: $\beta = \mu > 0$; κ is the rate of jumps.

$a(z)$ is probability of transition $x \to x+z$; $\sum_z a(z) = 1)$; $a(z) = a(-z)$

Generator of the underlying random walk: $\mathcal{L}\psi(x) := \sum_{z \neq 0} a(z)(\psi(x+z) - \psi(x))$

Central result: If $\beta = \mu$ (equilibrium between birth and death rates):

Steady state exists iff the underlying random walk is *transient*.

In other words, migration must be sufficiently active.

In dimension $d = 2$, this means jump distribution must be heavy-tailed (many long jumps).

Without this, population will undergo infinitely strong clusterization.

V. Backward approach to ergodic thm. (cont.)

Strategy of proof:

Take single particle at $x \in \mathbb{Z}^d$.

Let $n(t, x, \Gamma) = \#(\text{particles it generates at } t \geq 0 \text{ in } \Gamma \subset \mathbb{Z}^d)$.

R.v.s $n(t, x, \Gamma)$, $x \in \mathbb{Z}^d$, are independent. $n(t, \Gamma) = \sum_{x \in \mathbb{Z}^d} n(t, x, \Gamma)$.

For generating function, $u_z(t, x, \Gamma) = E_x z^{n(t,y,\Gamma)}$, we have KPP-type equation:

$$\frac{\partial u_z}{\partial t} = \mathcal{L} u_z + \beta (u_z - 1)^2$$

$$u(0, x, \Gamma) = \begin{cases} z, & x \in \Gamma \\ 1, & x \notin \Gamma \end{cases}$$

Differentiation over z and evaluation at $z = 1$ gives moment equations for $m_1(t, x, \Gamma) = E_x n(t, \Gamma)$, $m_2(t, x, \Gamma) = E_x n(n-1)$, ...

V. Backward approach to ergodic thm. (cont.)

To find Carleman estimates for cumulants $\varkappa_l(n(t,\Gamma))$:

Calculate cumulants $\varkappa_l(n(t,x,\Gamma))$ of independent r.v.s $n(t,x,\Gamma)$ using estimates of factorial moments for $n(t,x,\Gamma)$

Use relation $\varkappa_l(n(t,\Gamma)) = \sum_{x\in\mathbb{Z}^d} \varkappa_l(n(t,x,\Gamma)), \quad l=1,2,\dots$

Existence of limits of $m_l(t,x,\Gamma)$, $t\to\infty$ follows from explicit formulas for factorial moments.

This method works with small modifications for all branching random processes on $\mathbb{R}^d$ (or $\mathbb{Z}^d$), including KPP model, contact processes, etc.

VI. The problem of stability of the steady state

Clearly, assumption of criticality $\beta = \mu$ not realistic for applications

All models without immigration are unstable.

Theorem 1.4 (Kondratiev-Kutoviy-Molchanov). *Assume that*

$$\beta(x) = \beta_0 + \varepsilon\xi(x); \qquad \mu(x) = \beta_0 + \varepsilon\eta(x)$$

where $\xi(x)$ *and* $\eta(x)$ *are independent for different* $x \in \mathbb{Z}^d$*; and for some* δ

$$P\{(\xi - \eta)(x) > \delta\} > 0.$$

Then, $n(t, \Gamma) \to \infty$*, P-a.s.*

Central element here is the localization theorem for the Hamiltonian

$$H = \mathcal{L} + \varepsilon(\xi(x) - \eta(x)) = \mathcal{L} + \varepsilon V(x, \omega)$$

and existence of localized states with eigenvalues $\lambda_i(\omega) > 0$.

Corresponding eigenstates are concentrated on "happy islands" where $\xi(x) - \eta(x) \geq \delta > 0$.

VI. Stability of the steady state (cont.)

Consider now the local perturbation $\beta(x) = \mu(x) \equiv \beta_0$, $x \neq 0$; $\beta(0) - \mu(0) = c_0 > 0$.

Theorem 1.5. *If the underlying random walk with the jump distribution $a(z)$ is recurrent (which is possible for $d = 1, 2$), then, for arbitrary $c_0 > 0$ the Hamiltonian $H = \mathcal{L} + c_0\delta_0(x)$ has a positive eigenvalue $\lambda_1(c_0)$ and, as a result, $n(t, \Gamma) \to \infty$, P-a.s.*

(Note: random walk is always transient for $d \geq 3$ and in low dimensions $d = 1$, $d = 2$ under additional assumptions: that distribution $a(z)$ has heavy and regular tails, i.e., belongs to domain of attraction of symmetric stable law with parameter $\alpha < 2$ for $d = 2$ or $\alpha < 1$ for $d = 1$).

If random walk is transient, then, a spectral bifurcation occurs:

For $c_0 > c_{cr}$: positive eigenvalue exists and system is supercritical

For $c_0 \leq c_{cr}$: spectrum of $H = \mathcal{L} + c_0\delta_0$ is pure a.c.
Most likely indicates that steady state exists and represents small perturbation of initial steady state but this fact still has no complete proof.

VII. Globalization

Definitions:

Random graph:

Collection V of m vertices linked by set E of bidirectional edges.

Edges created probabilistically such that between any two vertices i and j edge e_{ij} exists with probability p independently of the existence of any other edge.

Degree d of a vertex: number of other vertices to which it is directly linked.

$Ed = p(m-1)$.

Component: set of vertices linked directly or indirectly to each other but to no other vertices

Erdös-Renyi Theorem (1960): Above the critical value for the expected degree, $Ed = 1$, a giant component, i.e., a component including most vertices, emerges. Below the critical value there is no giant component.

VII. Globalization (cont.)

Random graph with 150 vertices: