SANGKALAN

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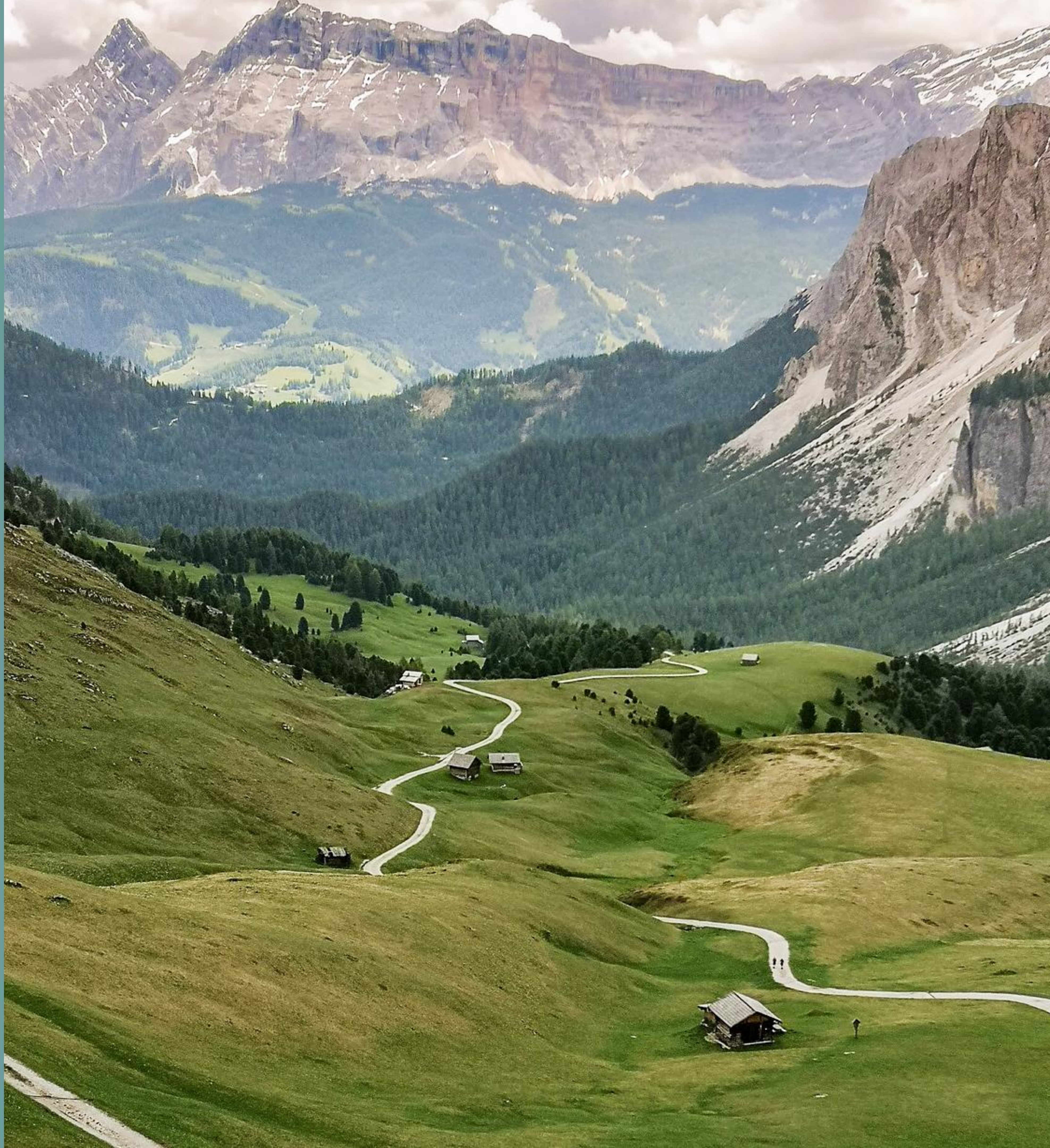
Oleh karena itu, mohon untuk tidak menyebarluaskan materi ini dalam bentuk apa pun kepada siapa pun; materi ini hanya untuk penggunaan pribadi mahasiswa peserta mata kuliah ini.

INTRODUCTION TO

METAPOPULATION ECOLOGY

LANDSCAPE PATTERN

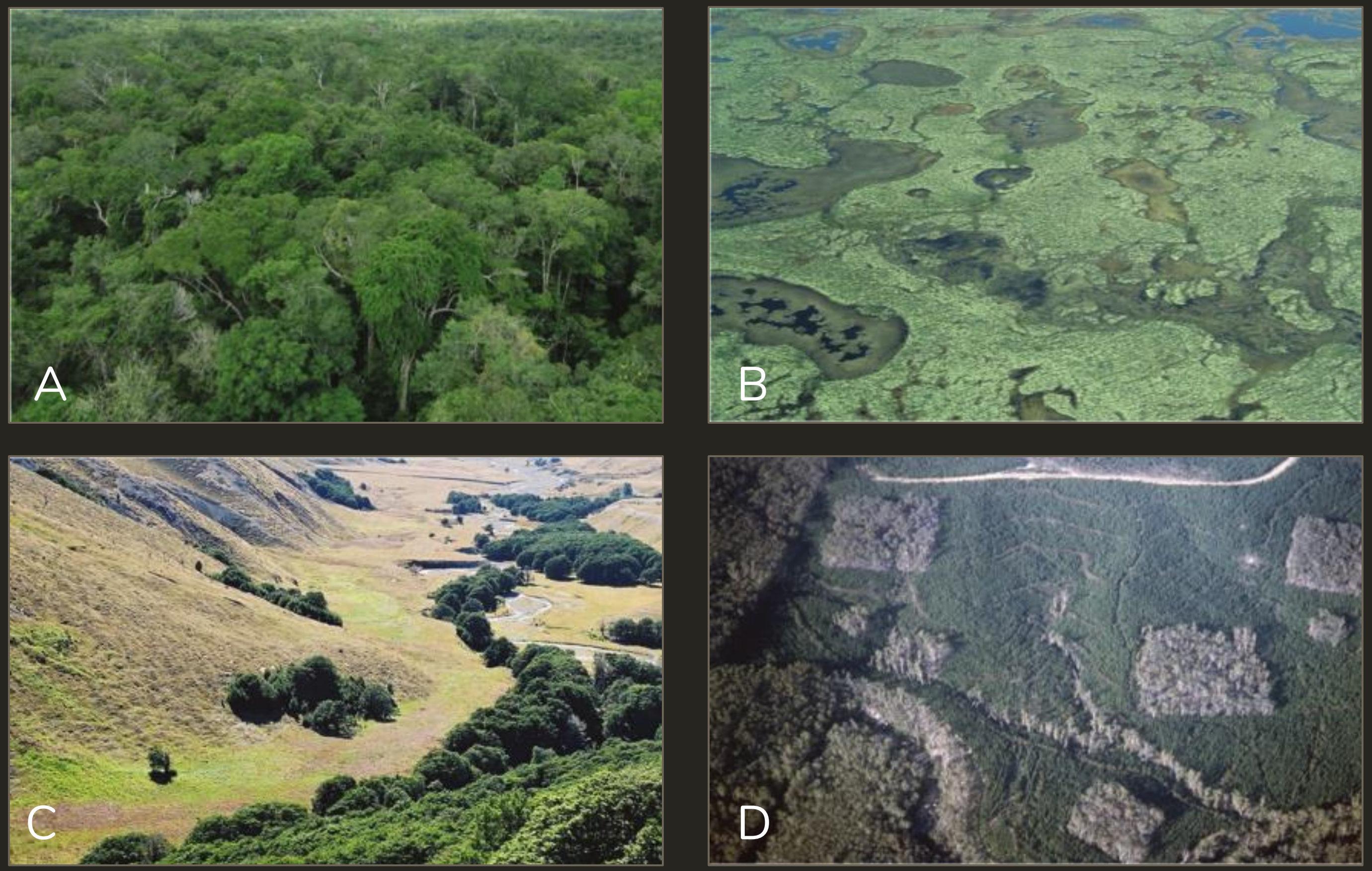
Patches arrangement and connectivity



Consequences of habitat change

- Human activities alter natural landscape.
  - Conversion into an artificial life support (urbanization and industry).
- Results of the alterations:
  - Increase of environmental heterogeneity.
  - Reduction of habitat availability for species.
  - Fragmentation of species habitat and populations.

Landscape heterogeneity



Examples of relatively intact landscapes (A and B) and highly modified ones (C and D). (A) Brazilian tropical lowland forest; (B) Natural mosaic of Canadian boreal forest and wetland; (C) fragmented New Zealand southern beech forest/anthropogenic grassland mosaic with strong landscape contrast and hard structural edges; (D) fragmented Australian Eucalyptus forest/pine plantation mosaic with weak landscape contrast and soft structural edges.

([Figure 1, with modifications], Brudvig et al., 2016, DOI: 10.1111/ecog.02543)

- Can be identified as:
  - Distinct boundaries of a mosaic of patches & corridors distributed in the landscape; or
  - A gradient in which discrete boundaries cannot be recognized, and a fuzzy boundary is observed.
- Occurrence can be natural or man-made.
- Has a complex and unique structure, not a random distribution of objects.

Habitat disturbance and landscape heterogeneity

- Disturbance can modify and fragment a landscape.
- Fragmentation reduces connectivity.
  - May have a negative result on biodiversity.
  - Characterized by a strong contrast between vegetation patches and their surrounding matrix.

Terms used in landscape ecology

Landscape MOSAIC

A composite of the landscape elements (differentiated by their substrate, internal dynamics, and human activities).

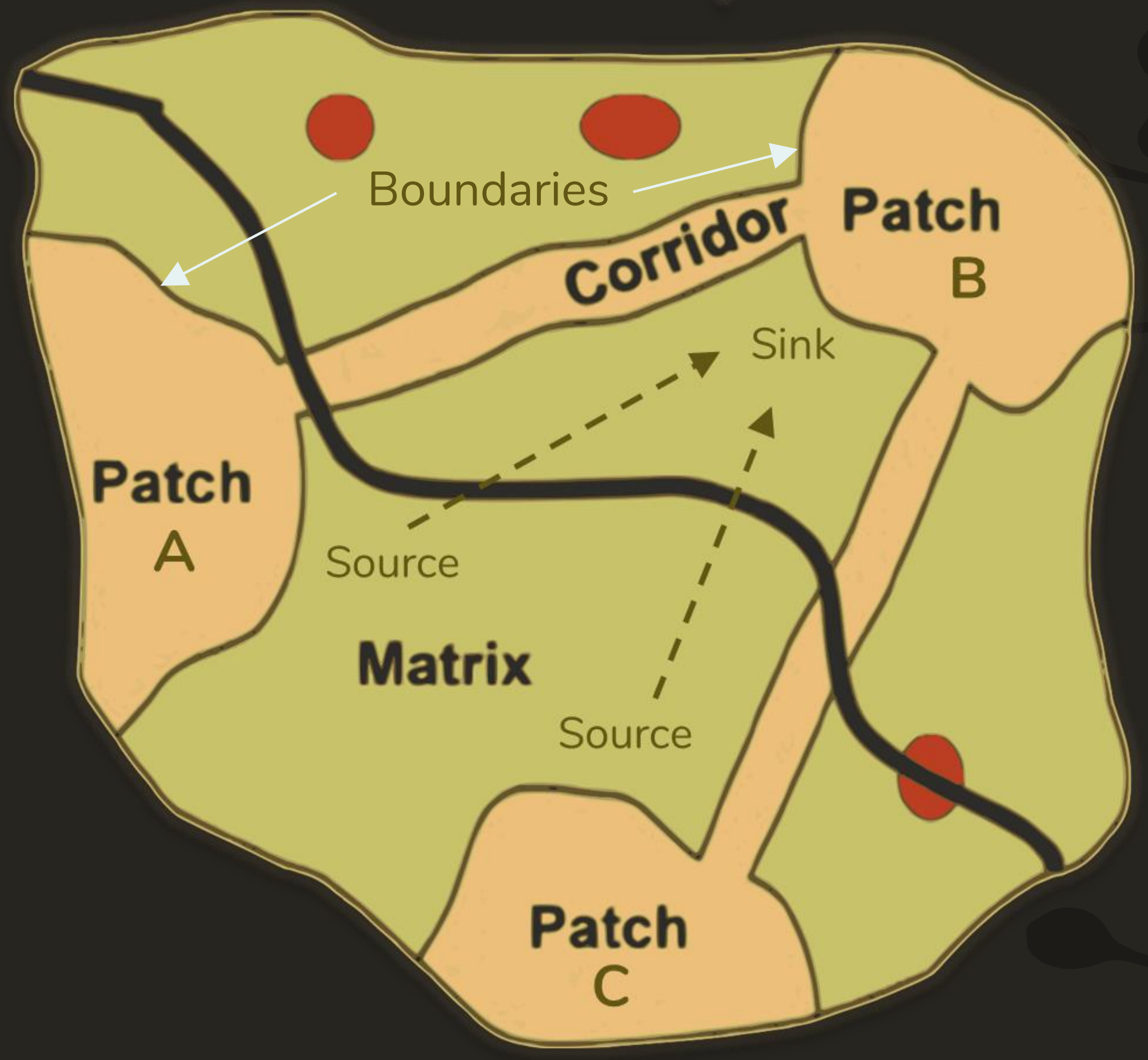
Landscape MATRIX

The "background" of a landscape, with a high degree of **connectivity**. Characterized by an extensive cover with a major control over processes.

Habitat CORRIDORS

Strips of habitat that is similar to the patches which they connect; act as dispersal pathways.

A landscape mosaic



[Figure 1, with modifications], Lausch et al., 2015, DOI: 10.1016/j.ecolmodel.2014.08.018, used under a Fair Use rationale.

Habitat/landscape PATCHES

Homogenous areas of a certain land cover type with own individual characteristics and functions; connected to the edges of adjacent patch/matrix by patch **boundaries**.

Habitat CONNECTIVITY

The measure of how connected or spatially continuous a corridor, network, or matrix is.

SOURCE and SINK habitats

Terms related to rates of colonization and extinction within patches (B+I, D+E); dynamics (sink ↔ source).

HABITAT FRAGMENTATION

Consequences on the spatial structure

Habitat fragmentation

- Habitat destruction typically leads to fragmentation.
  - The division of habitat into smaller and more isolated fragments separated by a matrix of human-transformed land cover.
- Results of fragmentation:
  - Habitat loss;
  - Increase in isolation;
  - Greater exposure to human land uses along fragment edges;
  - In general: changes to the structure and function of the fragments.

Effects of fragmentation

- Physical effects
  - Reduction in the size of habitat patches and increase in their spatial isolation.
- Demographic and population genetic effects
  - Reduced patch size and inter-patch dispersal result in smaller effective population sizes within fragments; prone to genetic drift and inbreeding.
- Community effects
  - Disruption of species interactions; small fragments loose species, especially large vertebrates and habitat specialists.

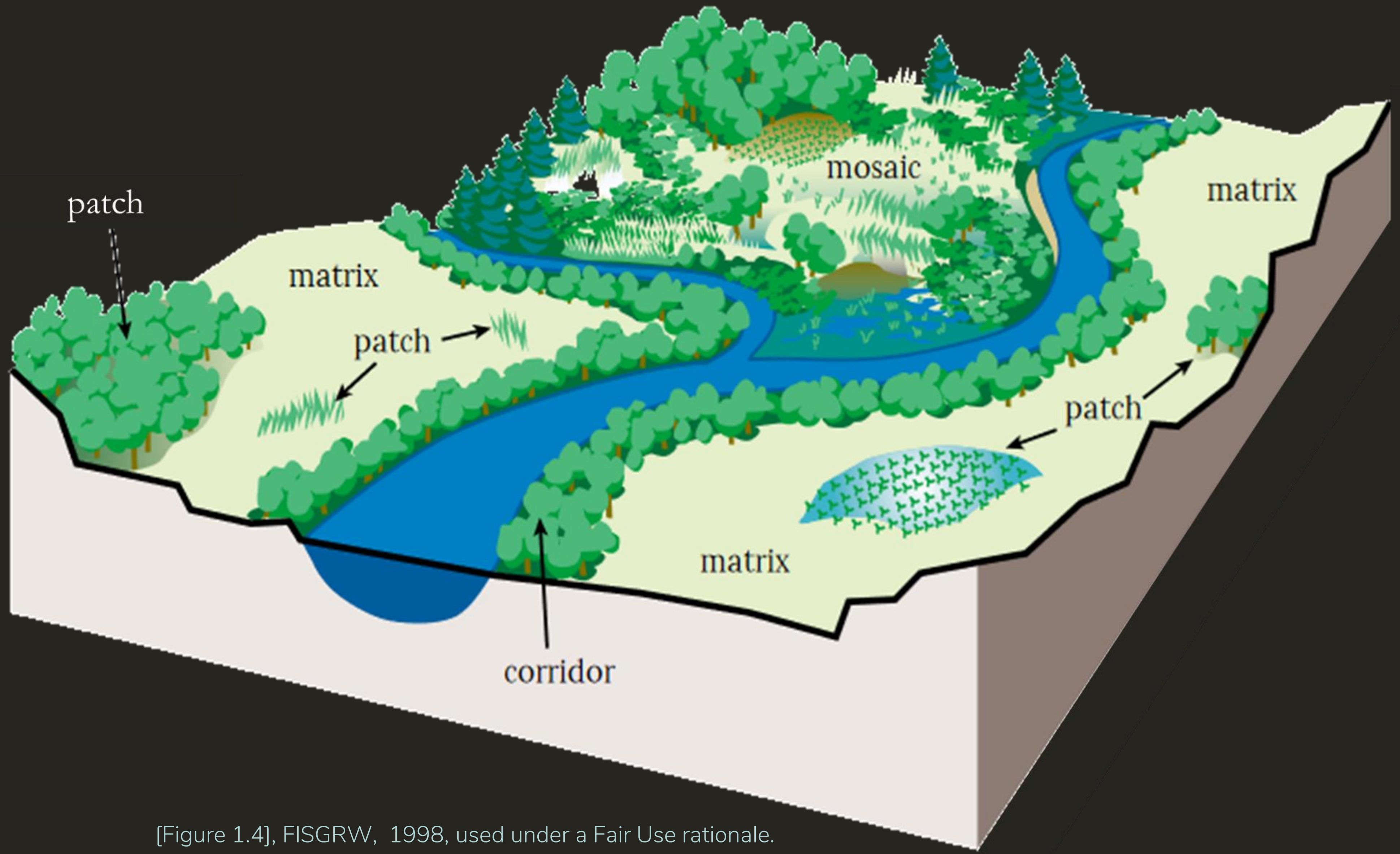
Fragmentation and isolation of Poole Basin, Dorset, England. Between 1759 and 1978, the area lost 86 percent of its heathland, changing from 10 large blocks separated by rivers to 1084 pieces.

[Figure 19.7], Smith & Smith,. 2015, Elements of Ecology, 9th ed. Essex (UK): Pearson Education Ltd, used under a Fair Use rationale.

Cheptou et al. 2017. Phil. Trans. R. Soc. B 372: 2016003720160037. DOI: 10.1098/rstb.2016.0037

Landscape spatial structure

- Landscape structure or landscape pattern emerge from composition and configuration of patches.
  - **Landscape composition:** the number, proportional frequency, and variety of land cover types of patches.
  - **Landscape configuration:** the spatial aspects of the patch mosaic (patches size & shape, spatial arrangement, patches connectivity).

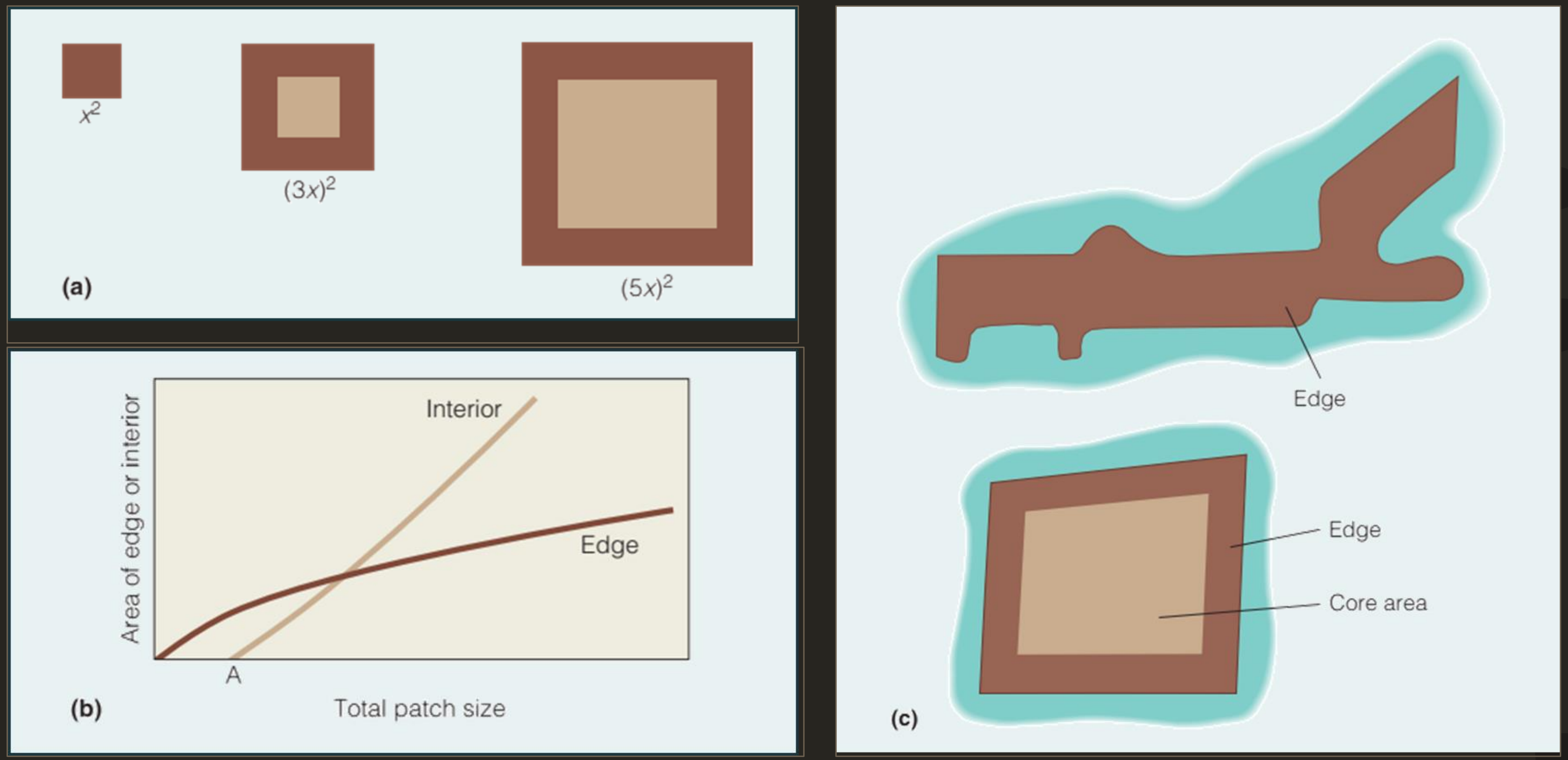


[Figure 1.4], FISGRW, 1998, used under a Fair Use rationale.

Effect of a patch size

- Large patches of habitat contain a greater number of individuals and species than do small patches.
- Larger patches are more likely to contain variations in topography and soils.
  - Greater diversity of plant life (both taxonomic and structural)
  - Create a wide array of habitats for animal species.
- Size and shape of patches affect the relative abundance of edge (or perimeter) and interior environments.
  - Ratio of boundary to interior

Effect of a patch size



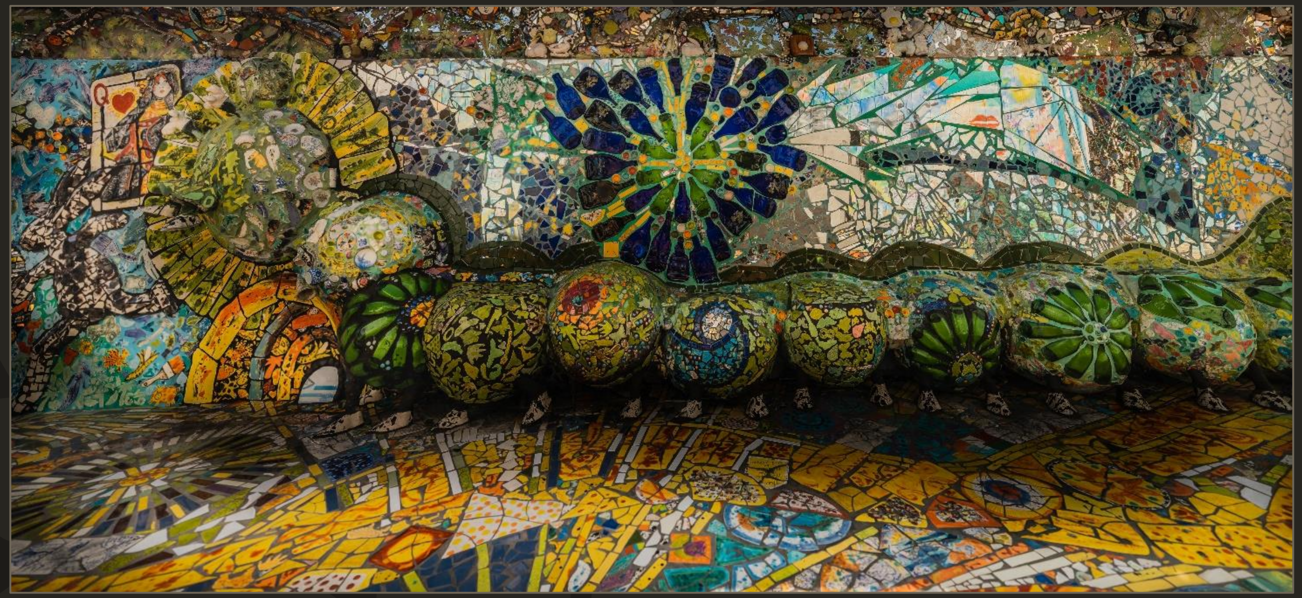
Relationship of habitat patch size to edge and interior conditions. Only when a patch becomes large enough to be deeper than its boundary can it develop interior conditions.

[Figure 19.17], Smith & Smith,. 2015, Elements of Ecology, 9th ed. Essex (UK): Pearson Education Ltd., used under a Fair Use rationale.

- (a) Assuming that the depth of the edge remains constant, the ratio of edge to interior decreases as the habitat size increases.
- (b) The general relationship between patch size and area of edge and interior. As size increases, interior area increases, and the ratio of edge to interior decreases.
- (c) This relationship applies for a square or circular habitat patch; long, narrow habitats are all edge communities, even though the area may be the same as that of square or circular ones.

Landscape mosaic

- A patchwork of different types of land cover.
  - An analogy of mosaic art.
- Landscape mosaic is dynamic.
  - Patches and their boundaries interact in a variety of ways and they change through time.
- A landscape with a certain number of potentially <u>habitable patches</u> of habitat can form a metapopulation.



METAPOPULATION

Structure, dynamics, and models

Metapopulation

- Discrete subpopulations (or local populations) in patches connected by occasional migration between patches.
  - **Patches**: areas with the necessary resources & conditions for a population to persist.
- Constantly fluctuates.
  - Modified by populations processes (B+I and D+E).
  - Thus, vulnerable to extinction (if D+E >> B+I), and recolonization.

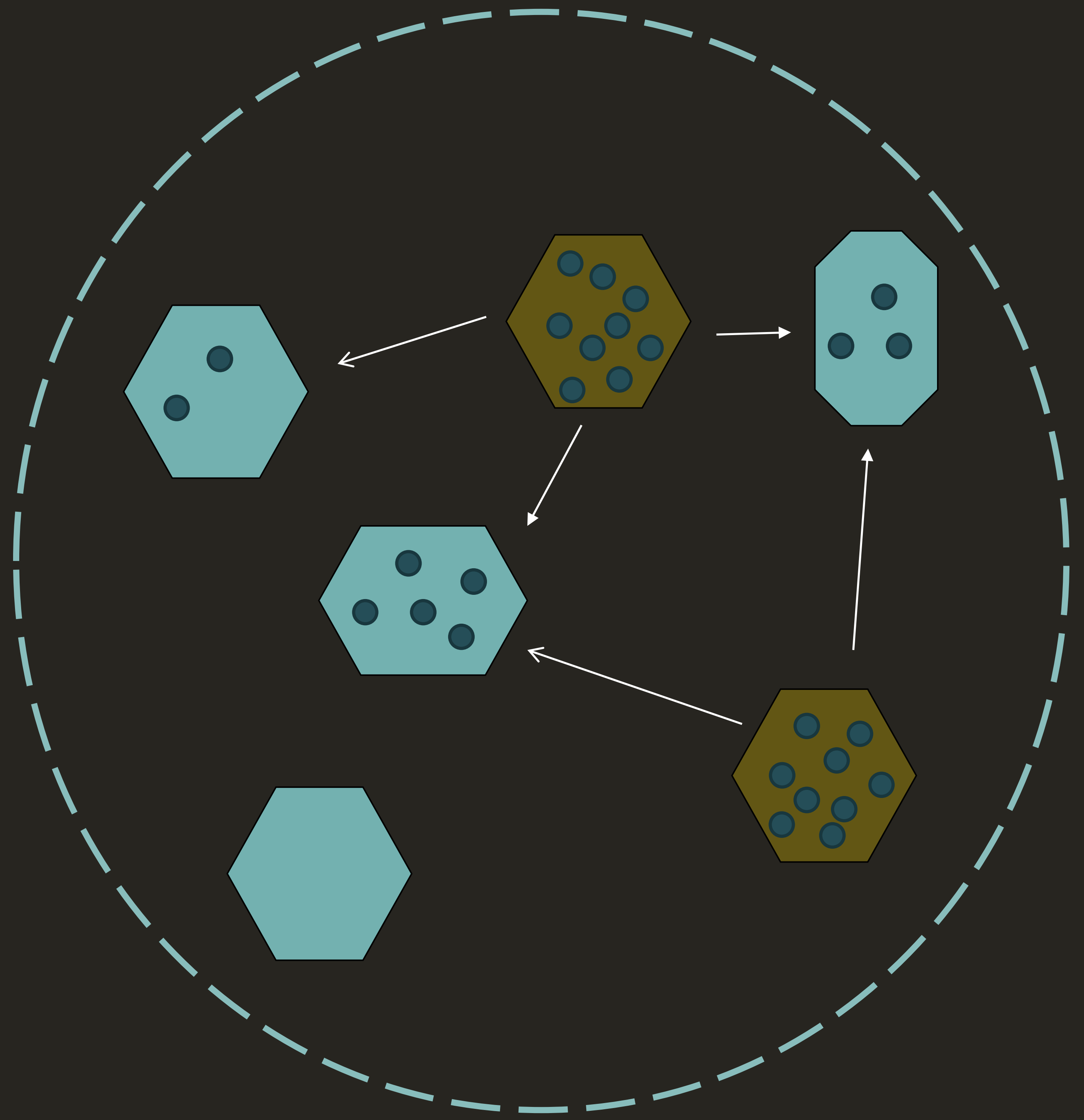
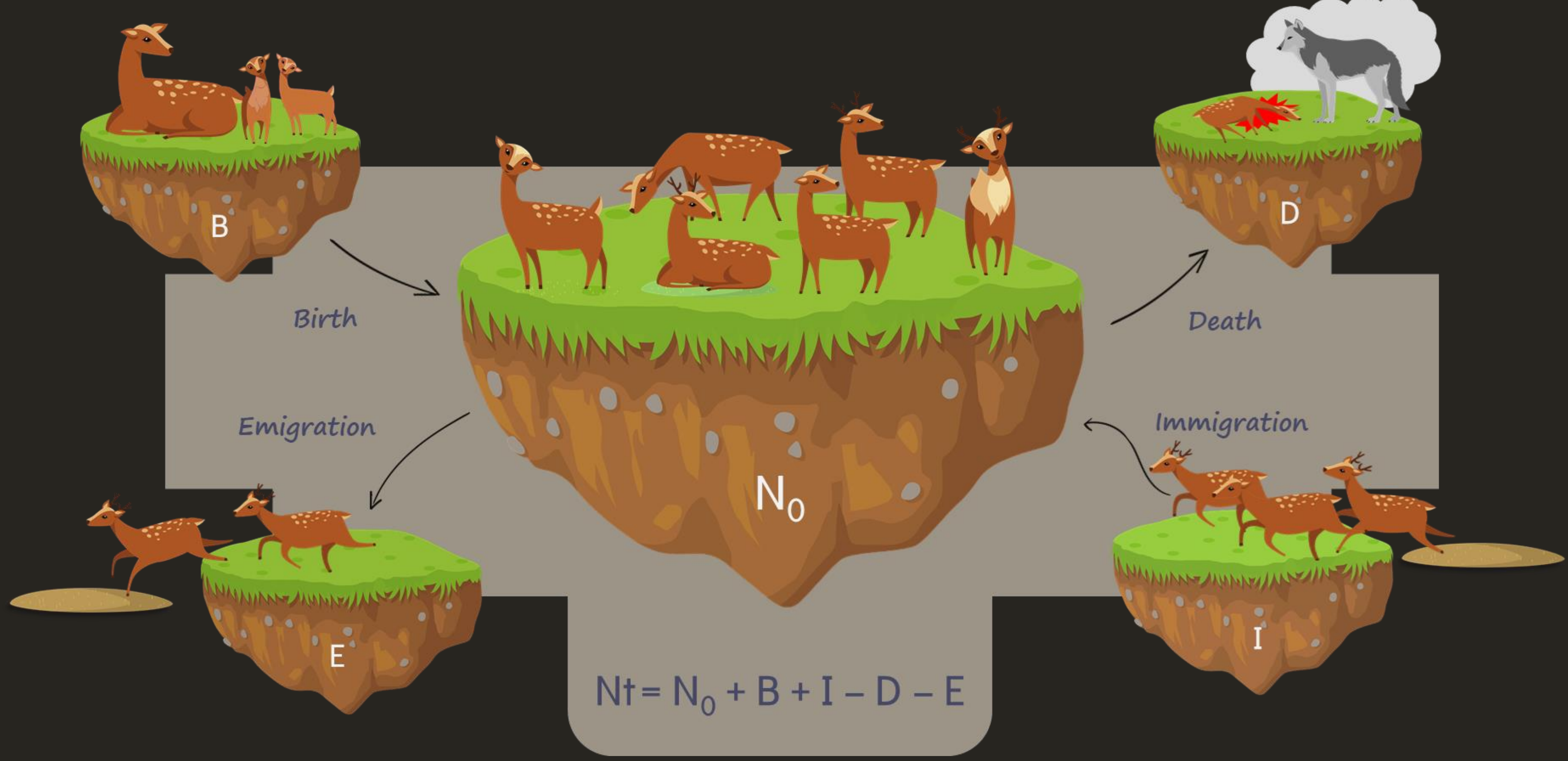


Illustration of a metapopulation. Metapopulation is everything inside dashed circle; shapes are habitable habitat patches; a group of individuals of a species (blue dots) occupying a patch is called subpopulation; shapes in blue filled with dots are patches receiving immigrations; shapes in brown are patches sending migrants; arrows show the direction of individual species movements.

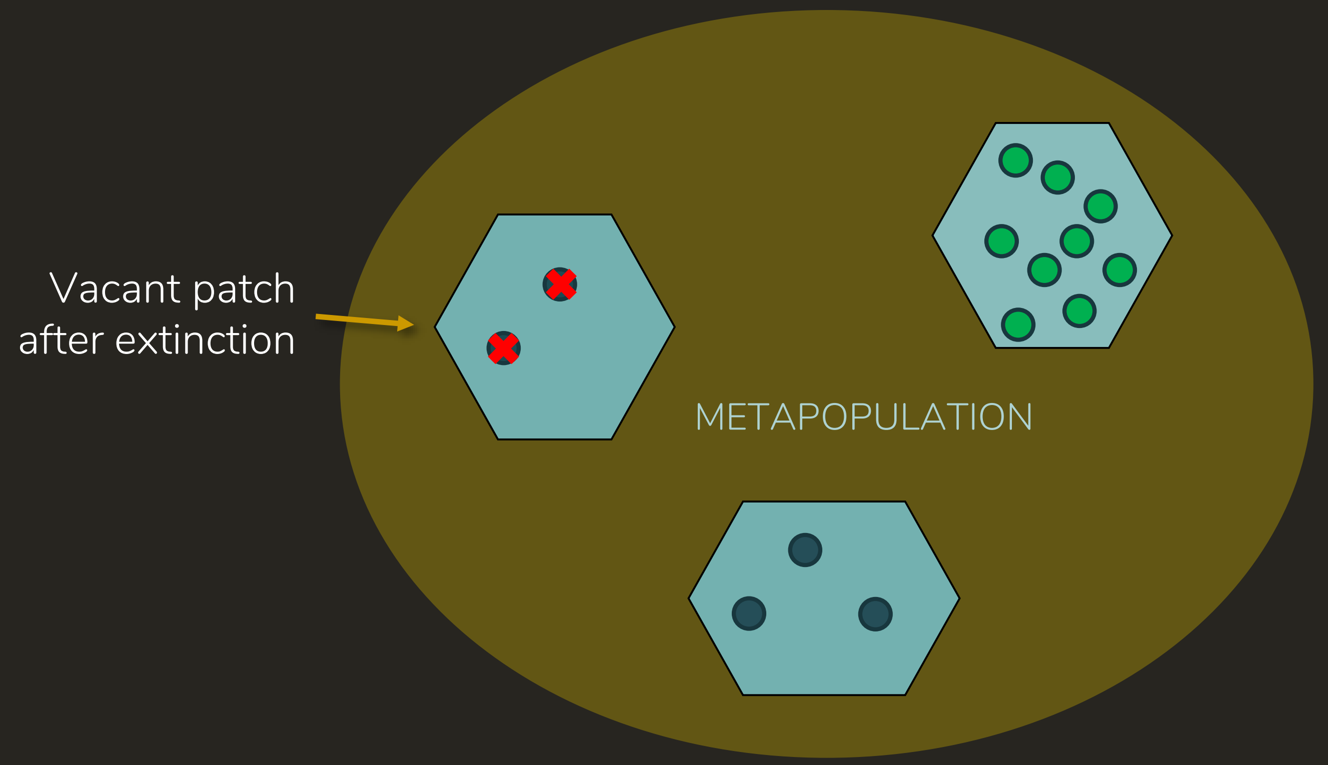
Metapopulation dynamics

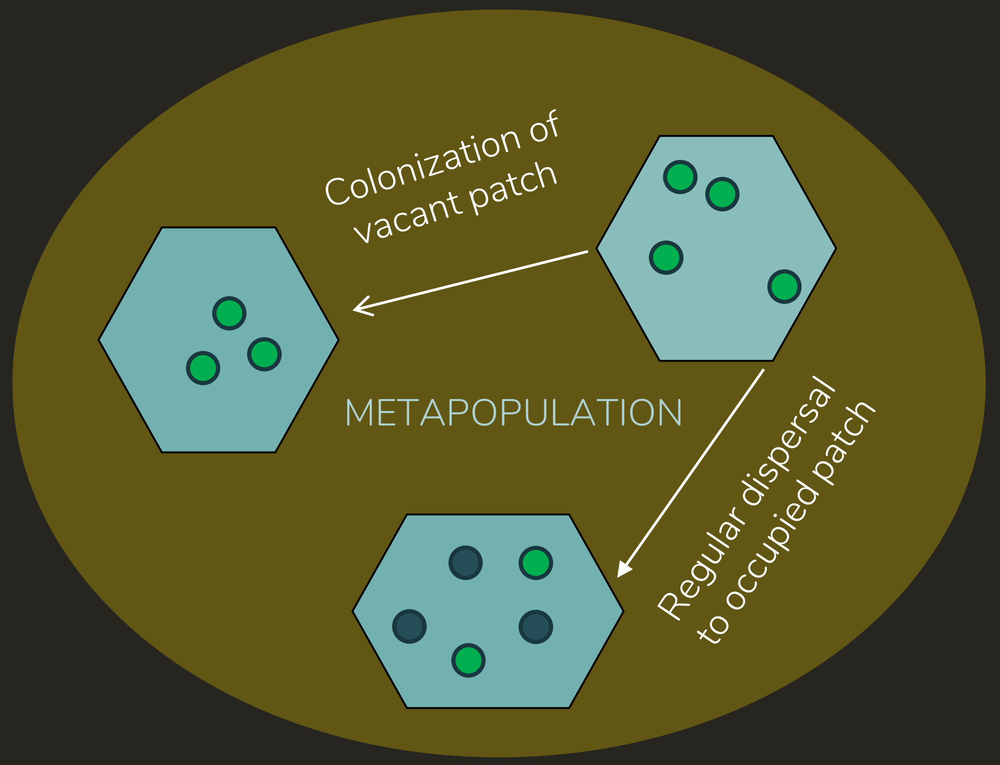
- Populations are subject to demographic (or population) processes.
  - Birth + immigration = population increase.
  - Death + emigration = population decrease.
- Populations may be naturally patchy in distribution.
  - From variation in resources, physical gradients, biological characteristics.



Metapopulations dynamics

- A balance between extinction and colonization among patches.
- Dispersal ability of organisms determines metapopulation boundaries.
- Extinction-colonization process.
  - When a habitat patch becomes vacant through extinction and is then recolonized by individuals from other subpopulation.





Extinction-colonization

Metapopulation structure affects its dynamics

- Metapopulation structure involves characteristics of patch size and density.
- Metapopulations may fluctuate in their level of patch occupancy.
- The level of genetic variation in a metapopulation is determined by interaction between population size, extinction, and colonization.

Metapopulations and evolution

- Reduction in habitat can drive local adaptation and rapid evolution.
- Habitat patches with larger population sizes allow enough time for organisms to adapt before stochastic extinction.
- Extinction event depends on population sizes and gene flow between populations.

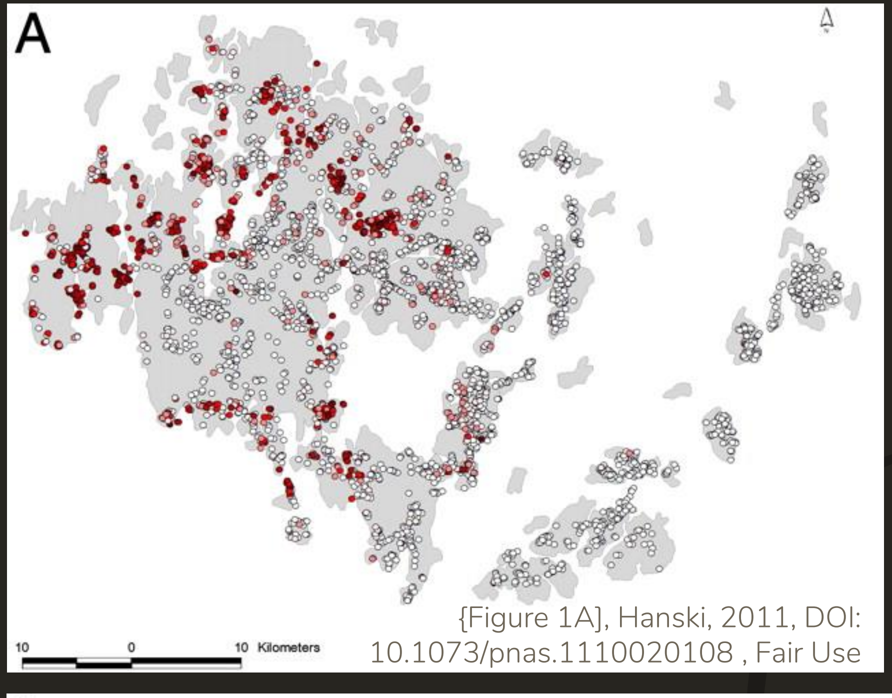
[Forest fragments in an Ontario boreal forest], Per Breiehagen via National Audubon Society

Key processes in metapopulation dynamics

Extinction	• Constant risk multiplied by number of occupied patches.
Colonization	• Dependent on number of occupied (source) and empty (target) patches.
Turnover	• Extinction of local populations and establishment of ones in empty habitat patches by migrants from existing local populations.
Rescue effect	• When immigration from another population allows a local population to avoid extinction; reduces chance of all populations going extinct at once.

Glanville fritillary butterfly metapopulation

- Habitat occurs in discrete patches.
- Endangered; all populations have risk of extinction.
- Dispersal occurs among all patches.
- Patch dynamics are asynchronous.



{Figure 1A], Hanski, 2011, DOI: 10.1073/pnas.1110020108 , Fair Use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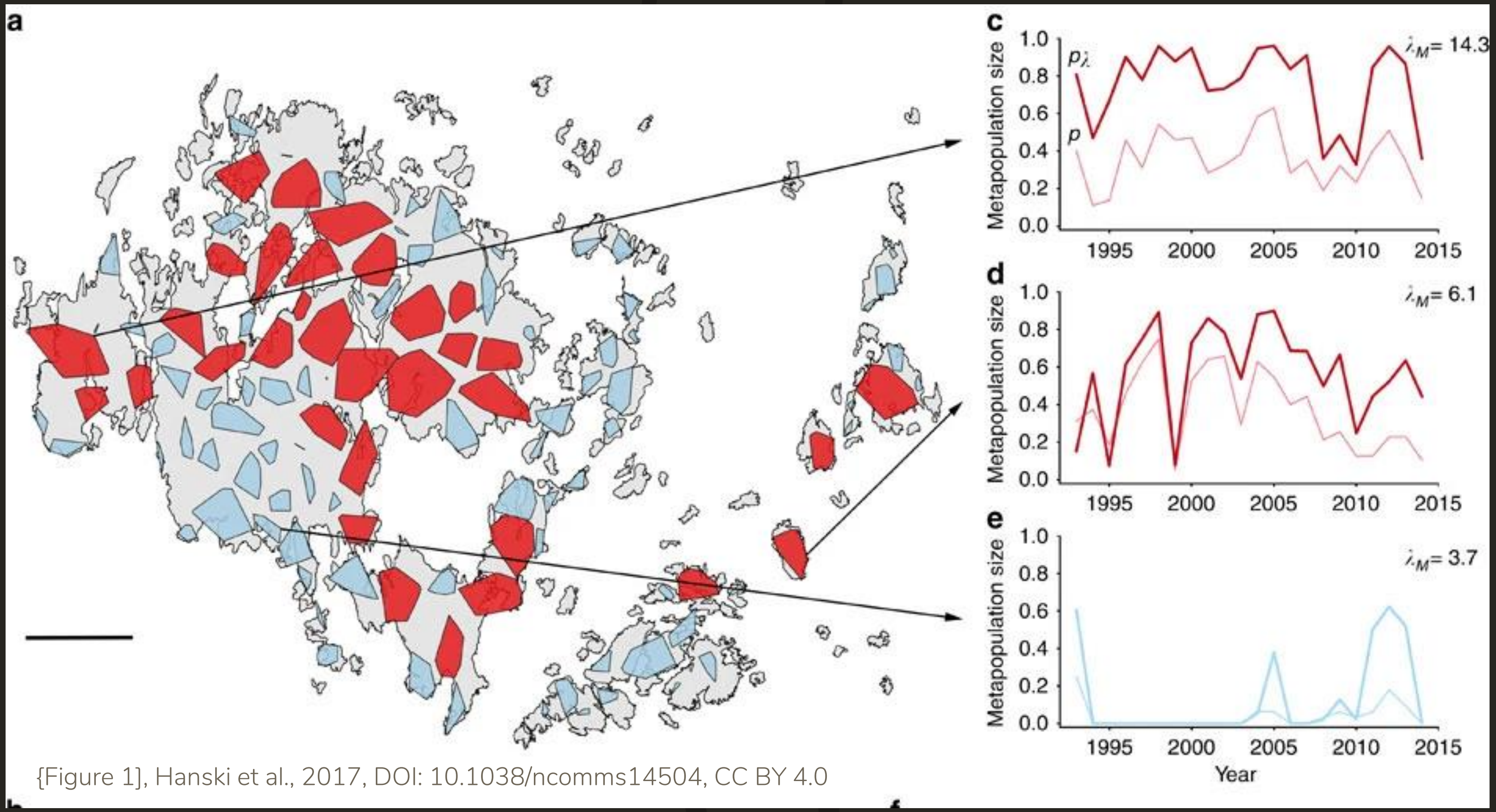


{Figure 1], Hanski et al., 2017, DOI: 10.1038/ncomms14504, CC BY 4.0

Map of Glanville fritillary *Melitaea cinxia* habitat patch network in the Åland Islands, Finland.

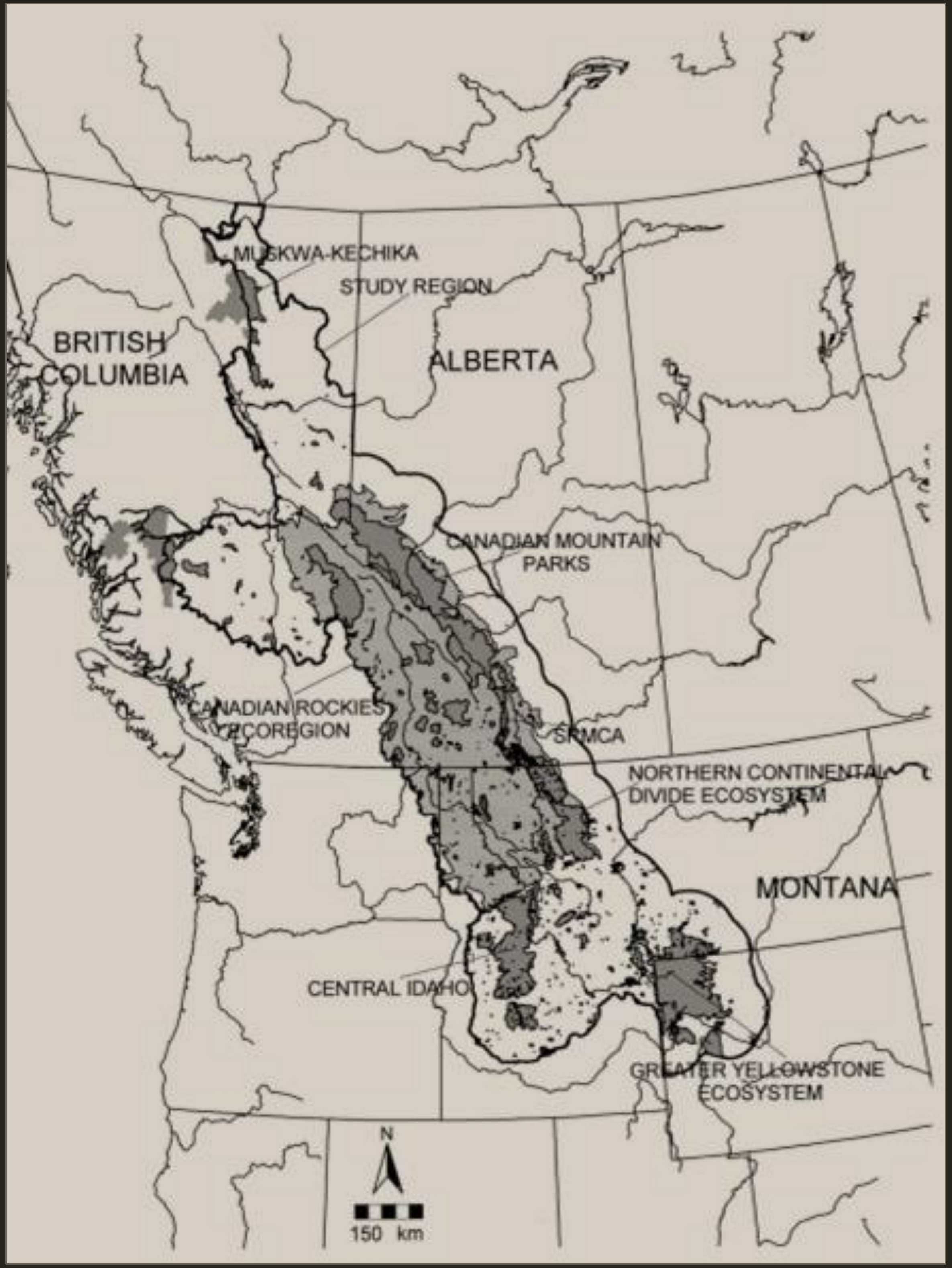
Southern California spotted owl metapopulation

[Figure 12.14], Ricklefs, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company. Used under a Fair Use rationale.

Kameron Perensovich, Los Padres ForestWatch, Fair Use

- Southern California spotted owls are distributed as a metapopulation over patches of suitable old-growth forest habitat in the mountains of southern California.
- Lines are possible dispersal routes.
- Numbers are the estimated carrying capacities.

Large carnivores in Rocky Mountains

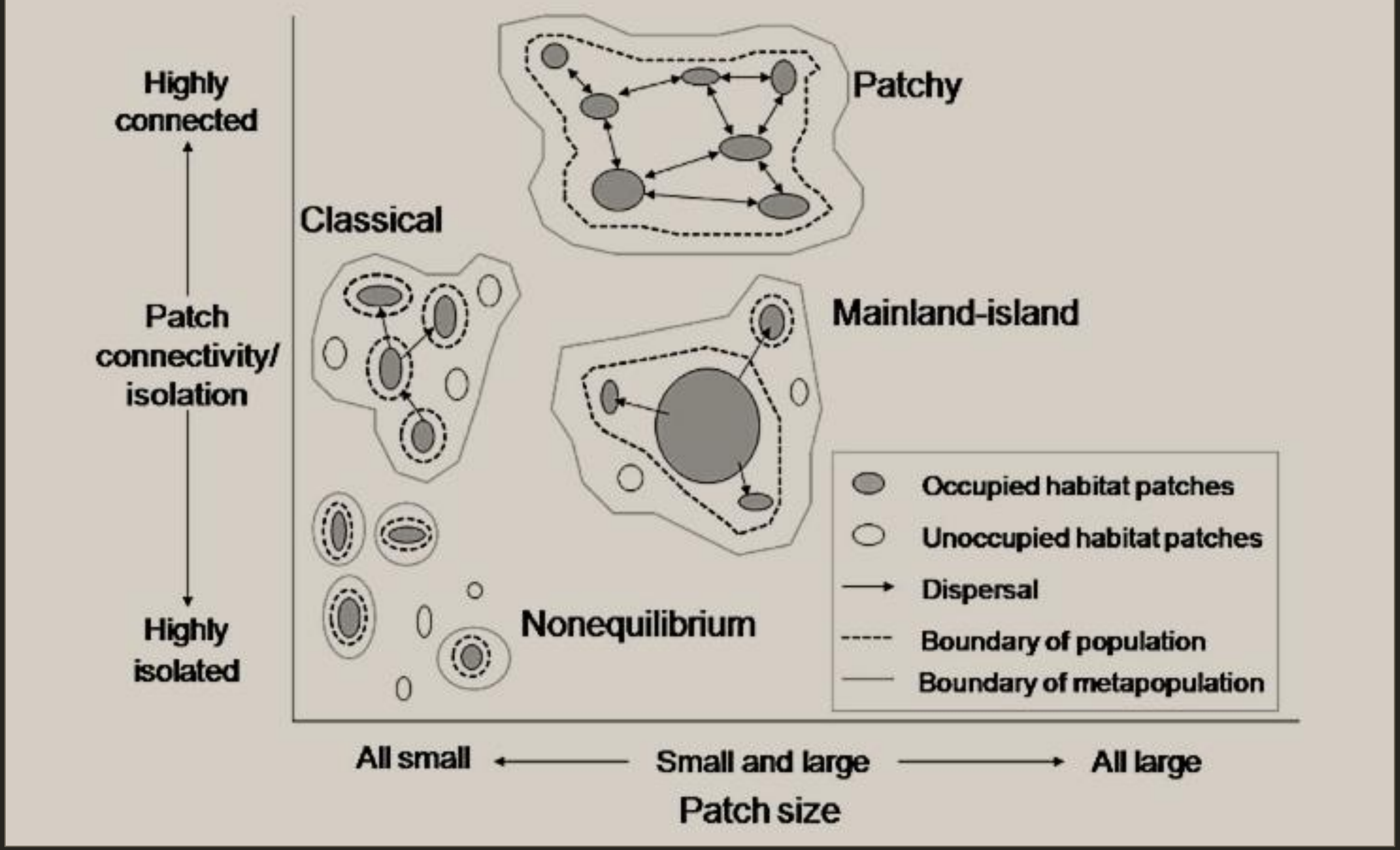


- Series of protected areas link carnivore species.
- Small, isolated populations in southern range margins.
- Conservation efforts have focused on retaining landscape connectivity in this region.

[Figure 1], Carroll et al., 2003, Ecol Appl 13(6): 1773–1789, Fair Use.

Types of metapopulation structure

[Figure 1], Aycrigg & Garton, 2014, DOI: doi.org/10.1644/12-MAMM-A-300, Fair Use.

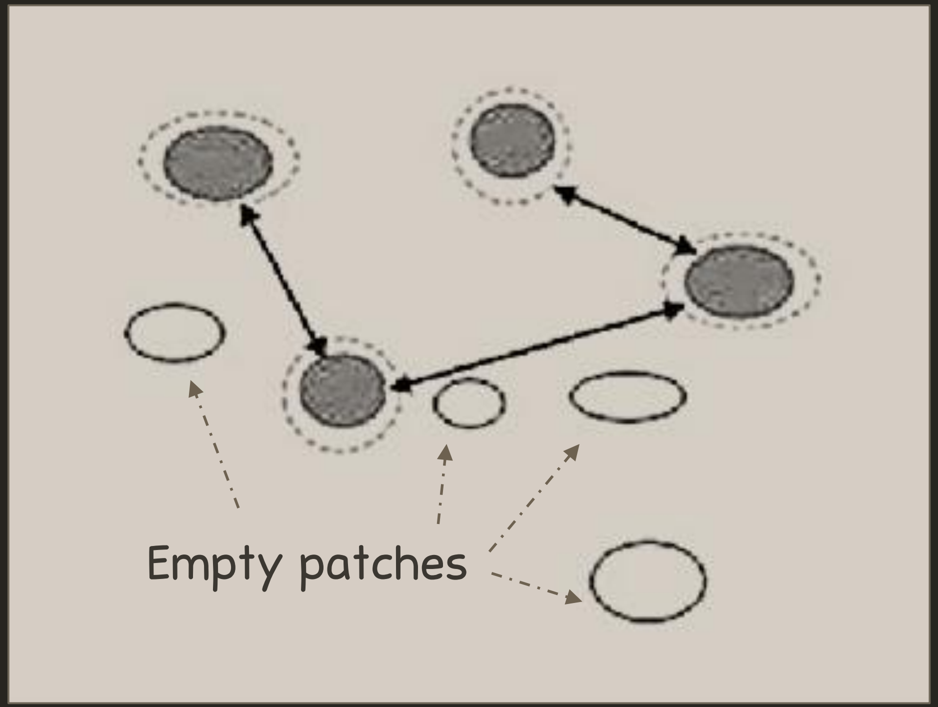


Patch connectivity (Y-axis) represents the dispersal distance (relative to interpatch distances)

1. Classical model (Levins metapopulation model)
2. Mainland-island model (Boorman-Levitt metapopulation)
3. Patchy model
4. Non-equilibrium model

1. Classical metapopulation model

Metapopulation concept was first introduced by Richard Levins (1970) to define a large network of similar, isolated habitat patches, with local dynamics occurring at a much faster time scale than metapopulation dynamics.



Moderate connectivity; all small patches

ASSUMPTIONS

- Homogeneous discrete patches (all patches are equally large and interchangeable).
- Extinction and colonization are insensitive to spatial context.
- No time lags (metapopulation growth responds instantaneously to changes in P).
- Very large number of patches (global extinction is not possible).

1. Classical metapopulation model

$$\Delta P/\Delta t = C - E$$

$$C = [mP(1-P)] \qquad E = eP$$

$$\Delta P/\Delta t = [mP(1-P)] - eP$$

$$\hat{P} = 1 - \frac{e}{m}$$

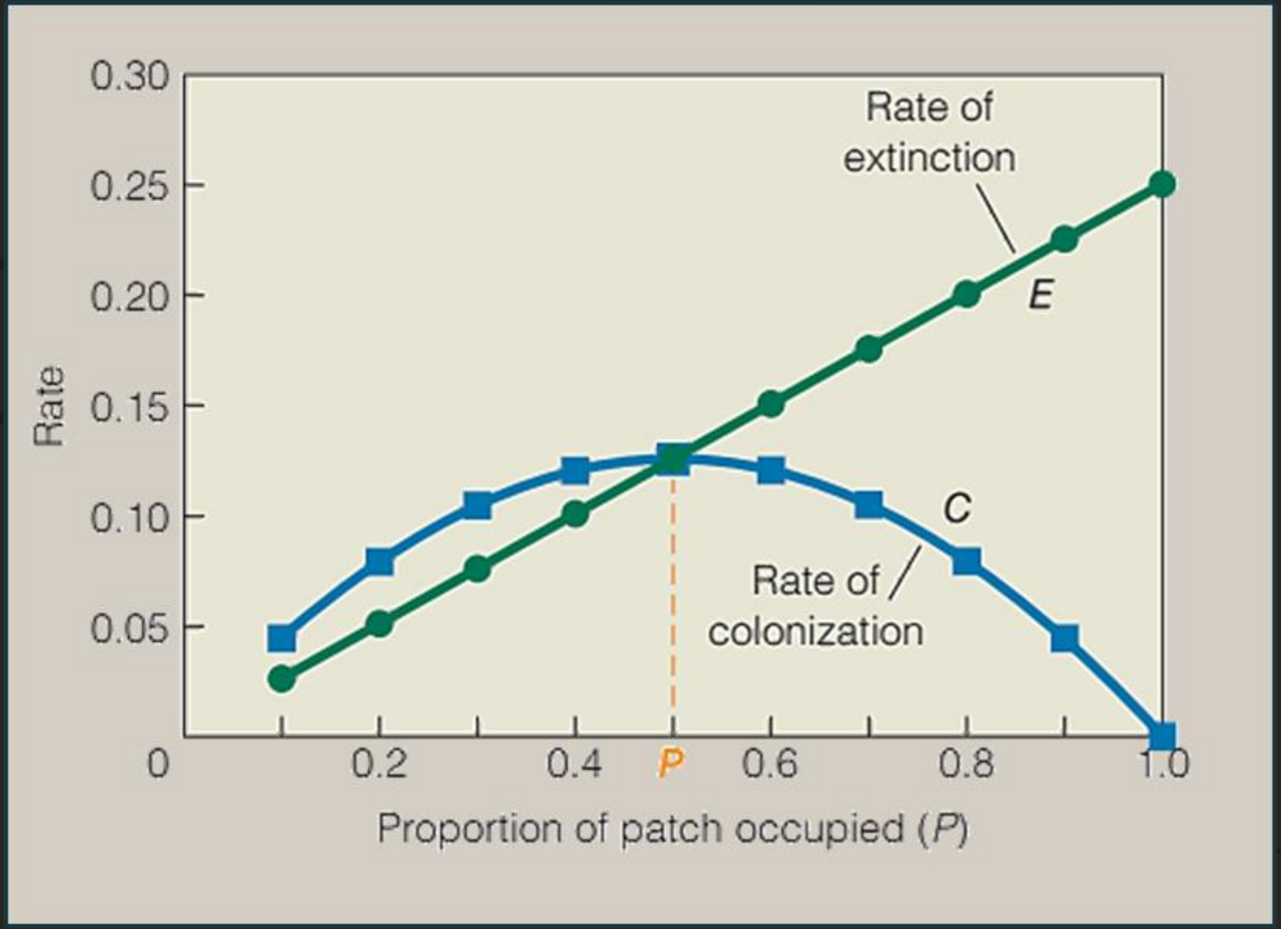
Metapopulation in an equilibrium state

P	Fraction of occupied habitat patches.
t	Time interval.
$\Delta P/\Delta t$	Change in the fraction of patches occupied by subpopulations through time.
C	Colonization rate of empty patches.
E	Extinction rate of subpopulations.
m	Colonization probability.
e	Extinction probability of subpopulations.
$\hat{P}$	Metapopulation equilibrium value.

Metapopulation will go extinct if $e > m$.
Metapopulation persists if $e/m < 1$.

1. Classical metapopulation model

- P increases with increasing patch area.
  - Caused by decreasing extinction.
- P increases with decreasing distance among patches.
  - Caused by increasing colonization.
- Rescue effect in Levins metapopulations:
  - Rate of extinction e decreases when fraction of occupied patches P increases.



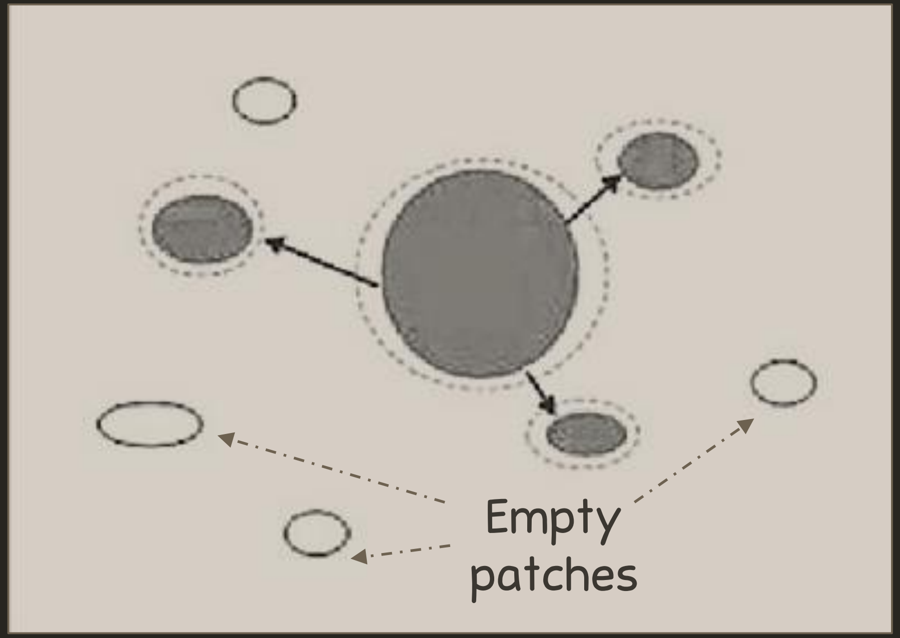
Rates of extinction and colonization as a function of patch occupancy (P) under the Levins model of metapopulation. The equilibrium value of patch occupancy ($\hat{P}$, where $C = E$) in this example is 0.5. At $P > 0.5$, the rate of change is negative, and P declines. At $P < 0.5$, the rate of change is positive, and P increases with time.

[Figure 19.26], Smith & Smith,. 2015, Elements of Ecology, 9th ed. Essex (UK): Pearson Education Ltd. Used under a Fair Use rationale.

2. Mainland-island metapopulation model

$$\Delta P/\Delta t = [m(1-P)] - eP$$

e and m are constant.



Moderate connectivity; small and large patches

Note: the equilibrium theory of island biogeography is a multispecies version of the mainland-island model.

ASSUMPTIONS

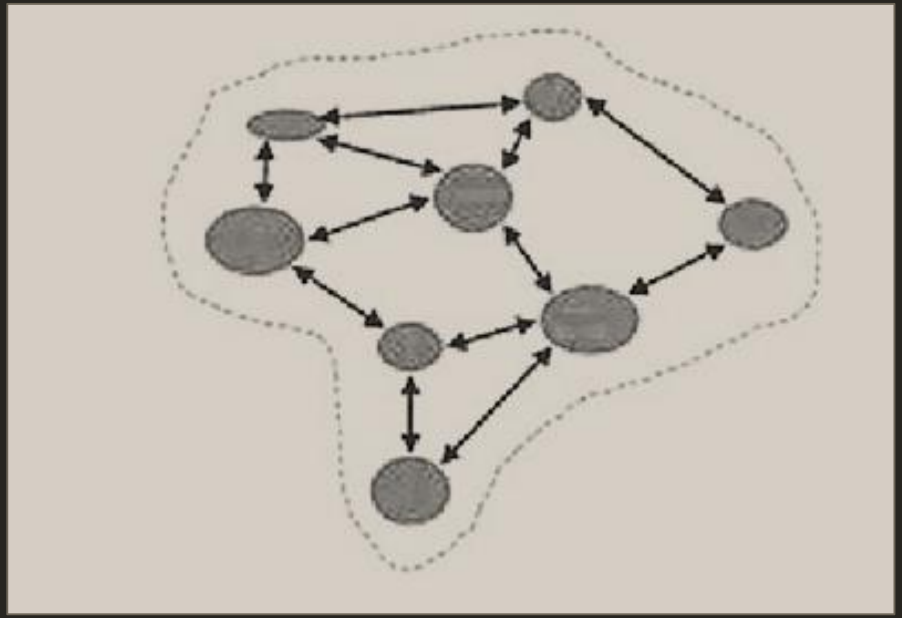
Large and invulnerable source population on the "mainland," from which individuals migrate to smaller habitat patches ("islands")

There may or may not be migration among the island populations; island populations depend on immigrants from the mainland.

Mainland population never goes extinct, and therefore, this metapopulation type generally never goes extinct.

3. Patchy metapopulation model

- When a subpopulation goes extinct, it is not noticed because it is part of a large continuous metapopulation.
- However if the single large subpopulation goes extinct, so does the metapopulation.
- Many do not consider this a metapopulation.



High connectivity;
small and large patches

ASSUMPTIONS

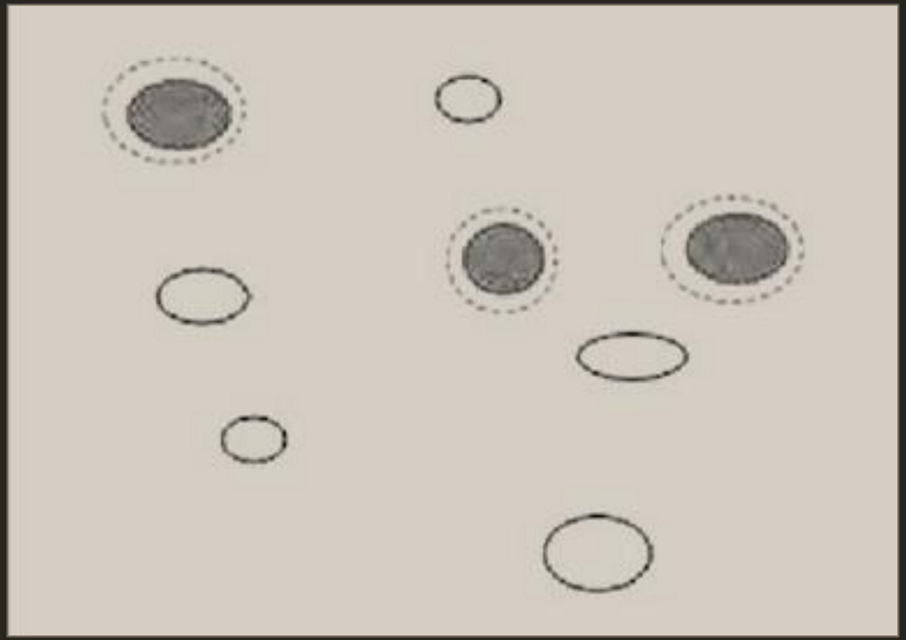
All subpopulations are sufficiently close to function as a single subpopulation.

Subpopulations are not independent; their demographics are closely linked.

Dispersal between patches is high; subpopulations are not at risk of going extinct (C > E).

4. Non-equilibrium metapopulation model

- The subpopulations are separated by large interpatch distances so that no migration occurs; when a subpopulation goes extinct it does not get recolonized.
- When extinction occurs, the subpopulation and the metapopulation go extinct.



High isolation;
All small patches

ASSUMPTIONS

Each subpopulation acts as a separate metapopulation.

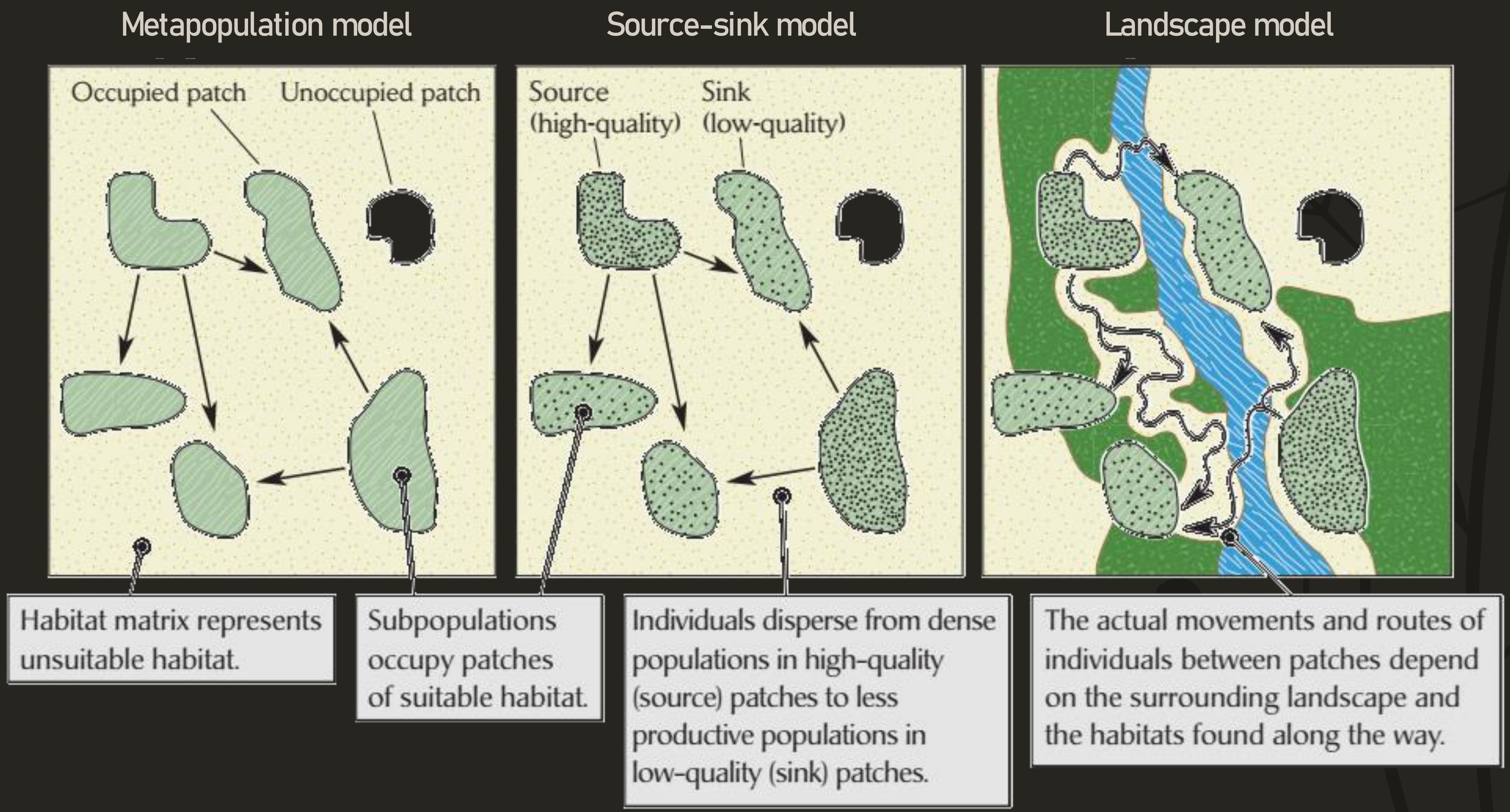
Each metapopulation is extinction-prone because of its isolation and small size (E > C)

Subpopulations are completely independent and their demographics are not linked.

Rescue effect

- A process explaining how immigration of individuals from large, productive subpopulations to declining subpopulations can reduce the chance of extinction.
  - Promoting the long-term persistence of the network of populations.
- In metapopulation models:
  - The rate of extinction (E) decreases as the fraction of occupied patches (P) increases.
- Further highlights the importance of patch connectivity to the persistence of metapopulations.

Models of population spatial structure

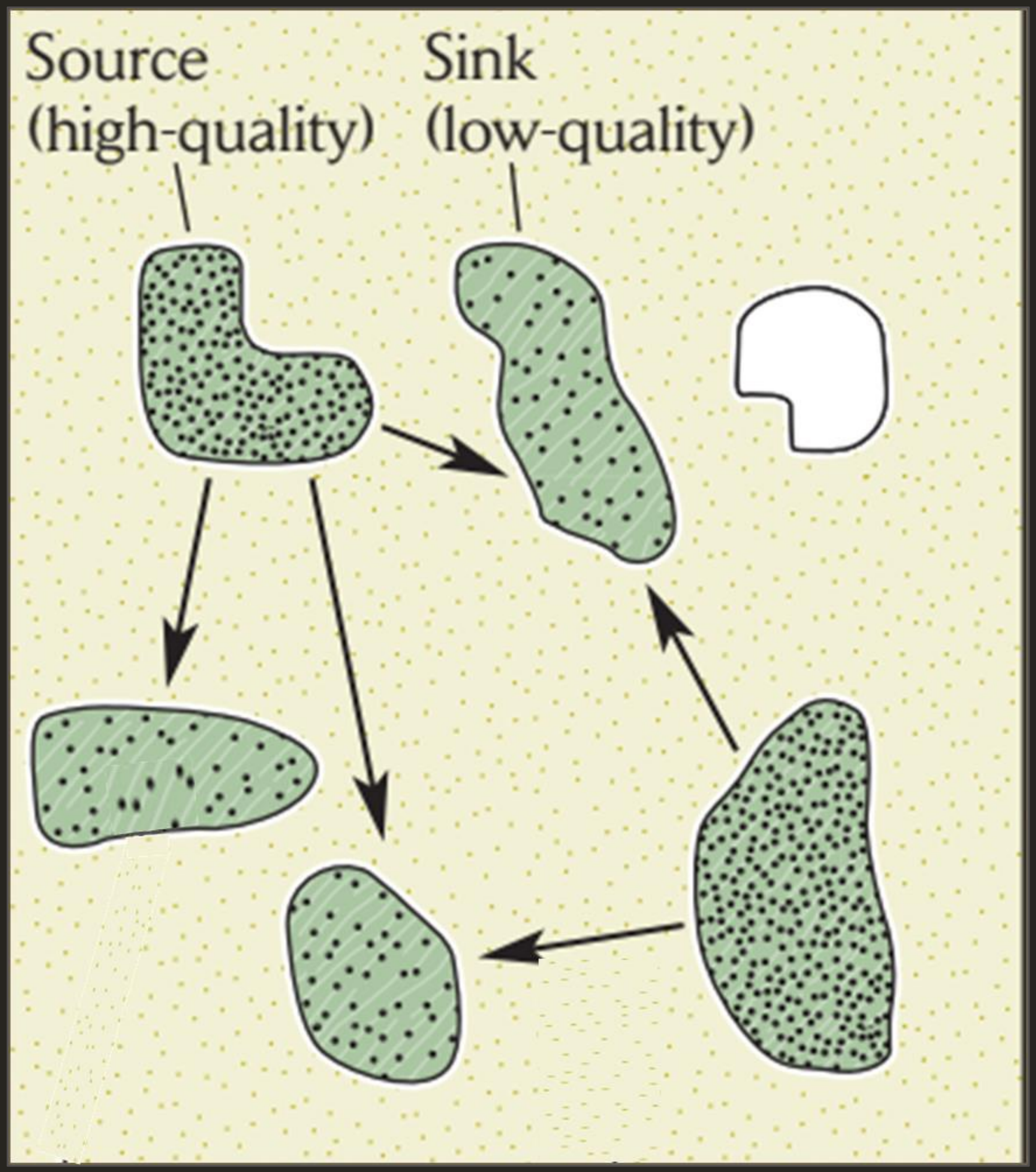


Three models of spatial population structure, based on variation in habitat patch quality and in the intervening matrix. Arrows represent movements of individuals between patches.

[Figure 10.18], Ricklefs, 2008, The Economy of Nature. 6th ed. NY: W. H. Freeman and Company, used under a Fair Use rationale.

Source-sink metapopulation dynamics

- System where at low density there are subpopulations with negative (in absence of dispersal) & positive growth rates.
- Persistence of a local population (sink) depends on migration from a nearby population (source).
  - True sink vs pseudo-sink population/habitat.
  - Source-sink relationship is not fixed; a source one year can be a sink the next.
- Empty patch is susceptible to colonization.



Other models: Spatially realistic metapopulation

- Similar to Levins' model, with some differences:
  - Accounts for variation in size of patches, total patch number and their spatial arrangement.
  - At equilibrium, depends on metapopulation capacity and probabilities that different patches are occupied.
- Spatially realistic models are often complex and rely on detailed data.

Other models: Spatially explicit metapopulation

- Assumes that local populations interact only with nearby local populations.
- Migration is distance dependent.
- Can be useful for understanding:
  - Response of a population to landscape change.
  - Areas of highest vulnerability to decline or extinction.
  - Location of population source areas.
  - Response of populations to alternative conservation strategies.

Metapopulation persistence

- Because of the rescue effect, metapopulation persistence increases with overall number of populations.
- Numerous factors can impact survival of populations:
  1. Environmental uncertainty (stochasticity).
  2. Natural catastrophe.
  3. Genetics.
  4. Demographic uncertainty (stochasticity).

Factors affecting the survival of populations

1. Environmental uncertainty
   - Resource fluctuations.
   - Seasonal variations.
   - Densities of competitor/other species.
2. Natural catastrophes
   - E.g.: earthquakes, fire, flood, landslide.

Factors affecting the survival of populations

3. Genetics
   - Genetic drift.
   - Founder events.
   - Inbreeding.
4. Demographic uncertainty
   - Skewed sex ratio.
   - Age structure; i.e. populations dominated by old or juvenile individuals.

Minimum viable population (MVP)

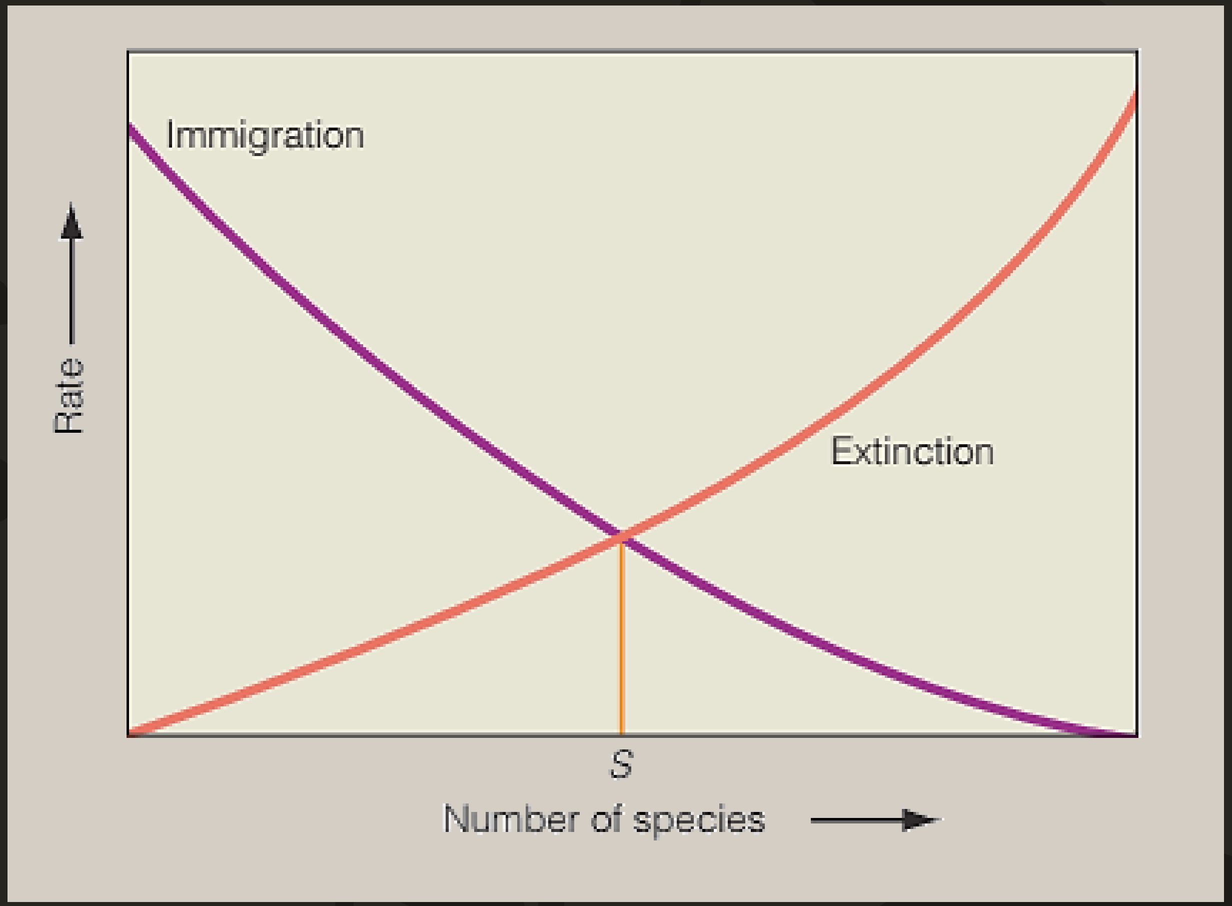
- Population size below which probability of extinction is increased.
- In metapopulations:
  - Minimum number of interacting local populations necessary for long-term persistence of metapopulation.

Minimum viable metapopulation

- Metapopulation persistence increases when:
  - Number of available patches increases.
  - Fraction of occupied patches becomes larger.
- In a classic (Levins) metapopulation model:
  - Persistence increases with *P* (fraction of occupied habitat patches)
  - At least 10 to 15 well-connected patches are needed for long-term persistence.

Island biogeography applies to landscape patches

- When immigration and extinction rates are equal, an equilibrium is reached.
- Number of species does not change, but there is still turnover.
  - What changes is the species themselves.



Species equilibrium plot according to the theory of island biogeography. Immigration rate declines with increasing species richness (x-axis) and extinction rate increases. The balance between rates of extinction and immigration (immigration rate = extinction rate) defines the equilibrium number of species (*S*) on the island.

[Figure 19.24], Smith & Smith,. 2015, Elements of Ecology, 9th ed. Essex (UK): Pearson Education Ltd., used under a Fair Use rationale.

Metacommunity as an extension of metapopulation concept

- **Metacommunity**: a set of local communities occurring in discrete patches, linked by dispersal.
  - Each habitat patch on the landscape is composed of a set of species that define the local community.
- Metacommunity ecology examines how local dynamics of ecological communities are associated with regional dispersal of species.

Metacommunity vs metapopulation

- Metapopulation theory
  - Examine what determines the persistence of the metapopulation in a system of connected habitat patches,
- Metacommunity theory
  - Examine what regulates the co-existence of multiple species in that same system of connected habitat patches.
- Metacommunity focus elements:
  - Multiple potentially interacting species;
  - Multiple patches at which interaction may occur;
  - Dispersal by at least some of the species to link interactions among the sites.

Analysis of metacommunity dynamics

- Interaction among communities is influenced by:
  - Size, shape, and spatial arrangement of the habitat patches and the matrix in which they are embedded.
- Effect of size:
  - Small fragmented communities: low species diversity, few trophic levels.
  - Large fragmented communities: greater species diversity, more trophic levels.

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