

Metapopulations

History

- Nicholson and Bailey (1935) unstable host-parasitoid models yield metapop dynamics
- Wright (1940) shifting balance theory
- Andrewartha & Birch (1954) ephemeral insect pops
- Huffaker (1958) predator & prey mites on oranges
- den Boer (1968) ‘spread the risk’ via asynchrony of local pop dynamics and dispersal
- Levins (1970) metapopulation = a population of populations and island occupancy model
- Gilpin & Hanski (1991) symposium & book

Metapopulations

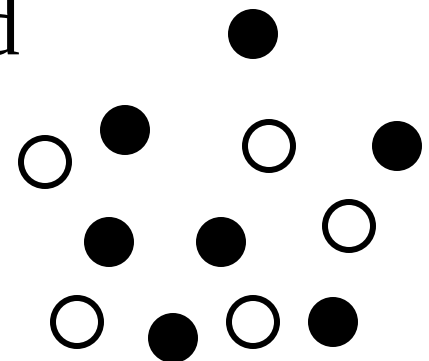
Metapopulation – a group of several local populations linked by immigration and emigration

local extinction vs regional extinction

f = fraction of population sites occupied

p_i = prob of local colonization

p_e = prob of local extinction



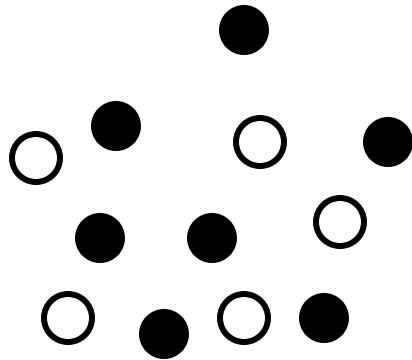
Metapopulations

Model variation: internal colonization

Levins' model (a Levins metapopulation)

- Assumes large no. of habitat patches such that stochasticity is unimportant
- Patches equidistant and identical
- Patch-level pop dynamics rapid so either empty (0) or occupied at K (**incidence models**)
- Biological processes are limited to colonization and local extinction
- All colonization is internal to metapop (local... only source of colonists are other occupied sites)

Metapopulations



● Occupied
○ Empty



Simplest Models

Assume all patches equivalent

Assume all patches equally
connected so spatial orientation
doesn't matter (hypersphere)

Metapopulations

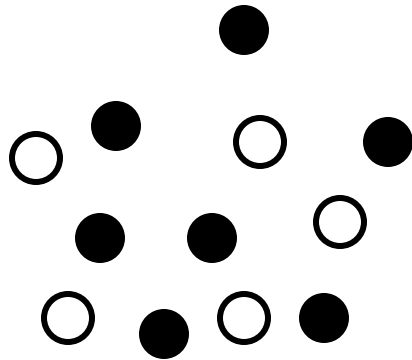
Consider: Given 2 populations, what is the probability at least one will persist? Same as $(1 - \text{prob both go extinct})$:

$$P_2 = 1 - (p_e)(p_e) = 1 - p^2$$

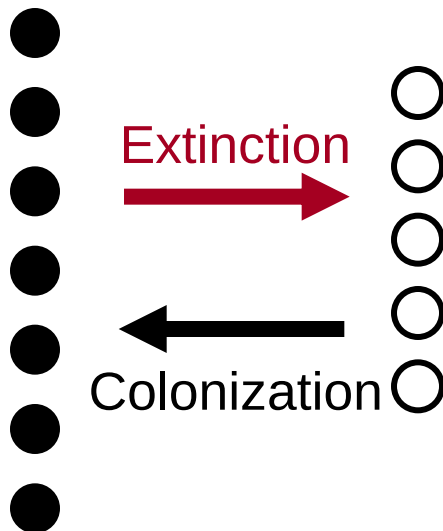
$$P_x = 1 - (p_e)^x$$

	Population 1		
		E (p_e)	P ($1-p_e$)
	E (p_e)		
	P ($1-p_e$)		

Metapopulations: Extinction



● Occupied
○ Empty



Each occupied patch has probability p_e of going extinct each time step

Decrease in f due to extinction:

$$E = fp_e$$

Metapopulations

f =fraction of population sites occupied

p_i =prob of local colonization

p_e =prob of local extinction

Consider dynamics of regional population:

$I = p_i(1-f)$ Immigration rate

$E = p_e f$ Extinction rate

Thus, I and E are functions of f and $df/dt = I - E$:

$$\frac{df}{dt} = p_i(1-f) - p_e f$$

Assumes: *homogeneous patches*

No spatial structure (spatial arrangement does not affect p_i , p_e)

No time lags

Constant p_e , p_i

Regional f affects local p_i and p_e

Large number of patches

Metapopulations

Model variations: Island-Mainland

Island-mainland model - assumes p_i and p_e are constants (not affected by f because of a large stable source of propagules... a 'mainland')

Propagule rain – constant supply of immigrants with p_i fixed from mainland source

Solve for equilibrium f : $\frac{df}{dt} = p_i(1 - f) - p_e f$

$$df/dt = 0 = p_i - p_i f - p_e f$$

$$p_i = p_i f + p_e f$$

$$\therefore \hat{f} = \frac{p_i}{p_i + p_e}$$

Metapopulations

Model variations: Island-Mainland

Thus, f is a balance of immigration and extinction

Note $\hat{f} > 0$ over large p_e , even with small p_i
because of prop rain from mainland

Metapopulations

Model variation: internal colonization

Only source of colonists are other occupied sites,
leading to:

$$p_i = if$$

where i = slope of probability of colonization relative to f

$$df/dt = if(1-f) - p_e f \quad (\text{from general eqn } df/dt = I - E)$$

$$p_e f = if(1-f)$$

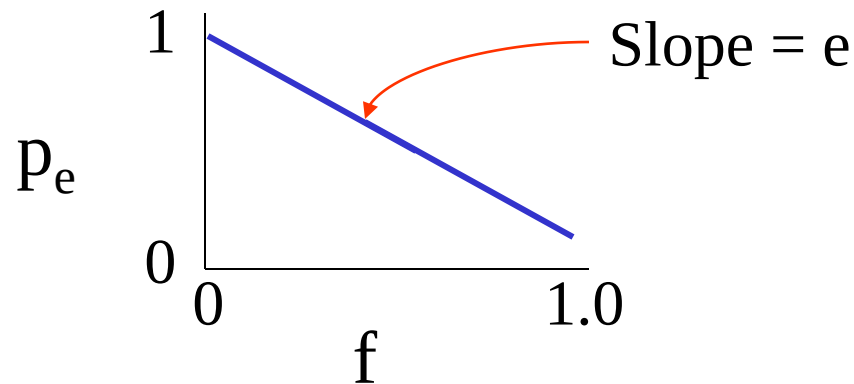
$$\begin{array}{l} p_e = i - if \\ if = i - p_e \end{array} \longrightarrow \hat{f} = 1 - \frac{p_e}{i}$$

$\hat{f}$ may go to 0 if i does not exceed p_e
 $i > p_e$ required for persistence

Metapopulations

Model variation: internal colonization with rescue

Rescue effect = reduction in prob of extinction (e) as a decreasing function of f



$$\hat{f} = \frac{p_i}{e}$$

See text for details of derivation

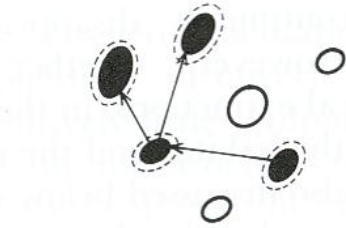
Metapopulations

Other extensions of Levins' model:

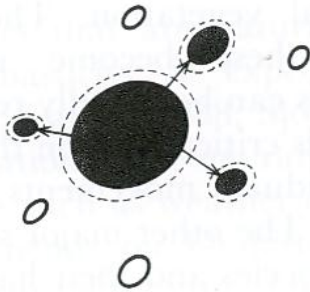
- Patch models
 - Two competitors
 - Predator-prey models
 - One spp drives others to local extinction, but leads to possibility of 'patchy coexistence'
- However, general application of Levins model is questionable

Metapopulations

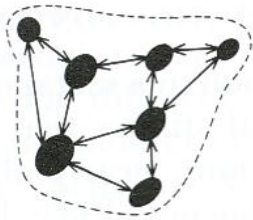
Consider these arrangements from Harrison (1991)



A



B



C

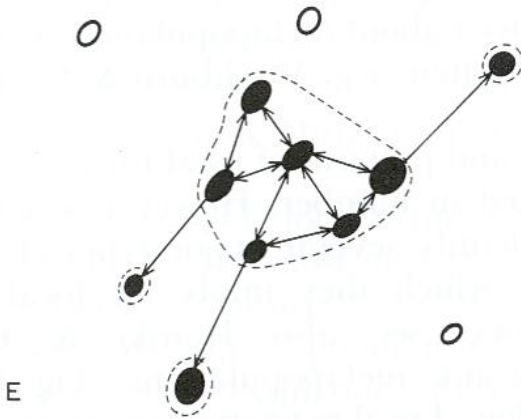
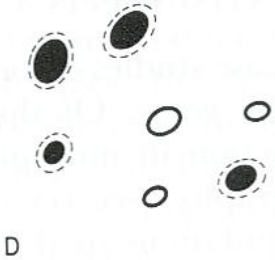
- A. Levin's metapop: % occupied sites determined by balance of extinction and re-colonization (uncommon in nature, prob because of environ fluctuation)
- B. Island-mainland or source-sink: central stable pop re-establishes islands, which go extinct regularly (propagule rain)
- C. Patchy population: high rate of dispersal among pops scattered over patchy habitat ($i > e$)

Metapopulations

Consider these arrangements from Harrison (1991)

D. Non-equilibrium metapopulation: no recolonization or inadequate to balance extinction... habitat degrading or sp declining (local extinction $i < e$)

E. Dynamic regional balance (hybrid of B and C)



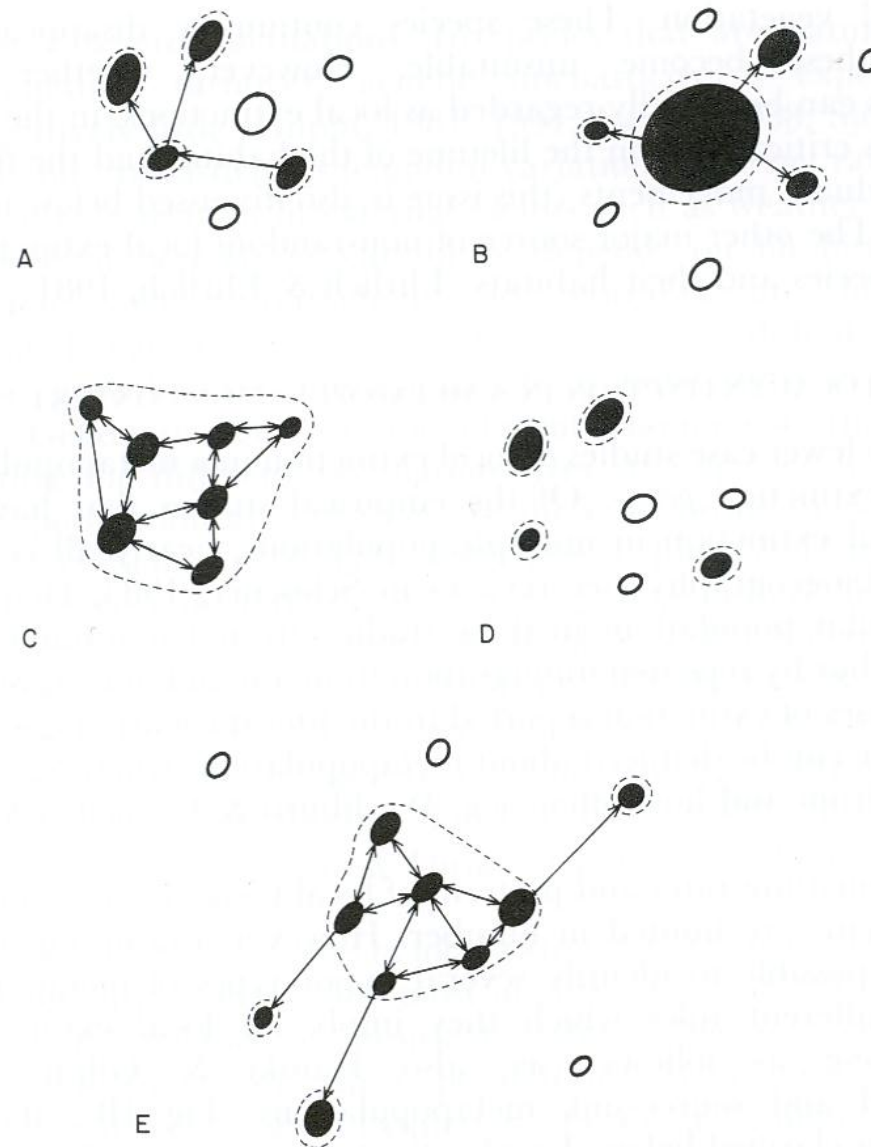


Figure 1. Different kinds of metapopulations. Closed circles represent habitat patches; filled = occupied, unfilled = vacant. Dashed lines indicate the boundaries of 'populations'. Arrows indicate migration (colonization). A, Levins metapopulation. B, Core-satellite (Boorman-Levitt, 1973) metapopulation. C, 'Patchy population'. D, Non-equilibrium metapopulation (differs from A in that there is no recolonization). E, An intermediate case that combines B and C.

Metapopulations part deux

Empirical work and other concepts

How do we study this stuff?

- must measure extinction and colonization rates
- could use e/m to estimate p IF able to identify ALL patches (not likely)
- quantitative prediction of global stability with local extinction is key
- but, is Levins' model structure generally applicable?

Metapopulations

Incidence Models

Notes from the literature:

- Real metapopulations often have local pops that never go extinct (mainland-island structure)
 - Natural or the result of habitat fragmentation?
 - Local extinction/colonization may have limited effect on regional persistence
 - Patch size may affect likelihood of habitation
 - Patterns of occupancy may not be related to geographical range and proximity of range limits

Metapopulations

Beyond Incident Models

- Species occupying naturally patchy habitats or transient habitats are often good dispersers (including visiting multiple patches in lifetime)
 - Examples: insects of dung, carrion, weedy host plants; amphibians in temporary ponds
- Important area of research is mortality rate while dispersing among patches... the greater mortality, the greater dynamical sensitivity to patch arrangement
- Species with high dispersal can have interaction of local and regional dynamics via:
 - Variable propagule supply
 - Local processes that include competition for space, Allee effects related to fertilization success
 - Source-sink dynamics
 - Commonly assumed that competition-dispersal trade off

Metapopulations

Spatially Structured Populations

- Habitat fragmentation can lead to local isolation over evolutionary time (natural ex: Mammals on mountaintops by Brown, 1971. Am Nat 105:467-478)
 - Mountain habitats appear isolated since Pleistocene
 - Fauna diversity reduced since isolation by ecological processes NOT tied to colonization-extinction balance
 - These processes include population size, body size, diet, and habitat requirements
- Regional extinctions are inevitable because of habitat fragmentation by humans (Hanski. 1985. Ecology 66:335-343... must manage each subpop as isolated entity)

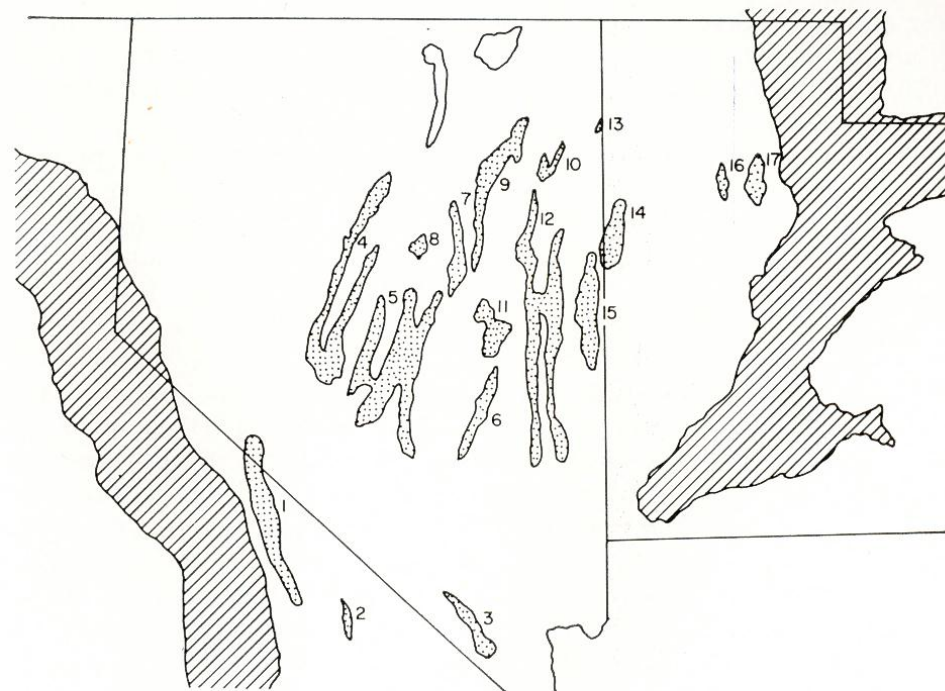


FIG. 1.—The Great Basin, with the montane islands lying between the Sierra Nevada (left) and Rocky Mountains (right). The shaded islands were used for the present analysis and are identified in table 1. The two unshaded islands were not used because they lie on the northern perimeter of the Great Basin and their faunas are poorly known.

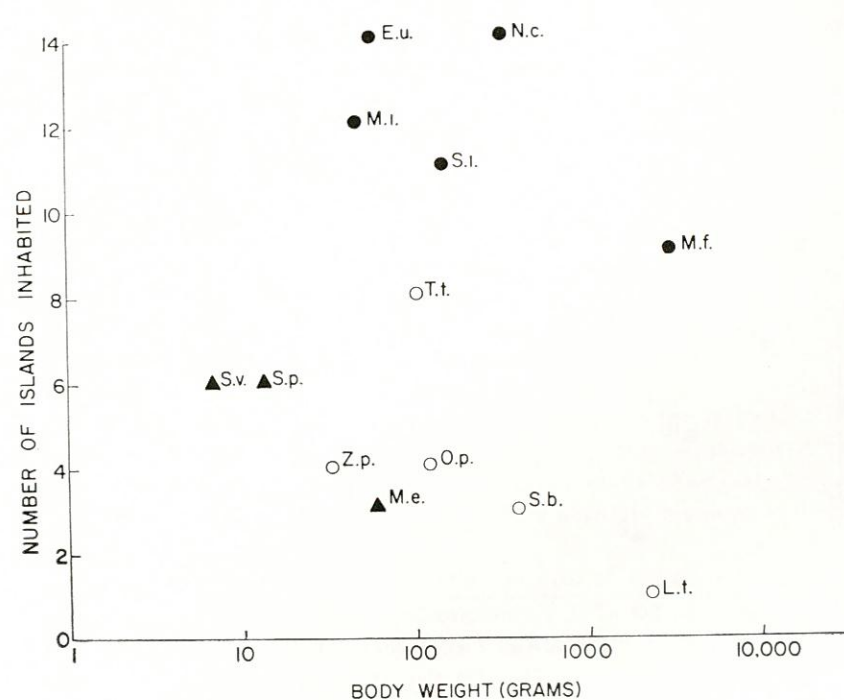


FIG. 3.—Frequency of occurrence on the montane islands of species of boreal mammals plotted against their body weight; shaded circles represent herbivores which are found in most habitats, unshaded circles indicate herbivores with specialized habitat requirements, triangles denote carnivores. The abbreviations are of species names which can be identified by reference to table 2.

TABLE 2
CHARACTERISTICS AND DISTRIBUTION IN THE GREAT BASIN OF THE FIFTEEN SPECIES OF BOREAL MAMMALS CONSIDERED

SPECIES	BODY WEIGHT (g)	HABITAT AND DIET	ISLANDS INHABITED																	TOTAL NO. ISLANDS INHABITED
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	
<i>Sorex vagrans</i> *	6.7	Carnivore	...	...	...	x	...	...	...	...	x	...	...	x	...	x	x	...	x	6
<i>Sorex palustris</i>	14	Carnivore	x	...	...	x	x	...	...	x	...	...	...	...	...	...	x	...	...	6
<i>Mustela erminea</i>	58	Carnivore	x	...	...	x	...	...	...	...	...	...	...	...	...	...	x	...	...	3
<i>Marmota flaviventer</i> ...	3,000	General herbivore	x	...	...	x	x	...	...	...	x	...	x	x	...	x	x	x	...	9
<i>Spermophilus lateralis</i> ..	147	General herbivore	x	...	x	x	x	x	x	...	x	x	x	x	...	x	x	...	...	13
<i>Spermophilus beldingi</i> ..	382	Meadow herbivore	...	...	...	x	x	...	...	...	x	...	...	...	...	...	...	...	...	3
<i>Eutamias umbrinus</i> † ...	57	General herbivore	x	...	x	x	x	x	x	x	x	x	x	x	...	x	x	...	x	14
<i>Thomomys talpoides</i>	102	Deep soil herbivore	x	...	...	x	x	...	x	...	x	...	x	x	...	x	x	...	x	8
<i>Microtus longicaudus</i> ...	47	General herbivore	x	...	...	x	x	x	...	x	x	...	x	x	...	x	x	x	x	12
<i>Neotoma cinerea</i>	317	General herbivore	x	x	x	x	x	...	x	...	x	x	x	x	x	x	x	...	...	14
<i>Zapus princeps</i>	33	Riparian herbivore	...	...	...	x	...	...	...	x	...	...	...	...	...	...	...	x	...	4
<i>Ochotona princeps</i>	121	Talus herbivore	x	...	...	x	x	...	...	...	x	...	...	...	...	...	...	...	...	4
<i>Lepus townsendi</i>	2,500	Meadow herbivore	...	...	...	...	...	...	...	...	x	...	...	...	...	...	...	...	...	1

* On island 17 the species is *Sorex obscurus*, a Rocky Mountain form, which forms a superspecies with *S. vagrans*.

† On island 3 the species is *Eutamias palmeri*, an endemic, which forms a superspecies with *E. umbrinus*.

Metapopulations

Notes continued

- Regional extinctions are inevitable because of habitat fragmentation by humans (Hanski. 1985. Ecology 66:335-343... must manage each subpop as isolated entity)

TABLE 1. Different components of habitat fragmentation and examples of how they may influence population dynamics.

Main component	Habitat change	Consequences for population dynamics
Distance-area or population-level effects	Reduced connectivity, insularization, increased interfragment distance	Directly affecting dispersal, reduces the immigration rate
	Reduced fragment size, reduced total area	Directly affecting population size, increases the extinction rate
Landscape or community-level effects	Reduced interior-edge ratio	Indirectly affecting mortality and production through increased pressure from predators, competitors, parasites and disease
	Reduced fragment-matrix ratio	
	Reduced habitat heterogeneity within fragments	Indirectly affecting population size through reduced carrying capacity within the fragment
	Increased habitat heterogeneity in surrounding matrix	Indirectly affecting mortality and production through increased carrying capacity of predators, competitors, etc. in the surrounding matrix
	Loss of keystone species from the habitat	Indirect effect through disruption of mutualistic guilds or food webs

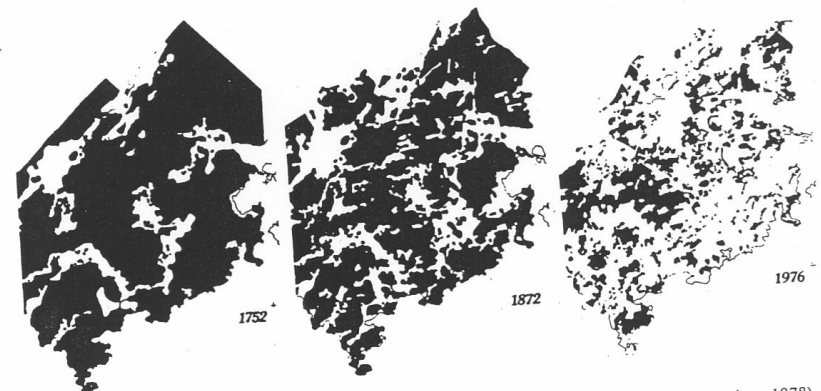


FIG. 5. Reduction and fragmentation of the woodland in Espoo, southern Finland (after Wuoreninne 1978).

Metapopulations

Notes continued

- Summary: Fragmented populations (natural or not) may not conform to metapopulation models and may not balance extinction and colonization
 - Caveat emptor!

Metapopulations

Movement Biology and Spatial Population Dynamics

How do you tell something is a metapopulation?

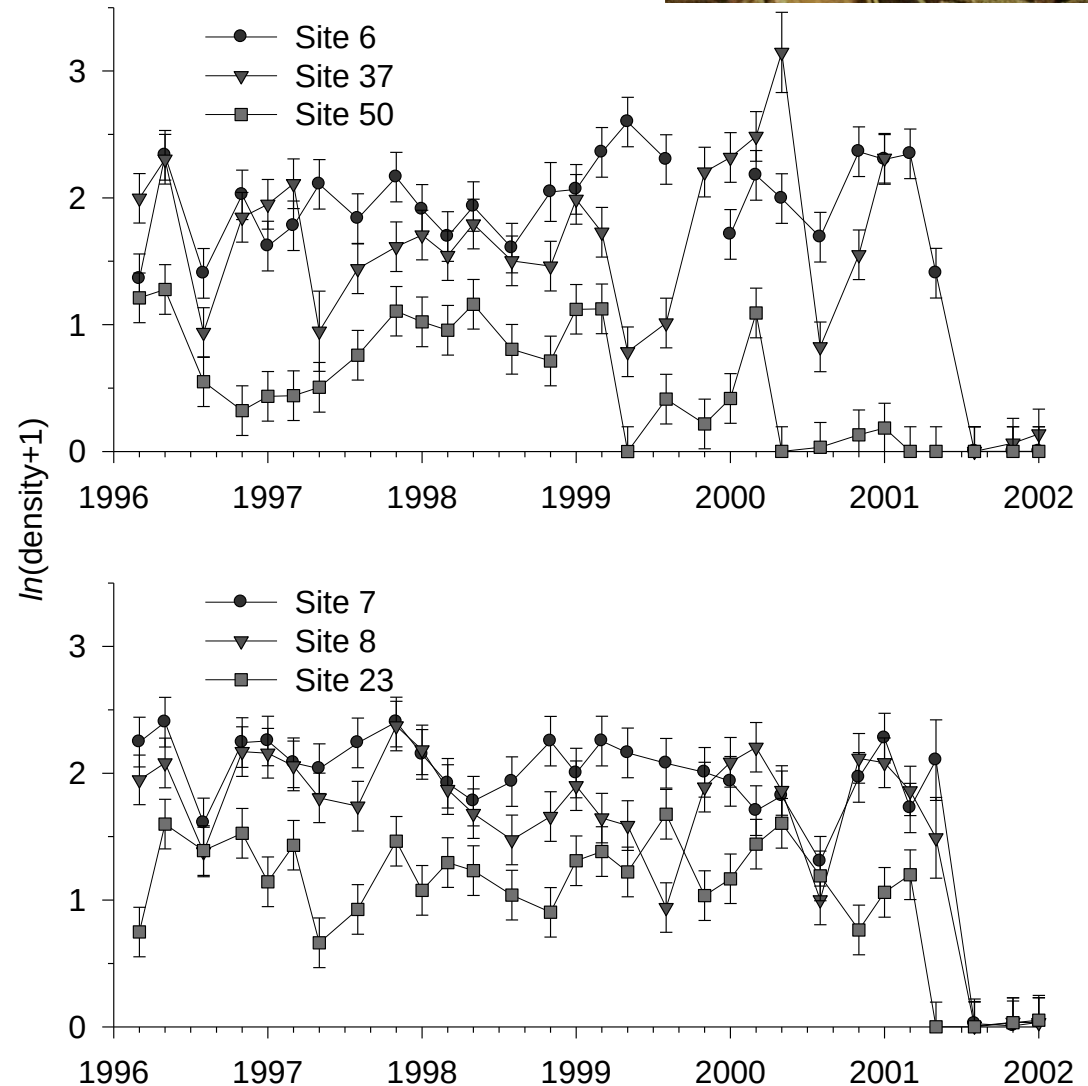
- Direct: mark-recapture (including genetic and isotopic markers)
 - Direct estimates of dispersal
 - Observe expansion of an introduced spp or colonization of a defaunated habitat
- Indirect:
 - species incidence/distribution pattern
 - Local abundance over time (look for local extinctions and failure of local populations to be replaced immediately when go extinct)
 - Population synchrony, Moran Effect

Metapopulations

Population Synchrony



- Spatiotemporal variation in the density (No./m²) of bluefin killifish in Shark River Slough. Error bars represent ± 1 SE. Least-squares means and standard errors were estimated based on the mixed linear model.

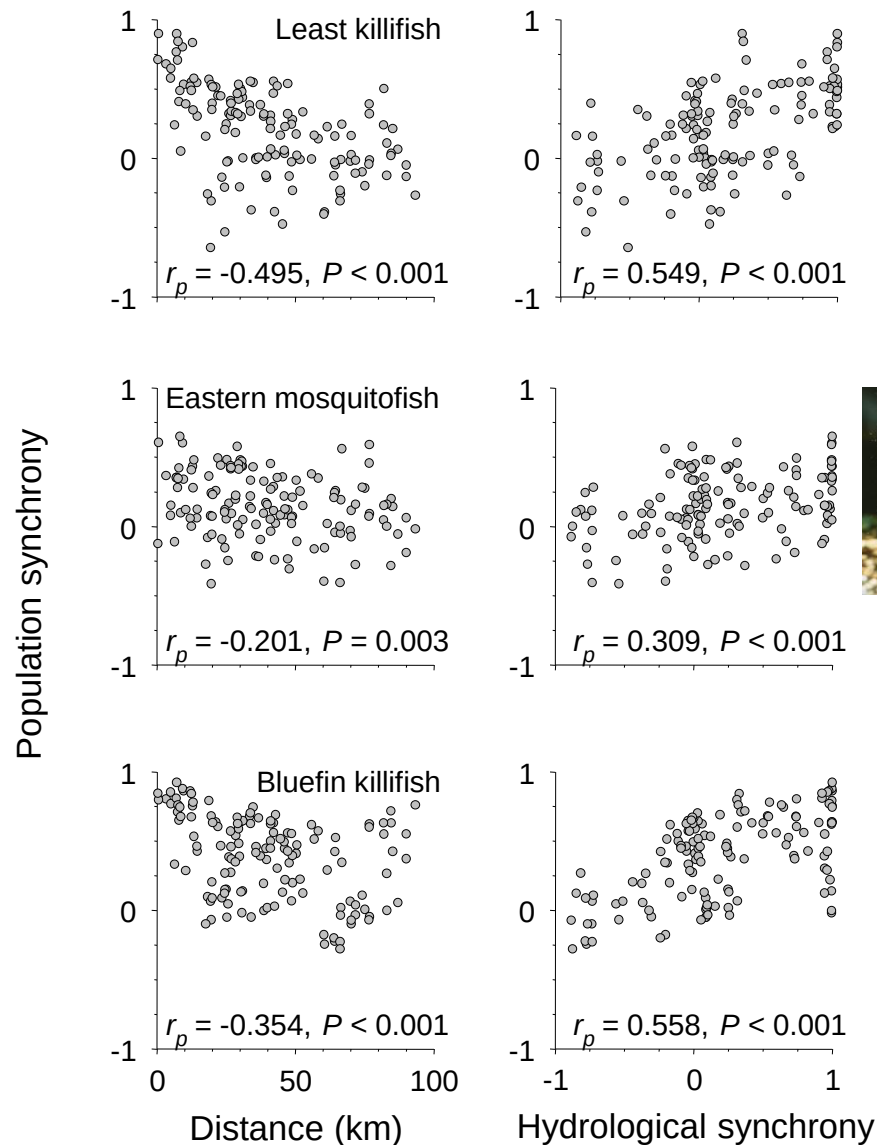


- Ruetz et al. 2005. JAE 74:322-332

Metapopulations

Population Synchrony

- Population synchrony is the correlation between fish densities for each pair of sites. Hydrological synchrony is the correlation between time since a dry down for each pair of sites, and r_p is the partial correlation coefficient. P-values were calculated using Mantel tests.
- Ruetz et al. 2005. JAE 74:322-332



Metapopulations

Notes continued

Why do local populations go extinct?

- Demographic stochasticity
- Environmental stochasticity
- Catastrophes... large-scale events
- Destruction of regional 'safe' sites

Local vs regional extinction

- Lifetime of habitats
- Dispersal: range and frequency
- Habitat fragmentation (Hanski 1985)
- Metacommunity dynamics: regional species pools

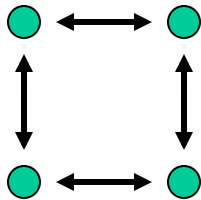
Metapopulations

heritage from population genetics

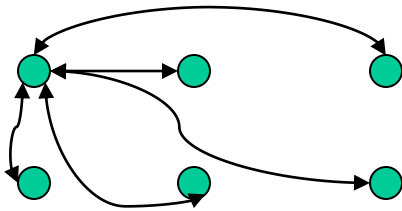
Patterns of dispersal



One-D stepping stone



Two-D stepping stone



Island and infinite island (connected pairs selected at random)

Metapopulations

Ecological Dispersal models

- Skellam-Fisher Model: passive diffusion as a random walk
- Directed Movement: Ideal-free distribution. Animals distribute themselves along gradients based on inequality of resource availability, move until return on foraging is no longer increased. IF distributions can apply to plants, too.
- Others: Lévy walk and related patterns (random turning, non-normal distributions of step lengths)

Random Walks

- Diffusional spread to fill a landscape ($D = \lambda^2/2\tau$ where D is diffusion coefficient, λ is mean speed on path, τ is mean time along path; turning angle is random.
- An appropriate null hypothesis to reject before evaluating more complex hypotheses

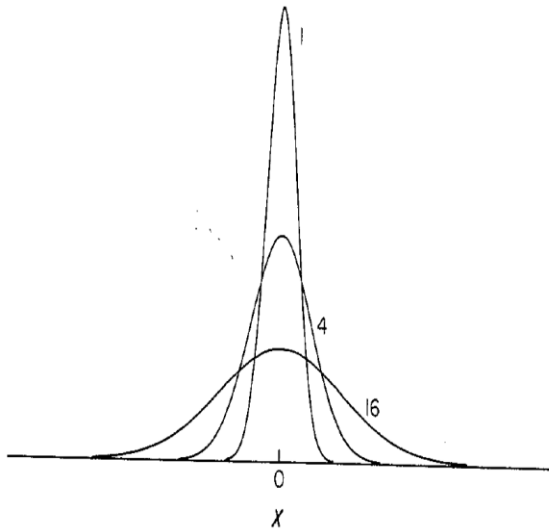


Fig. 1.3. The probability of finding particles at different points x at times $t = 1, 4$, and 16 . The particles start out at position $x = 0$ at time $t = 0$. The standard deviations (root-mean-square widths) of the distributions increase with the square-root of the time. Their peak heights decrease with the square-root of the time. See Eq. 1.22.

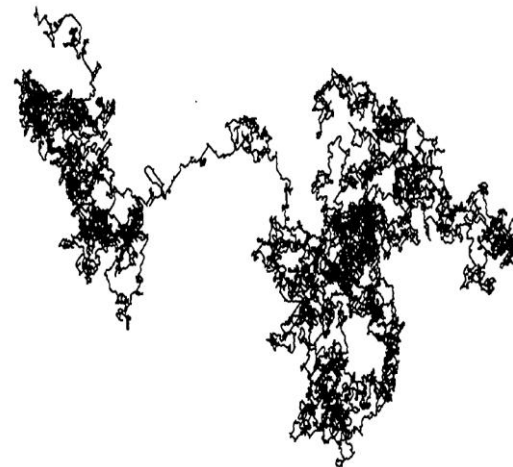


Fig. 1.4. An x, y plot of a two-dimensional random walk of $n = 18,050$ steps. The computer pen started at the upper left corner of the track and worked its way to the upper right edge of the track. It repeatedly traversed regions that are completely black. It moved, as the crow flies, 196 step lengths. The expected root-mean-square displacement is $(2n)^{1/2} = 190$ step lengths.

Two Random Walks

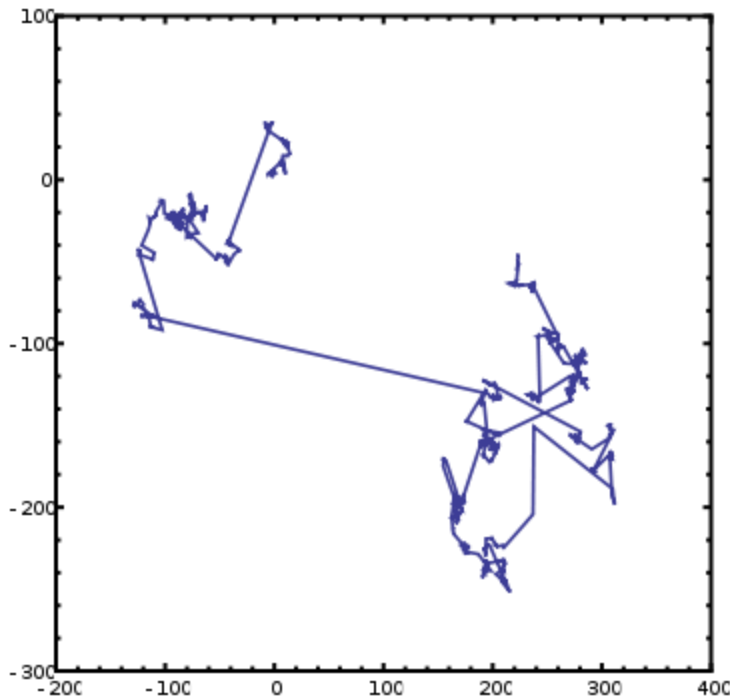


Figure 1. An example of 1000 steps of a Lévy flight in two dimensions. The origin of the motion is at $[0,0]$, the angular direction is uniformly distributed and the step size is distributed according to a Lévy (i.e. stable) distribution with $\alpha = 1$ and $\beta = 0$ which is a Cauchy distribution. Note the presence of large jumps in location compared to the Brownian motion illustrated in Figure 2.

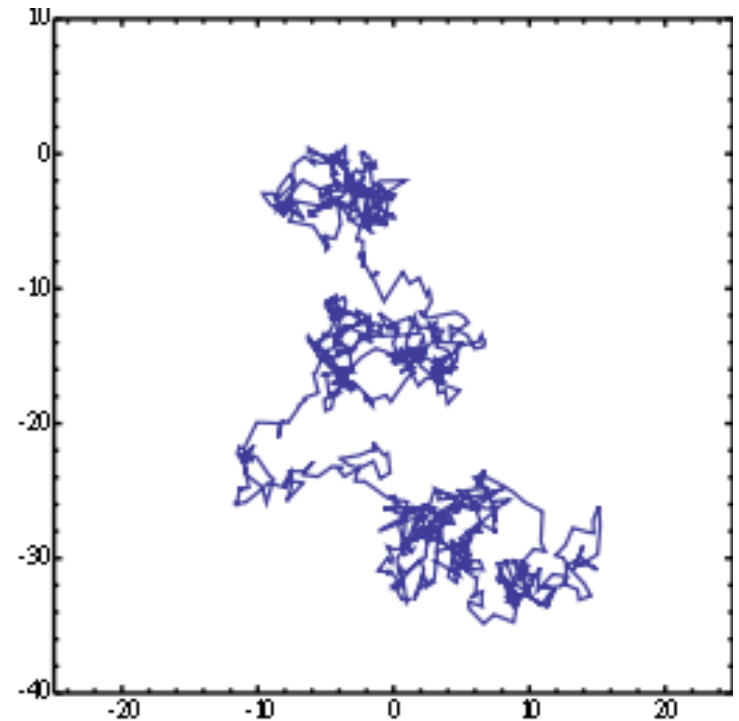


Figure 2. An example of 1000 steps of an approximation to a Brownian motion type of Lévy flight in two dimensions. The origin of the motion is at $[0, 0]$, the angular direction is uniformly distributed and the step size is distributed according to a Lévy (i.e. stable) distribution with $\alpha = 2$ and $\beta = 0$ (i.e., a normal distribution).

Metapopulations

heritage from population genetics

Sewell Wright – evolutionary interplay of gene flow and local differentiation

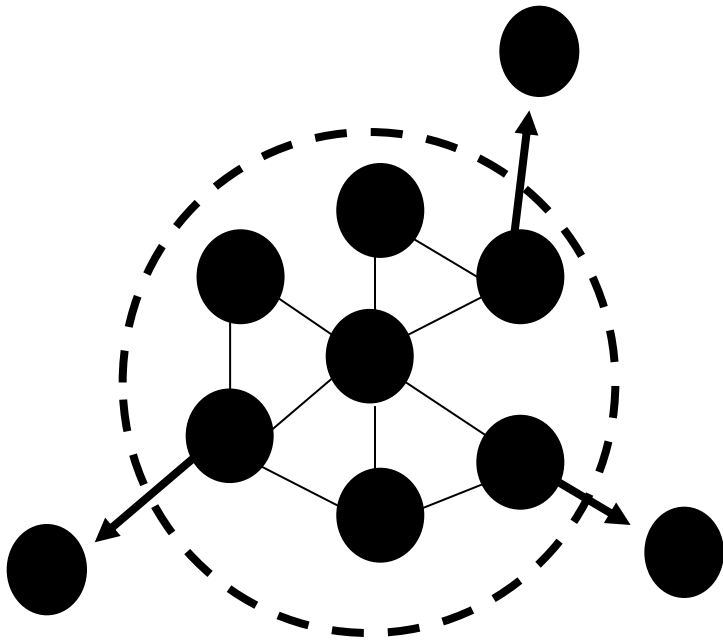
- founder effects, drift, selection

Recent work supports notion that extinction and colonization can promote genetic reorganization of spatial structure (Wade MJ, McCauley DE (1988) Extinction and recolonization: their effects on the genetic differentiation of local populations. *Evolution*, 42, 995-1005)

- propagule pool vs migrant pool

Conceptual Models of Migration

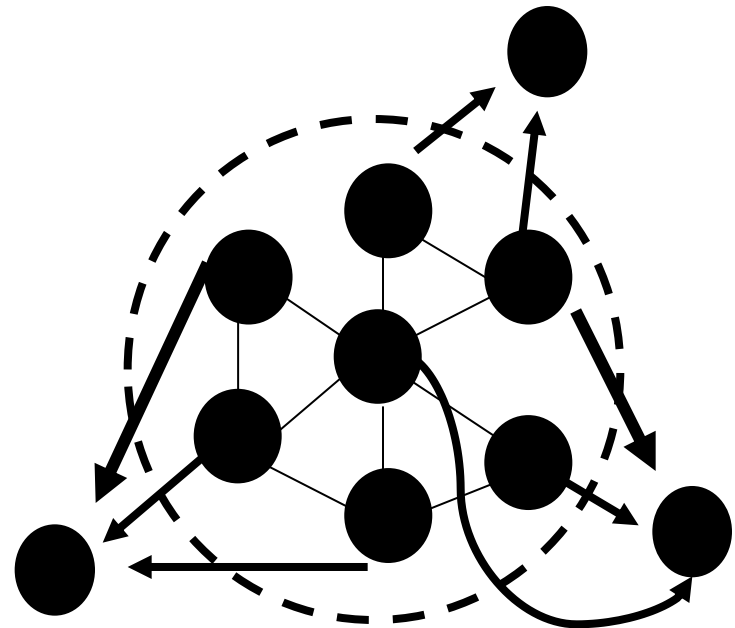
Is colonization different from routine movement?



Propagule Pool

Restricted source for colonists

Prediction: Increase
heterogeneity of recipient pops.



Migrant Pool

Diverse sources for colonists

Prediction: Homogenizes of
recipient pops

Metapopulations

heritage from population genetics

Resolution of genetic concepts and ecological ones not complete because of time scale difference.

Some techniques attempt to separate ecological and evolutionary time scale patterns in genetic diversity, but not same as ecological metapopulation concepts.