E-CONTENT PREPARED BY

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E-Content prepared for students of

M.Sc.(Semester-II) in Conservation Biology

Name of Course:
Biological Rarity Phenomena

Topic of the E-Content:
Fragmentation and Metapopulation

Habitat fragmentation and loss

- **Habitat fragmentation** describes the emergence of discontinuities (fragmentation) in an organism's preferred environment (habitat), causing population fragmentation and ecosystem decay.
- More specifically, habitat fragmentation is a process by which large and contiguous habitats get divided into smaller, isolated patches of habitats (Fahrig, 2003)
- The term habitat fragmentation includes five discrete phenomena:

a. Reduction in the total area of the habitat
b. Decrease of the interior: edge ratio
c. Isolation of one habitat fragment from other areas of habitat
d. Breaking up of one patch of habitat into several smaller patches
e. Decrease in the average size of each patch of habitat

Natural causes

Evidence of habitat destruction through natural processes such as volcanism, fire, and climate change is found in the fossil record. For example, habitat fragmentation of tropical rainforests in Euramerica 300 million years ago led to a great loss of amphibian diversity, but simultaneously the drier climate spurred on a burst of diversity among reptiles (Sahaney et al., 2010).

Human causes

Habitat fragmentation is frequently caused by humans when native plants is cleared for human activities such as agriculture, rural development, urbanization and the creation of hydroelectric reservoirs. Habitats which were once continuous become divided into separate fragments. After intensive clearing, the separate fragments tend to be very small islands isolated from each other by cropland, pasture, pavement, or even barren land. The latter is often the result of slash and burn farming in tropical forests. In the wheat belt of central-western New South Wales, Australia, 90% of the native vegetation has been cleared and over 99% of the tall grass prairie of North America has been cleared, resulting in extreme habitat fragmentation.

Processes of fragmentation

- Endogenous

A part of species biology so they typically include changes in biology, behavior, and interactions within or between species

changes to breeding patterns or migration patterns

Triggered by exogenous processes

- Exogenous

Independent of species biology and can include habitat degradation, habitat subdivision or habitat isolation

Habitat subdivision or isolation can lead to changes in dispersal or movement of species including changes to seasonal migration. These changes can lead to a decrease in a density of species, increased competition or even increased predation

Biological consequences of fragmentation

- Initial exclusion
- Crowding effect
- Insularization and area effects
- Isolation
- Edge effects
- Matrix effects
- The special problem of roads
  - Species invasions

Source: https://www.slideshare.net/sanbro/habitat-fragmentation-srm-130821796

Initial Exclusion

- Loss of endemic species due to fragmentation of specialized habitats

Crowding effect

- Fragmentation causes large populations to divide and relocate into smaller patches
- This leads to increase in density and causes crowding in small patches

Insularisation and area effect

- Decrease in species diversity occurs with decline in insular habitat i.e. islands can be a small area to sustain huge number of species, most animals have home ranges more than island area

Isolation

- Many species are specialized and need a mix of different habitats for their survival
- Thus fragmentation with construction of rail, road or other human barrier may lead to isolation of a particular habitat from natural resources thus threatening the survival of species living there

Edge effect

- Growth of unwanted species
- Outer boundary influenced by light and wind
- Shade intolerant species dominate in open edges between two habitats
- Extinction of inland species

Isolation

- Isolation leads to loss of genetic diversity
- Forces population to inbreeding depression
- Blocks migratory routes thus preventing genetic drift
- Re-colonization after a chaotic instability becomes impossible due to habitat fragmentation

Problem by roads

- Habitat fragmentation supplemented by road construction
- Effects of roads documented–
  - Mortality from road construction
  - Mortality from collision with vehicles
  - Modification of animal behaviour
  - Alteration of physical environment
  - Alteration of chemical environment
  - Spread of invasive species
  - Increase of edge effects
  - Barriers for animals

Source: https://www.slideshare.net/sanbro/habitat-fragmentation-srm-130821796

Species vulnerable to fragmentation

- Wide-ranging species
- Nonvagile species (with poor dispersal abilities)
- Species with specialized requirements
- Large-patch or interior species
- Species with low fecundity or recruitment
- Species vulnerable to human exploitation

Source: https://www.slideshare.net/sanbro/habitat-fragmentation-srm-130821796

Some species that have experienced genetic consequences due to habitat fragmentation are listed below:

- *Macquarie perch*
- *Macquaria australasica*
- *Fagus sylvatica*
- *Betula nana*
- *Rhinella ornata*
- *Ochotona princeps*
- *Uta stansburiana*
- *Plestiodon skiltonianus*
- *Sceloporus occidentalis*
- *Chamaea fasciata*

Metapopulation: Concept and dynamics

Reference: Ricklefs, R.E. and Miller, G.L. (2000) Ecology. 4th Edition, W.H. Freeman, New York

Simple implicit or classic model

The first simple model of metapopulation dynamics was presented by Levins (1969, 1970), and it serves as a basis for much of metapopulation theory (Hanski1991, 1997). In this model, the metapopulation is conceptualized as a group of local populations, each having a density of either 0 (extinct) or *K* (equilibrium density), where *K* is the patch carrying capacity. The carrying capacity of the patch is the number of individuals that can be supported by the resources in the patch for an indefinite period of time (the same concept of carrying capacity that was introduced in Chapter 16). The assumption that a patch has either no individuals or the carrying capacity is, of course, a simplification. At any time, some proportion, *p,* of the total number of patches in the metapopulation will be occupied, and the remaining fraction, 1 - *p,* will be unoccupied or extinct. The rate of change of *p* is given by

$$dp/dt = mp(l - p) - ep,$$

where *m* is the rate of patch colonization and *e* is the rate of patch extinction. When the rate of change of occupancy is 0, $dp/dt = 0$, and $p = 1 - e/m$, the equilibrium proportion of occupied populations (Levins 1969, 1970; Hanski 1991). The main prediction of this model is that species will not persist that is, $p < 0$- when extinction rate, *e,* is greater than colonization rate, *m,* in the metapopulation. Or, to put it another way, population persistence requires $e/m < 1$.

The Levins model has a number of simplifying assumptions

- The processes of population growth, resulting from the dynamics of birth and death, and of population regulation, resulting from the interaction of birth and death processes with the environment, in the local populations are not considered.
- All the patches are assumed to be equal in area and to be equally isolated from the other patches that is, the movement of individuals occurs with equal probability between any pair of patches.
- The populations within the patches are also assumed to be independent from other populations-that is, the population dynamics of one population are not affected by immigrants from another population. If populations are not independent, then extinction and colonization events may be correlated or synchronized. Such a situation becomes more likely as the rate of migration among patches increases.
- In the Levins model, it is only when immigrants enter an unoccupied patch (colonization) that their movement has an effect on the metapopulation dynamics.
- The extent to which individuals move from one patch to the next (immigration and emigration) is assumed to be neither extremely high nor extremely low. If movement

among local populations is extremely high, it is likely that extinction will be rare, in which case the metapopulation concept is not needed to explain population dynamics. Likewise, if movement among populations is extremely low, the populations are essentially unconnected, and thus represent individual, though possibly small, populations.

- Finally, the Levins model does not take into consideration variation in the ease with which individuals may move from one patch to the next. Such variation might arise as a result of landscape features For example, inhabitants of occupied habitat patch A, located equidistant from two unoccupied patches, B and C, may colonize B more quickly than C if there is a mountain between A and C.

Levins model is referred to as a patch metapopulation model/occupancy model because the local population dynamics are ignored; all that is considered is the proportion of occupied and unoccupied.

Comparison of Metapopulation and Logistic Population Models

Logistic Population Models	**Metapopulation**
depend upon the relationship between population density, *N*, and the carrying capacity, *K*	emphasize extinction-colonization dynamics rather than the dynamics of population density
highlights the population size and the factors controlling it	deals with its persistence time and how the migration and spatial heterogeneity will affect the persistence time
driving force in density dependent regulation and carrying capacity	Depends on migration: extinction ratio and can survive any kind of demographic or environmental stochasticity

Spatially Explicit Model:

The dynamics of meta-populations are affected not only by extinction and colonization rates, but also by the relationship of those rates to the spatial arrangement and density of the habitat patches (our reference to density here refers to the density of patches, not to the density of populations in patches).In order for a metapopulation to persist, the overall colonization rate must be greater than the extinction rate (1 <*elm*). But successful colonization requires that individuals move from an occupied site to one that is not occupied, and such movement may be prevented if there is a great distance between the occupied and unoccupied sites. The distance barrier may be overcome in .time if potential colonists arise continuously from an occupied site, thereby increasing the chance that one will make it to the distant unoccupied site.

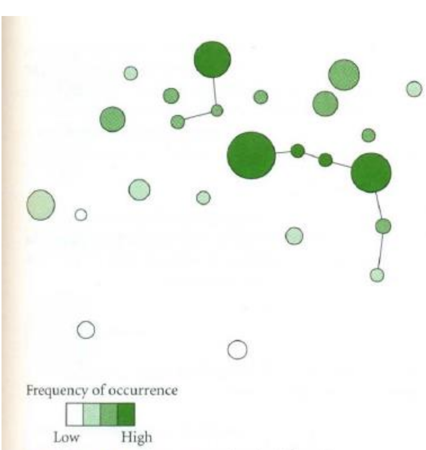


FIGURE 17-3 The pattern of probability of occupancy

But in order for this to happen, the colonizing population must persist, and in general, population persistence is related to population size. Small populations suffer a higher risk of extinction than do large populations.

Figure 17-3 depicts the relationship between the pattern of patch occupancy in a metapopulation and the spatial and size relationships among patches. The larger the patch, the more likely it is to be occupied. Small, isolated patches remain unoccupied because they are too isolated from occupied patches to be colonized. Patches of similar size that are located closer tooccupied patches are more likely to receive colonists.In general, where the patch density is high, the probability that a patch will be occupied is high, and that probability increases with patch size.

Mainland-island meta-populations are those in which a system of patches, or islands, is situated near another, larger, patch, the mainland, from which dispersers can reach all the islands. The assumption in these models is that the mainland population never goes extinct. Another type of metapopulation structure is the source-sink metapopulation, in which, some populations (sources) have a positive growth rate at low densities and other populations (sinks) have a negative growth rate in the absence of immigration.

Patch size and density (again, we are referring to the density of patches, not to the density of populationsin patches) may interact in a compensatory way to affect metapopulation persistence. This interaction can be shown with a modification of the basic metapopulation model, $dp/dt = mp(1 - p) - ep$ (Hanski1991). Suppose that the migration rate, *m*, is dependent on the degree to which a patch is isolated, measured as some distance, *D*. That is, migration to an unoccupied patch that is isolated from a colonizing patch (high D) is less likely than if the patch is in the proximity of a colonizing patch (low D). The exact relationship between *D* and *m* is not that important, so long as *m* declines as *D* increases. One possible relationship between the two is a negative exponential function, where

$$m = m_0 e^{-aD},$$

m_0 and *a* are parameters.

Now, let us suppose that the extinction rate, *e*, is dependent on the size of the patch, so that populations in larger patches have a lower chance of becoming extinct than do those in smaller patches. Thus extinction is related to patch area, A, in a negative exponential function as well, where

$$e = e_0 e^{-bA},$$

e_0 and *b* are parameters.

If we substitute these two equations into the equation for the equilibrium value of p, $p = 1 - e/m$, we obtain

$$\hat{p} = 1 - \frac{e_0 e^{-bA}}{m_0 e^{-aD}},$$

which may be simplified by factoring e_0 / m_0 from the right-hand term to obtain

$$\hat{p} = 1 - \left(\frac{e_0}{m_0}\right)e^{-bA+aD}.$$

If $a = b = 1$. Then, the term becomes $e^{-A+D.}$ If $A = l$ and $D =$ **1,** the term is $e^{-1+1} = e_0 = l$.

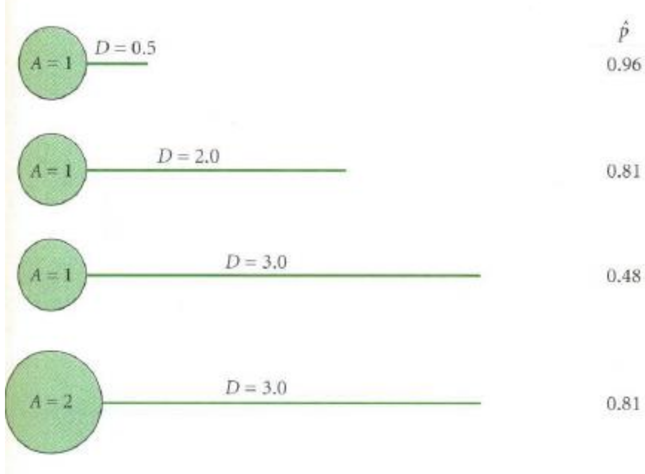


Figure 17-6 provides a schematic representation of what this means for meta population persistence. Inthis figure, $a = b = 1$, m_0= 0.7, and e_0= 0.05; thuse_0 / m_0= 0.071. If patch area A is 1 $(A = 1)$ and thepatch is isolated by a distance of $D = 1$ distance units,as in the first example, then p = **1** - $0.07e^{-l+l}$ =1 - 0.07 = 0.993. In that situation, the equilibrium patch occupancy is very high because of the proximity of patches to one another. If the isolation ofa patch of the same size $(A = 1)$ is twice that of the first example (D = 2), then $p = 1 - 0.07e^{-1+2}$ =1 - (0.07)(2.718) = 0.81, and the equilibrium occupancy declines. The decline is even greater $(p$ = 0.48) if D is increased to 3. However, if when $D = 3$, the size of the patch is increased to $A = 2$, then p is the same as for the situation in which $A = 1$ and D = 2(that is, p = 0.81). The greater patch area compensates for the greater isolation.

Thus explicit model focuses more on patch size and distance between the patches as also it encompasses the demography of each local population living in the patch. A population with low growth rate has a chance of extinction if it is closed without any migration especially immigration. Thus its ability to survive to any kind of demographic or environmental stochasticity is high, whereas in a meta-population if any of a small population gets extinct by any local effect it may get recolonized by migrants from other large patches which are closely placed to it. This will lead to the overall success of the metapopulation making it more **stable** than any small local population. This phenomenon of survival from extinction is known as **Rescue effect**.

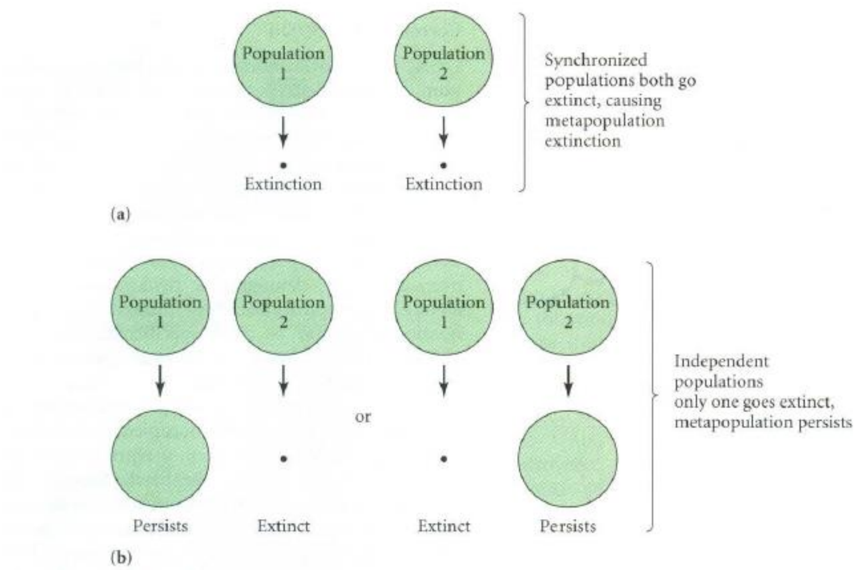


Figure 17- 12 depicts a simple metapopulation with just two patches, both occupied, in which the density of each local population is represented by thesize of the circle denoting the patch. Suppose that density is correlated with environmental conditions; that is, that density tracks environmental stochasticity. If the density of each local population responds to environmental variation in the same manner, then theywill both increase when conditions are good and decrease when conditions are poor. Further, let us assume that emigration is correlated with density, andthat greater emigration from either population increasesthe likelihood of movement from one patch tothe other. In such a situation, the metapopulation may be imperiled in times of low density because both populations will become too small to sustain movement between them (Figure 17- 12a). If the populationsbecome extinct as a result, this situation is referred to as **correlated extinction** (Harrison and Quinn 1989, Gilpin 1990).

Now, suppose that the two populations are more or less independent of each other - that is, that density is uncorrelated with environmental fluctuationandone population may increase while the other decreases (Figure 17-12b). If that were to happen, emigration from the population with the higher density might be sufficient to sustain the smaller populationvia the rescue effect, and the metapopulationas a whole might persist. To be sure, two independent populations might by chance simultaneously decline in density, creating a situation like the one shown inFigure 17 - 12a, in which the meta population becomes endangered. In general, however, when the demographicdynamics of populations are largely independent of one another, the metapopulation has a better chance of persisting (Harrison and Quinn 1989,Gilpin 1990).

Questions:

1. Define metapopulation?
2. Explain the classic metapopulation model. What are its drawbacks? Briefly state the new assumptions.
3. How can the explicit model explain the metapopulation dynamics better? What do you mean by source and sink concept?
4. Can mainland-island populations be considered as metapopulation? If yes, why?
5. What is rescue effect? Explain correlated extinction.
6. What are the four basic criterion of a metapopulation?
7. Explain spatially realistic model.
8. What is spatial heterogeneity? Differentiate local and stratified heterogeneity.
9. How habitat fragmentation differ from habitat loss?
10. What are the causes and effects of habitat fragmentation?
11. Point out the difference between local and metapopulation.
12. How logistic model is different form metapopulation model?
13. Define effective population size.
14. What is an idealized population?
15. What are the generalized attributes of an effective population size?

Meta-population: Definition, Models and theory

Spatial heterogeneity

- **Spatial heterogeneity** is a property generally ascribed to a landscape or to a population. It refers to the uneven distribution of various concentrations of each species within an area. A landscape with spatial heterogeneity has a mix of concentrations of multiple species of plants or animals (biological), or of terrain formations (geological), or environmental characteristics (e.g. rainfall, temperature, wind) filling its area. A population showing spatial heterogeneity is one where various concentrations of individuals of this species are unevenly distributed across an area; nearly synonymous with "patchily distributed.“
- Environments with a wide variety of habitats such as different topographies, soil types, and climates are able to accommodate a greater amount of species.
- Organisms can finely subdivide a landscape into unique suitable habitats, more species can coexist in a landscape without competition, a phenomenon termed "niche partitioning."

- Spatial heterogeneity could be either local or stratified
- **Spatial local heterogeneity**, referring to the phenomena that the value of an attribute at one site is different from its surrounding, such as hotspot or cold spot
- **Spatial stratified heterogeneity**, referring to the phenomena that the within strata variance is less than the between strata variance, such as ecological zones and land use classes. Spatial local heterogeneity can be tested by LISA, Gi and SatScan, while spatial stratified heterogeneity of an attribute can be measured by geographical detector *q*-statistic:

$$q = 1 - \frac{1}{N\sigma^2}\sum_{h=1}^{L} N_h \sigma_h^2$$

where a population is partitioned into $h = 1, ..., L$ strata; N stands for the size of the population, σ^2 stands for variance of the attribute. The value of q is within [0, 1], 0 indicates no spatial stratified heterogeneity, 1 indicates perfect spatial stratified heterogeneity. The value of q indicates the percent of the variance of an attribute explained by the stratification.

- We know about population growth models
- Exponential growth which is dependent on population size N and intrinsic rate of growth r, where

  r = b-d (b = birth rate and d = death rate), thus the equation

  dN/dt = rN
- Logistic growth came into existence as the previous growth model is not realisitic, as all populations are affected by environment
- Thus came the new model

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

- There are certain factors which are essential for population growth

- Factors affecting population size

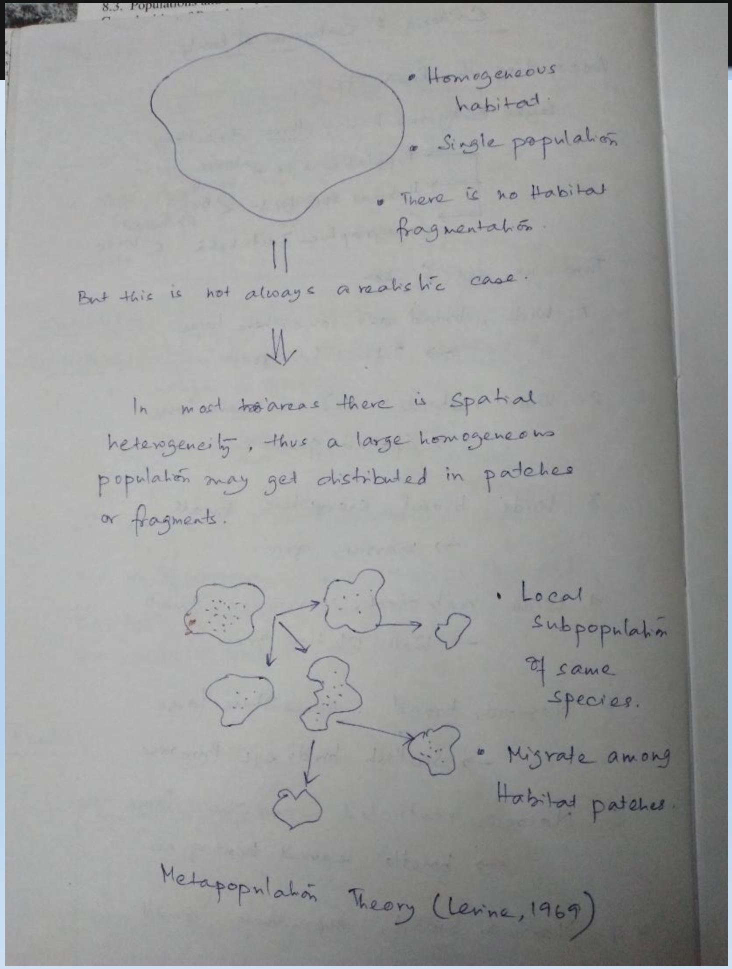
  Deterministic: directly affects size of a population

  stochastic: indirectly affects the same
- Mark Shaffer identified four uncertainties/stochasticities

  Genetic, demographic, environmental and natural catastrophes
- Demographic, environmental and natural events control the population size of large populations but genetic events like inbreeding, genetic drift mainly affect small population. Genetic stochasticity affects those populations that are small and are spatially separated.
- Therein came the concept of Metapopulation: population of populations

✓ A metapopulation is a group of same individual living in different places forming "patches" , but movement of individuals from one population to another occurs regularly.

- In metapopulations, local populations are found in "patches" of suitable habitat.
- These islands of suitable habitat are surrounded by intervening, unsuitable habitat called the matrix.
- Mortality risk is generally higher in the matrix, limiting movement between local populations.



Local Population:

- Closed population
- Group of same individuals living in same places at a same time
- Here the individuals are added only through birth and loses through death.
- Interact takes place within the a subpopulation

Metapopulation:

- Open population
- Group of same individual living in different places at a same time.
- Here the individuals are added through immigration and loses through emigration
- For interaction, migration from one local population to other patches is possible.

https://www.slideshare.net/TRIDIPBORUAH1/metapopulation

Four Conditions define a Metapopulation (Hanski)

1. Suitable habitat only found in discrete patches
2. All subpopulation have a risk of extinction
3. Patches close enough to be recolonized
4. Local populations growth dynamics not synchronized

Dynamics of Metapopulation

- It is governed by two sets of processes operating at two distinctive spatial scales.

  1. Local scale
  - Within patch
  - Individuals move
  - Population changes and regulation
  - Governed by demographic processes (birth and death)

  2. Regional scale
  - Interaction between patches
  - Governed by dispersion and colonization

https://www.slideshare.net/TRIDIPBORUAH1/metapopulation

Harrison (1991) types of spatially dynamic population

- Classical levins metapopulation
- Mainland island metapopulation
- Patchy population
- Non equilibrium population

https://www.slideshare.net/TRIDIPBORUAH1/metapopulation

The Classic Levins Metapopulation (1969)

- "A nexus of patches, each patch winking into life as a population colonizes it, and winking out again as extinction occurs." (Wilson 1980)
- Much higher levels of interaction between individuals within a patch than between patches
- All patches relatively small
- All patches have a nontrivial probability of local extinction.

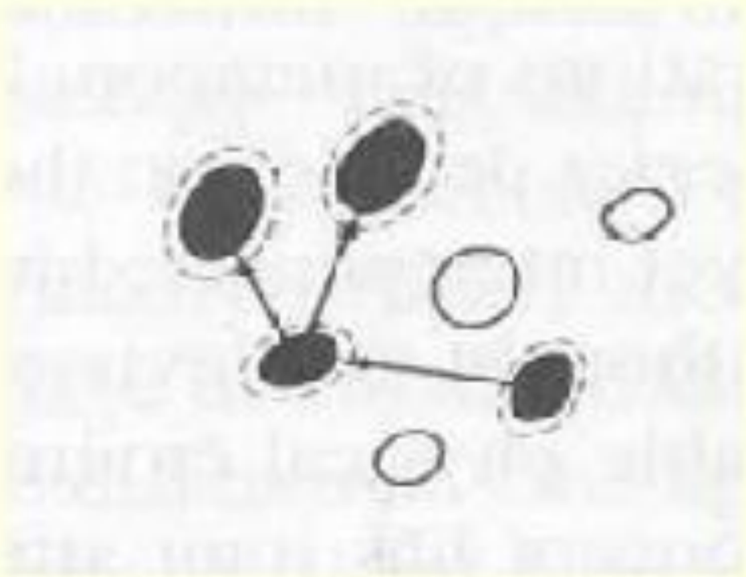


Fig. 1a. Harrison and Taylor 1997.

1970s when Levins (1970) offered the first intentional definition of a metapopulation as "any real population [that] is a population of local populations which are established by colonists, survive for a while, send out migrants, and eventually disappear" (Figure 8.7).

Also known as Spatially implicit model, but this model has certain limitations which will be discussed in upcoming slides

Levine's Model

- Population separated into spatially discrete units.
- Individual units suffer periodic extinction
- Recolonised by dispersers from neighbouring patch.
- Thus population size N determined by.
  - ⇒ Extinction rate
  - ⇒ migration rate.

Population size = N

Total number of units/sites = T

migration rate = m

∴ No. of populations newly established in vacant units through migration

$$mN\left(1 - \frac{N}{T}\right).$$

here $\left(1 - \frac{N}{T}\right)$ is probability that site reached is vacant.

Ex: Probability of migrants reaching another site is 50% i.e. m = 0.5 /year

N = 100 T = 200

∴ annual number of new population established

$$= 0.5 \times 100 \left(1 - \frac{100}{200}\right)$$

$$= 0.5 \times 100 \times 0.5 = 25$$

However some populations are eliminated by local extinction with a ~~rate~~ probability E and rate EN. ~~E popd~~

∴ population size

$$\frac{dN}{dt} = mN\left(1 - \frac{N}{T}\right) - EN$$

and.

Population will reach equilibrium. When.

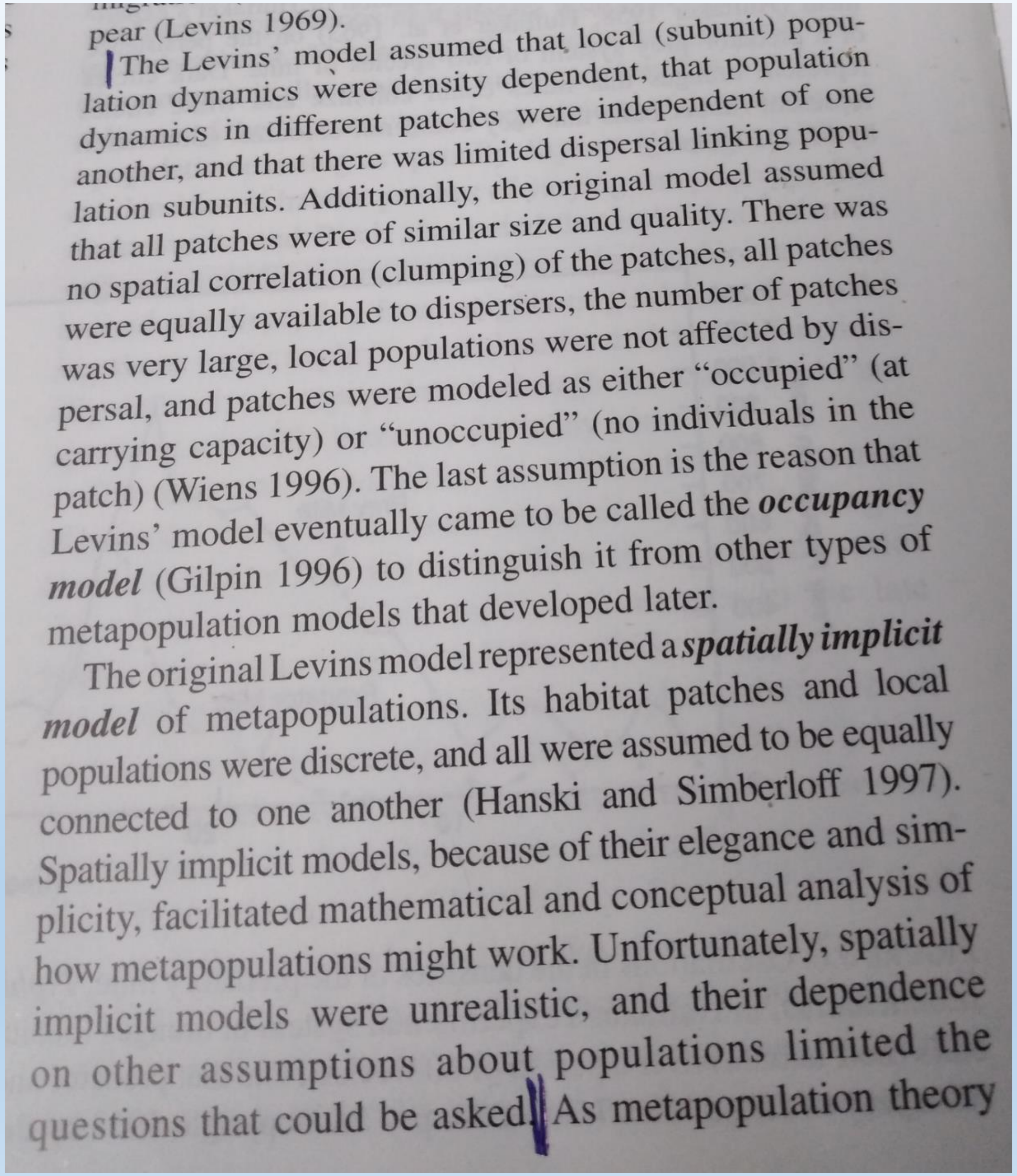
$$N_{eq} = T\left(1 - \frac{E}{m}\right).$$

Thus a metapopulation will persist over ti
only when.

⇒ $m > E$

⇒ N_{eq} will be established $E = m$.

Limitations and new assumptions


pear (Levins 1969).

The Levins' model assumed that local (subunit) population dynamics were density dependent, that population dynamics in different patches were independent of one another, and that there was limited dispersal linking population subunits. Additionally, the original model assumed that all patches were of similar size and quality. There was no spatial correlation (clumping) of the patches, all patches were equally available to dispersers, the number of patches was very large, local populations were not affected by dispersal, and patches were modeled as either "occupied" (at carrying capacity) or "unoccupied" (no individuals in the patch) (Wiens 1996). The last assumption is the reason that Levins' model eventually came to be called the ***occupancy model*** (Gilpin 1996) to distinguish it from other types of metapopulation models that developed later.

The original Levins model represented a ***spatially implicit model*** of metapopulations. Its habitat patches and local populations were discrete, and all were assumed to be equally connected to one another (Hanski and Simberloff 1997). Spatially implicit models, because of their elegance and simplicity, facilitated mathematical and conceptual analysis of how metapopulations might work. Unfortunately, spatially implicit models were unrealistic, and their dependence on other assumptions about populations limited the questions that could be asked. As metapopulation theory

Limitations

New assumptions

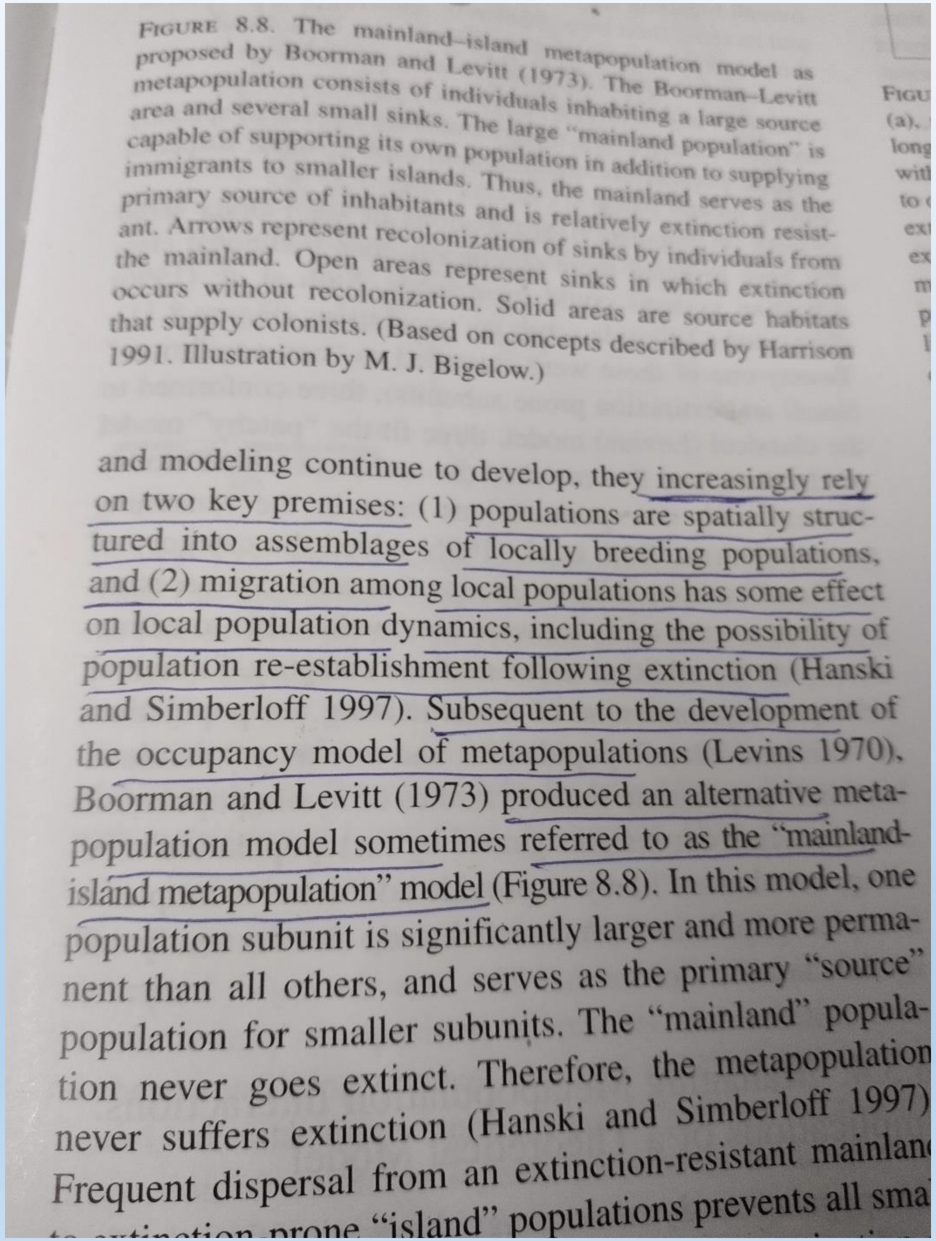


FIGURE 8.8. The mainland–island metapopulation model as proposed by Boorman and Levitt (1973). The Boorman–Levitt metapopulation consists of individuals inhabiting a large source area and several small sinks. The large "mainland population" is capable of supporting its own population in addition to supplying immigrants to smaller islands. Thus, the mainland serves as the primary source of inhabitants and is relatively extinction resistant. Arrows represent recolonization of sinks by individuals from the mainland. Open areas represent sinks in which extinction occurs without recolonization. Solid areas are source habitats that supply colonists. (Based on concepts described by Harrison 1991. Illustration by M. J. Bigelow.)

and modeling continue to develop, they increasingly rely on two key premises: (1) populations are spatially structured into assemblages of locally breeding populations, and (2) migration among local populations has some effect on local population dynamics, including the possibility of population re-establishment following extinction (Hanski and Simberloff 1997). Subsequent to the development of the occupancy model of metapopulations (Levins 1970), Boorman and Levitt (1973) produced an alternative metapopulation model sometimes referred to as the "mainland-island metapopulation" model (Figure 8.8). In this model, one population subunit is significantly larger and more permanent than all others, and serves as the primary "source" population for smaller subunits. The "mainland" population never goes extinct. Therefore, the metapopulation never suffers extinction (Hanski and Simberloff 1997). Frequent dispersal from an extinction-resistant mainlan to extinction-prone "island" populations prevents all sma

The Mainland-Island Metapopulation

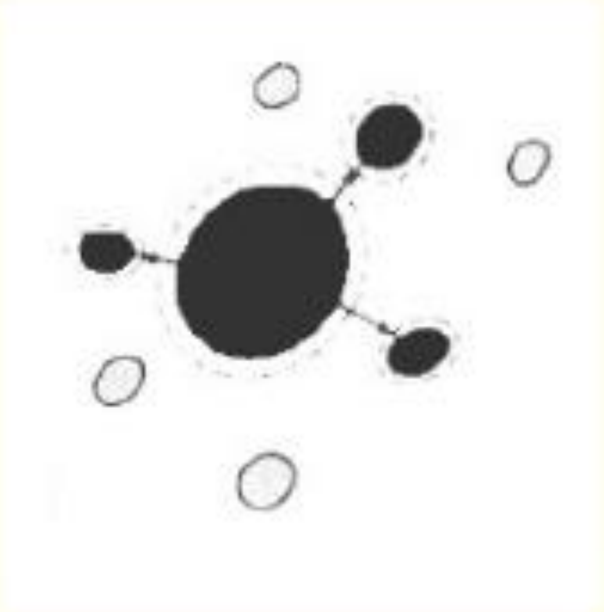


Fig. 1b. Harrison and Taylor 1997.

- Several small “island” patches are within dispersal distance of a much larger “mainland” patch.
- Though smaller patches have a high probability of local extinction, there is a highly improbable chance that the mainland population will ever become extinct.
- A steady migration of organisms out of the mainland to the islands, called propagule rain, is independent of the number of patches vacant or filled.
- Helps explain source-sink dynamics observed in some metapopulations

Sources and Sinks

- Source patches- At low density and without immigration, pop. growth rate is positive.
- Sink patches- At low density and without immigration, pop. growth rate is negative.
- Without emigrants leaving source patches, sink patches would decrease to extinction.
- “Rescue effect” allows for the persistence of local populations with negative growth rate.

Patchy Population

- Local populations exist in habitat patches, but dispersal between patches is high.
- Population structure is clumped, but interbreeding between patches is frequent
- The metapopulation concept is not very useful under this scenario, and most researchers do not consider this a metapopulation.

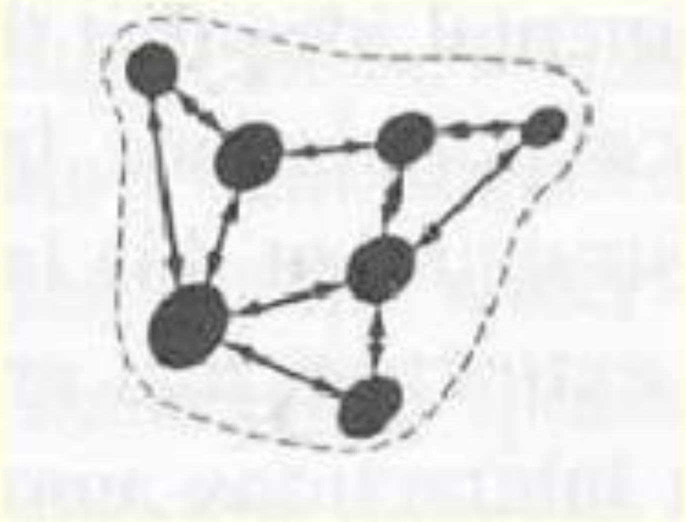


Fig. 1c. Harrison and Taylor 1997.

Non-Equilibrium Population

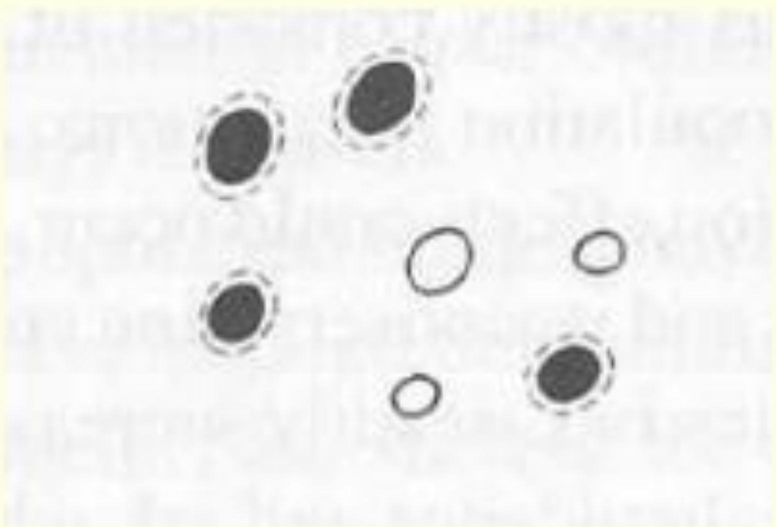


Fig. 1d. Harrison and Taylor 1997.

- Local populations are patchy, but local extinctions greatly exceed recolonization
- Vacant patches are rarely or never recolonized
- Not considered a functional metapopulation
- Frequently found in anthropogenic fragmented landscapes (e.g. formerly forested agricultural fields)

Spatially-Implicit Model

- Type of model used in Levins (1969)
- Simple assumptions, including all local populations are equally connected and have independent local dynamics
- Instead of focusing on distance between patches and population density of each patch, the model keeps track of the proportion of patches occupied at any one time.

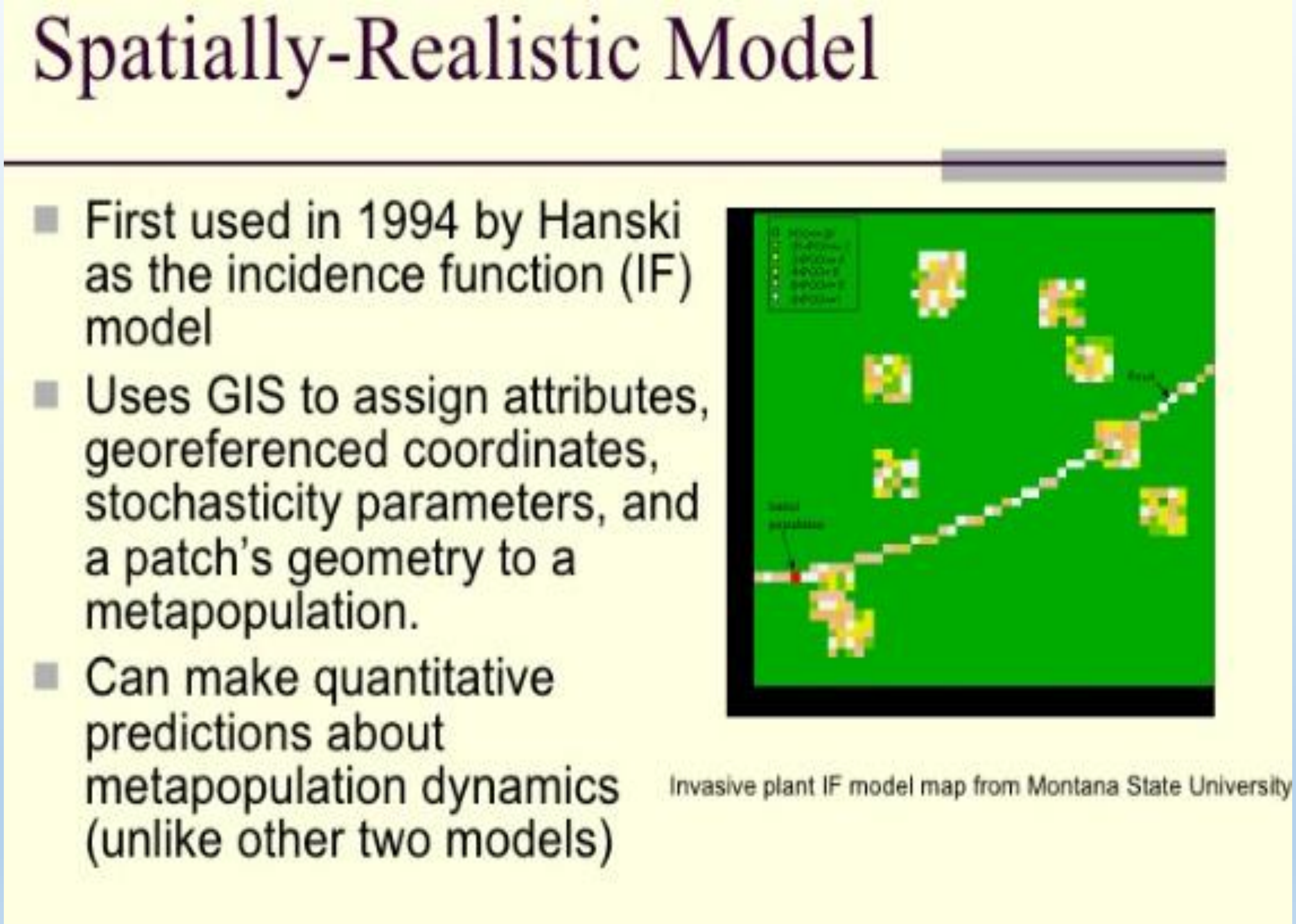
Already explained in previous slide with equation

Spatially-Explicit Model

- More complex than spatially-implicit models
- Can model density-dependent migration by organizing patches as cells on a grid
- Assumes that local populations are only interacting with nearest patch(es).
- Also only considers presence/absence of a species in each patch

Assumptions:

- Different degrees of connectedness between population subunits
- Localized interactions i.e. population migration occurs within neighboring units only, but not to distant units
- Size and availability of resource, distance between the patches are also considered



- Finalized in 1997 by Hanski and Simberloff
- Considered specific geometry of particular patches
- Especially size, shape and arrangement of patches

Outcomes of meta-population concept

- Conservationists proposed that planning and management for extant taxa must include preservation of Habitat fragments
- More effort to be given in small patches of subpopulations of a meta population than large contiguous habitat blocks
- Population persistence depend on the ability of the individuals to disperse/migrate successfully among habitats
- Vacant habitats must be recolonized on regular basis and unoccupied habitat could be as important as occupied habitats in long term population persistence
- A fragmented group of population subunit could actually enhance population structure and persistence
- Spatial structure of a population is its key concept of dynamics

1. Calculate the persistence of Metapopulation when

- Rate parameters a=b= 1, extinction in any local patch = 0.05 and migration to a new patch = 0.7
- Area of a patch = 1, Distance between patches = 1unit

2. Calculate the persistence of Metapopulation when

- Rate parameters a=b= 1, extinction in any local patch = 0.05 and migration to a new patch = 0.7
- Area of a patch = 2, Distance between patches = 3unit

3. Calculate the persistence of Metapopulation when

- Rate parameters a=b= 1, extinction in any local patch = 0.02 and migration to a new patch = 0.5
- Area of a patch = 1, Distance between patches = 3unit

Paper: Biological Rarity Phenomena (MSCCONBC202)

Module: 202.5

EFFECTIVE POPULATION SIZE

The effective population size is the size of an idealized population that has the same amount of genetic drift as the natural population under study. An idealized population is one in which the following attributes must be present:

a. number of reproducing males and females is the same (1:1 sex ratio)
b. random mating occurs among males and females (that is, every male has an equal probability of mating with every female)
c. the rate of emigration and immigration is constant
d. no age structure

Usually effective population size is smaller than the idealized population i.e. $Ne < N$, but in real system this is not the case always. Two important factors control the effective population size of any population:

- ✓ relative reproductive success of males and females within the population
- ✓ variance in that success

Thus, to determine N_e, separate effective population sizes for males and females is calculated as follows

$$N_{\text{males}} = \frac{N_m K_m - 1}{(K_m + V_m/K_m) - 1}$$

$$N_{\text{females}} = \frac{N_f K_f - 1}{(K_f + V_f/K_f) - 1},$$

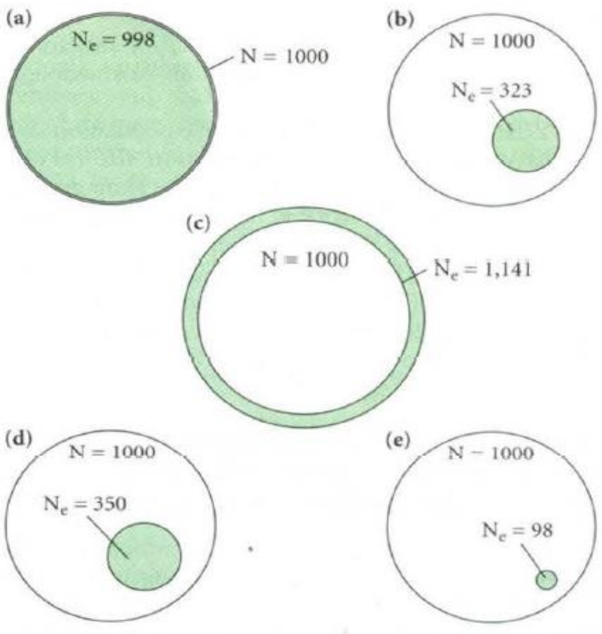
Where, N_m and N_f are the numbers of breeding males and females respectively, K_m and K_f are the average numbers of offspring produced by males and females in their lifetime, and V_m and V_f represent the variance in the number of offspring produced by each sex.

The separate values for males and females given in the equations above may be combined in the following way (here given without derivation) to calculate the overall effective population size (Lande and Barrowclough 1987):

$$N_e = 4\left[\frac{1}{N_{\text{males}}} + \frac{1}{N_{\text{females}}}\right]^{-1}.$$

One example of calculating effective population size and its diagrammatic explanation:

FIGURE 14-16 Calculations of effective population size, N_e, for five different hypothetical populations. $N = 1{,}000$ in each case. (a) The population contains an equal number of males and females, all individuals produce an average of one offspring during breeding, and the variance in the number of offspring produced is 1 ($N_m = N_f = 500$, $K_m = K_f = 1$, $V_m = V_f = 1$). In this case the effective population size is nearly equal to the total density of the population. (b) The same situation as depicted in a, except that the variance in the number of offspring produced is tripled ($N_m = N_f = 500$, $K_m = K_f = 1$, $V_m = V_f = 3$). This results in an effective population size about one-third the total density of the population. (c) The effective population size may be larger than the total density if all individuals breed and the average reproductive output of one of the sexes is high ($N_m = N_f = 500$, $K_m = 3$, $K_f = 1$, $V_m = V_f = 1$). (d) When only a portion of the population of one sex breeds and produces a small mean number of offspring, $N_e < N$ ($N_m = 100$, $N_f = 500$, $K_m = K_f = 1$, $V_m = V_f = 1$). (e) When a very small proportion of the population breeds and produces a small mean number of offspring, $N_e \ll N$ ($N_m = 50$, $N_f = 50$, $K_m = K_f = 1$, $V_m = V_f = 1$).



Source:

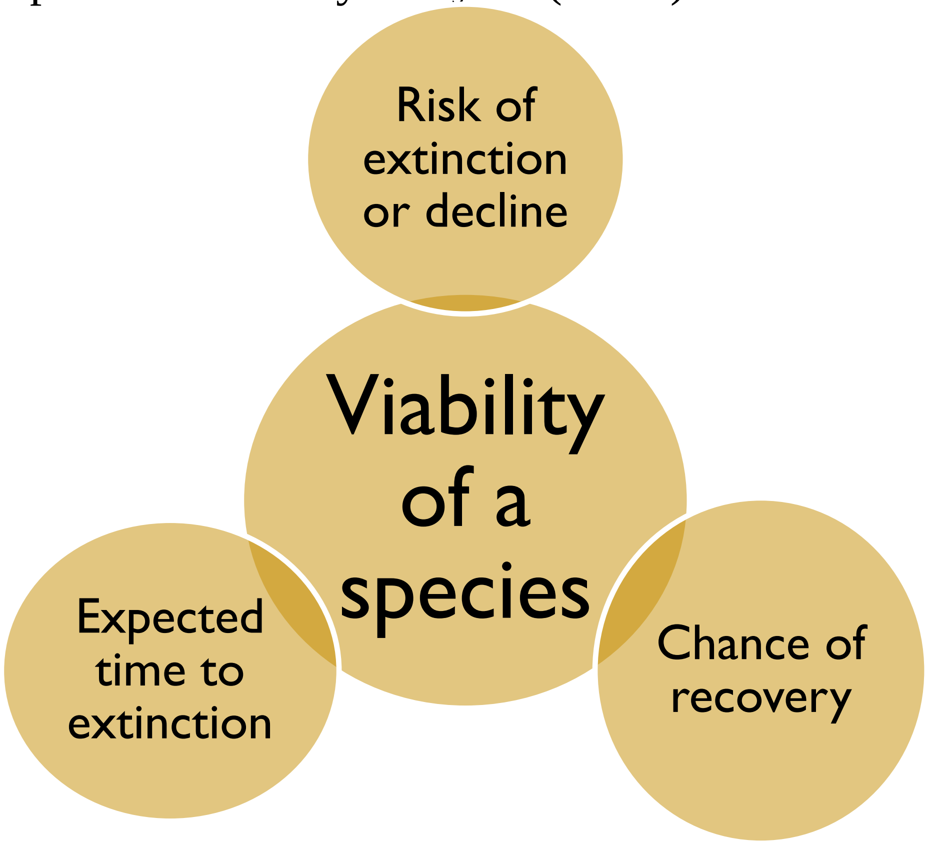
Ricklefs, R.E. and Miller, G.L. (2000) Ecology. 4th Edition, W.H. Freeman, New York

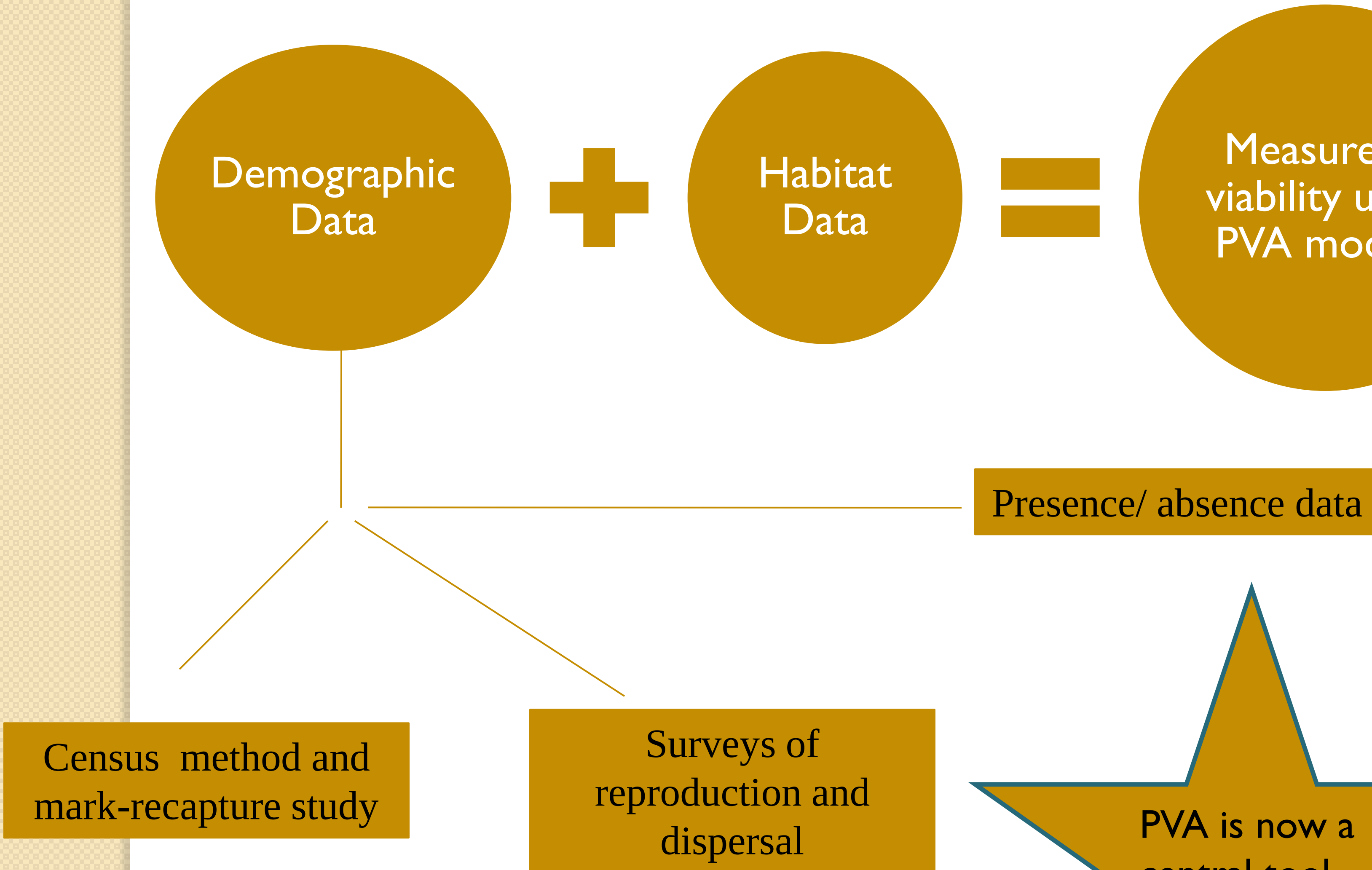
Population Viability Analysis

- Population viability analysis (PVA) is a collection of methods for evaluating the threats faced by populations of species, their risks of extinction or decline, and their chances for recovery, based on species-specific data and models.
- Compared to other alternatives for making conservation decisions, PVA provides a rigorous methodology that can use different types of data, a way to incorporate uncertainties and natural variability, and products or predictions that are relevant to conservation goals.
- The disadvantages of PVA include its single-species focus and requirements for data that may not be available for many species.
- PVAs are most useful when they address a specific question involving a focal (e.g., threatened, indicator, sensitive, or umbrella) species, when their level of detail is consistent with the available data, and when they focus on relative (i.e., comparative) rather than absolute results, and risks of decline rather than extinction

BACKGROUND

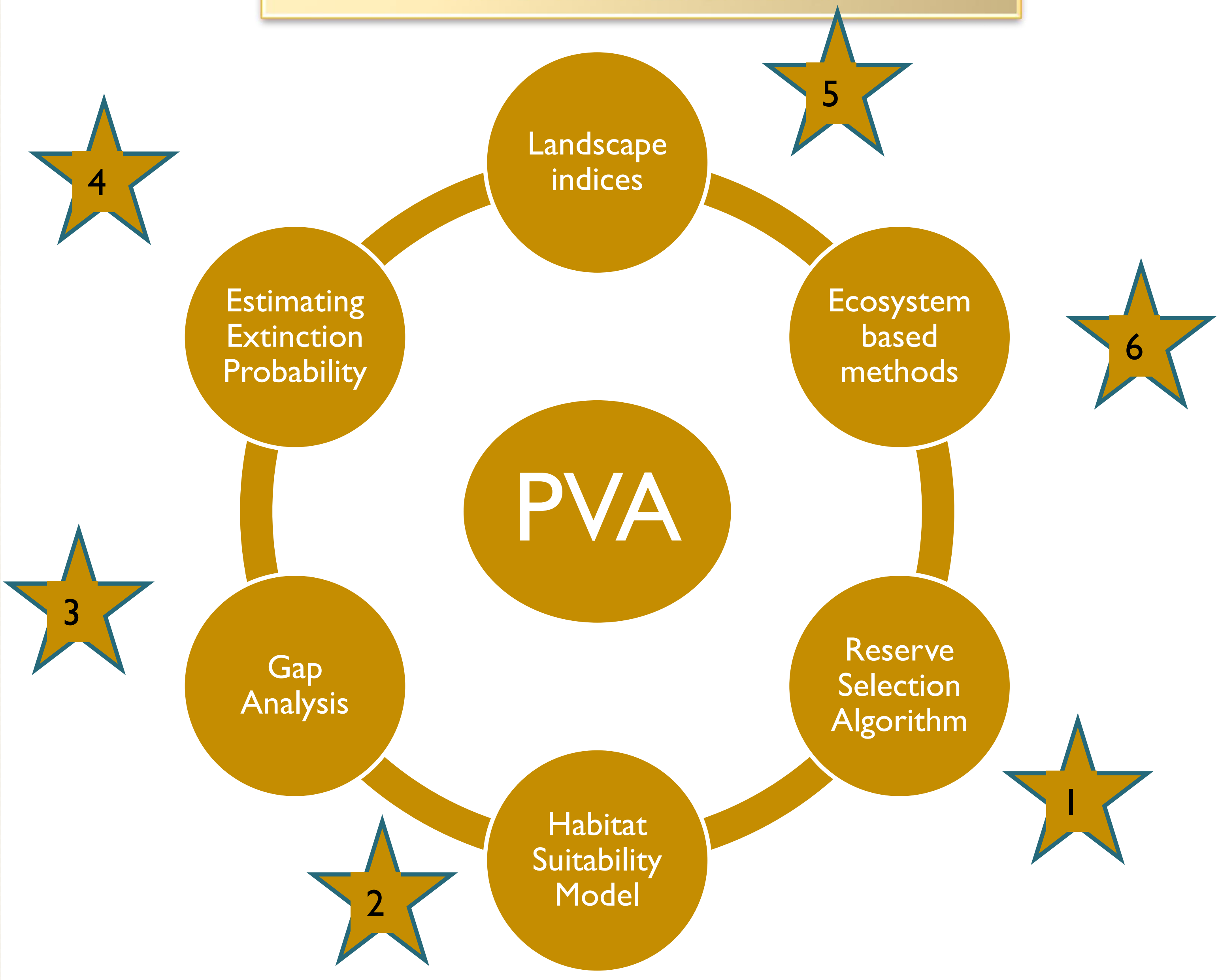
Practical problems in conservation planning and wildlife management are increasingly phrased in terms of questions about the viability of threatened or indicator species. Because of the nature of these questions, and the natural variation and uncertainty present in ecological data, risk-based methods are appropriate for population viability analyses (PVAs).





1. Need of threatened species
2. Use of indicator species
3. Potential for rigorous risk assessment using various data

METHODS



PVA
Landscape indices
Ecosystem based methods
Reserve Selection Algorithm
Habitat Suitability Model
Gap Analysis
Estimating Extinction Probability
1
2
3
4
5
6

These methods are designed to select nature reserves, i.e., choose a subset of available habitat patches for protection often using criteria that maximize the number of species included in the reserves.

The algorithms are usually based on the presence/absence of species in each habitat patch, and do not explicitly consider the viability of species in habitat patches, or the interaction among populations in different habitat patches (e.g., metapopulation dynamics).

The presence of a species in a particular patch does not necessarily indicate that the patch can support a viable population, or that the population will persist even if the neighboring habitat patches are not included in the reserve system.

Nevertheless, these methods are useful if the only available data are occurrences.

2

The aim of habitat suitability (HS) models is to predict a species' response to its environment. The response is usually the occurrence or abundance of the species at a certain locality or the carrying capacity of the habitat. The statistical procedures to obtain the HS model (such as multiple logistic regression) use species occurrence or abundance at each location as the dependent variable and the habitat characteristics as the set of predictive variables

One advantage of habitat suitability models is that they are statistically rigorous and can be validated. They can also be used to explore effects of environmental changes on habitat patch suitability, and to calculate probabilities of species occurrence

Another advantage is that they can use all the available habitat data (including point observations, GIS data of various types, satellite images, digital elevation maps, etc.), and incorporate nonlinearities of, and interactions among habitat variables

The main disadvantage of habitat suitability models is that suitability is only one component of viability, which also depends on demographic factors. However, habitat suitability models can be integrated with PVA models to identify habitat patches and characterize the spatial structure of meta-populations

3

A “gap” is the lack of representation or inadequate representation of a plant community or animal species in areas managed primarily for natural values.

Identification of a gap indicates potential risk of extinction or extirpation unless changes are made by land stewards in the management status of the element. Gap Analysis Program (GAP) is a process widely used by state agencies in the USA to identify such gaps. The process involves overlaying (intersecting) land cover and species distribution (element occurrence) coverage with the coverage of areas protected or managed primarily for natural values

The advantages of gap analysis are its widespread use, and its use of all available geographic information.

The major disadvantage of gap analysis is that it is not based on population dynamics, and does not utilize available demographic information. Hence, it does not provide a direct measure of viability

Another disadvantage is that it often relies on species-habitat associations and species distribution patterns that are not rigorously determined

These methods also try to estimate probabilities of extinction, but they work from a record of sightings, rather than the more detailed demographic information that PVA uses (Solow 1993)

The quantity estimated with these methods is the probability that the species is already extinct, rather than the probability that it will become extinct by a given future date.

5

These include metrics such as patch size distribution, fractal dimension, shape index, and other descriptions of spatial structure, which are calculated from digital raster maps of habitat types in the landscape. Although many of these indices may be informative in particular situations, there are three major problems with their general application to conservation issues.

First, the objects that form the structure (e.g., patches of forest habitat) are often arbitrarily defined.

Second, the spatial scale is often arbitrarily selected. Both the definition of "patch" and the selection of spatial scale require a specific phenomenon or focal species.

Third, and most important, the relationship between these metrics and conservation goals may be weak or very restricted

These methods deal with more than target or focal species.

The assessments are based on various methods, including point scoring sheets, expert opinion, rating systems, etc. Others focus on “emergent” properties such as nutrient cycling or various measures of species diversity

The clear advantage and appeal of the ecosystem approach is its comprehensiveness. The ultimate goal of most conservation efforts is the preservation of well-functioning, representative, natural ecosystems

The main disadvantage of the ecosystem approach is the complexity of interactions among species and our lack of understanding of community and ecosystem dynamics

TABLE 2.2 A classification of PVA methods reviewed in this handbook

Number of populations or EOs included in the analysis:	Type of data collected:	Minimum number of years of data per population or EO:	PVA method:	Where to look in this handbook:
One	Counts	10 (preferably more)	Count-based extinction analysis	Chapter 3
One	Demographic information	2 or more	Projection matrix models	Chapter 4
More Than One	Counts	10 (preferably more) for at least one of the populations	Multi-site extinction analysis	Chapter 5

After Morris et al., 1999

AIMS/OBJECTIVES OF PVA

Population viability analysis is often oriented towards the management of rare and threatened species, with two broad objectives.

The short-term objective is to minimize the risk of extinction.

The longer-term objective is to promote conditions in which species retain their potential for evolutionary change without intensive management

MANAGEMENT ORIENTED OBJECTIVES

Planning Research and data collection : PVA may reveal that population viability is insensitive to particular parameters. Targeting factors having important effect on extinction or recovery is main objective of research

Assessing vulnerability: Estimates the relative vulnerability of populations to extinction. Together with cultural priorities, economic imperatives and taxonomic uniqueness results lead to policy making

Impact Assessment: Assess the impact of human activities with or without the population level consequences of human activities

Ranking management options: Predicts the likely response of species to reintroduction, captive breeding, weed control, habitat rehabilitation or different designs for nature reserves or corridor networks

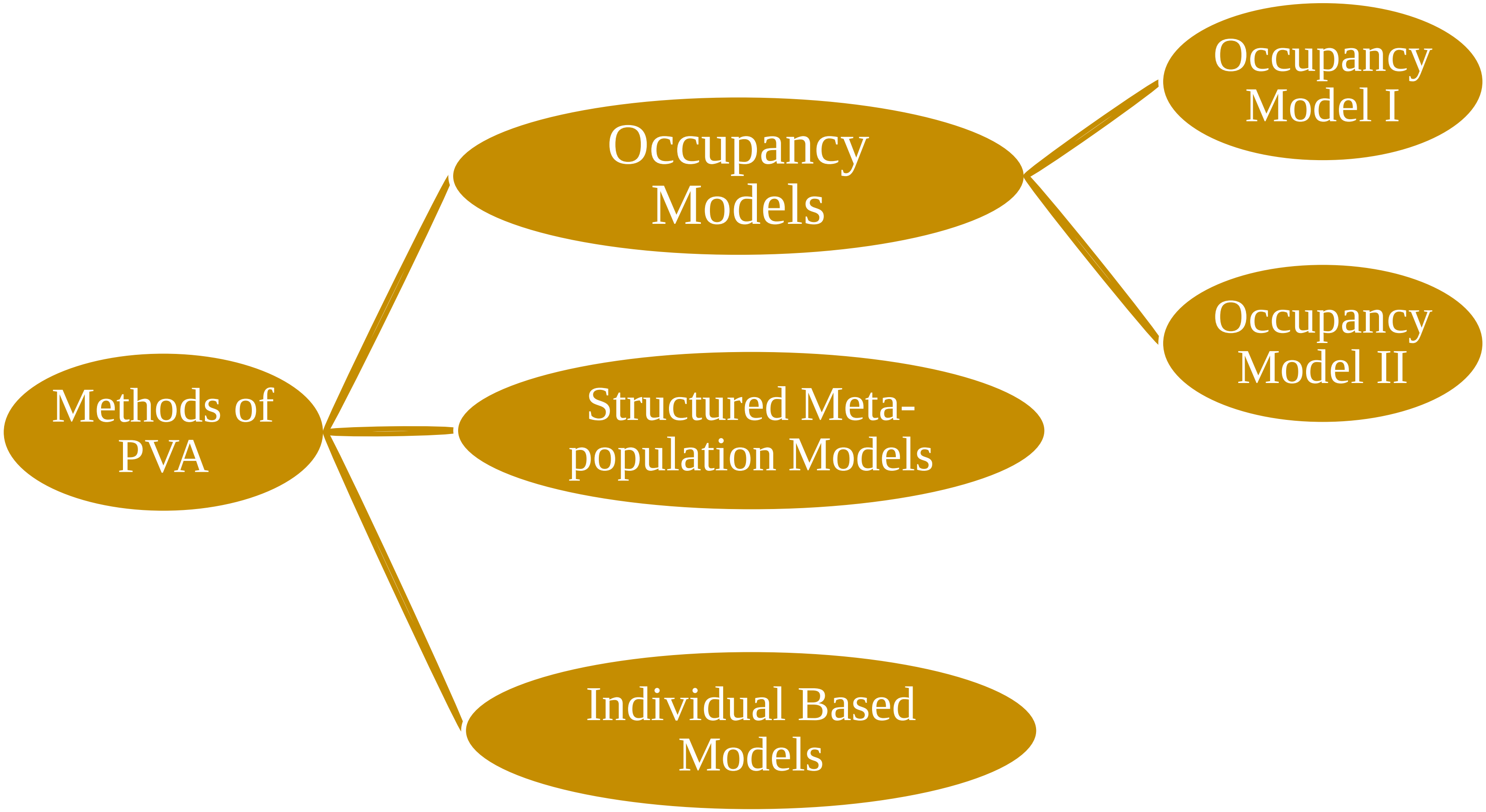
PVA is also an excellent tool for organizing the relevant information and assumptions about a species or a population which include:

- Extinction risk
- Time to decline
- Chance for recovery
- Persistence time
- Local and regional occupancy rate

Which measure to be used depends on the question

Most outputs from demographic PVAs are based on three variables

- The amount of decline (e.g., 100% or total extinction or partial decline)
- The probability of decline
- The time frame in which the decline is expected to take place


Methods of PVA
Occupancy Models
Structured Meta-population Models
Individual Based Models
Occupancy Model I
Occupancy Model II

Occupancy Models

The simplest metapopulation approach models the occupancy status of habitat patches in a geographic region (i.e., the presence or absence of the species in these patches).

This approach dates back to a model that was originally developed by Levins (1969) and that has been modified and expanded by several authors. Occupancy models are parameterized using data on the presence or absence of a species in habitat patches from one or more regional inventories. They may be advantageous to demographic models when demographic data are difficult to obtain. However, the management question and the ecology of the species, and not just data availability, should dictate the model used

Occupancy models require that the species has local populations confined to a clearly delimited habitat in a landscape. They ignore local population dynamics, and do not model fluctuations in size or composition of the local populations

Two general types of occupancy models, were proposed by Sjögren-Gulve and Hanski (2000)

Occupancy Model I

Incidence function models (Hanski 1994, 1999) require data on the areas and geographic locations of suitable habitat patches and the presence/absence of the species in these patches from at least one complete inventory. A habitat-suitability analysis of the species presence/absence pattern may be required for reliable habitat patch identification and delimitation. Based on these data, colonization and extinction probabilities are estimated for each patch using regression. These estimated probabilities are then used in simulations to predict metapopulation persistence and patch occupancy

Occupancy Model II

State transition models are conceptually related to the incidence function models discussed above. They require presence/absence data, but from two or more yearly inventories. Instead of relying on patch occupancy patterns, these models use patterns of patch state transitions. They predict state transitions (vacant to occupied as a result of colonization; and occupied to extinct, as a result of local extinction) from correlated environmental variables. Similar to habitat-suitability models, the patch transitions are modeled using predictive environmental variables discerned by multiple logistic regression

Structured Meta-population Models

Structured population models consider factors that may be important for the persistence of local populations by modeling the dynamics of each population occupying a habitat patch. As in the occupancy models discussed above, they also incorporate the spatial structure of the habitat patches (Burgman et al. 1993). In addition, they incorporate internal dynamics of each population (e.g., variation in age structure, immigration, emigration, density dependence, and environmental fluctuations), which often are important determinants of metapopulation persistence

- The main advantage of structured population models compared to occupancy models is their flexibility. In the local population dynamics, they can incorporate several biological factors and can represent spatial structure in various ways. Since they model demographic processes, the populations are the focal object rather than the habitat patches. Consequently, the species-habitat association need not be as strong as in occupancy models
- Another advantage is that, despite their realism, structured models are based on a number of common techniques or frameworks that allow their implementation as generic programs
- A third advantage is that structured demographic modeling allows careful risk assessment for species with very few local populations (occupancy models require a larger number), and under circumstances in which no extinctions have occurred and habitat patches are not easily identified

- The main disadvantage of structured models is that they require more data than occupancy models, including stage-specific survival and fecundity rates, and the temporal and spatial variation in these rates
- Another difficulty lies in the estimation of local vital rates for populations that may, in the future, colonize currently vacant patches

Individual Based Models

There are various types of individual-based models. In a commonly used approach, the behavior and fate of each individual is modeled in a simulation (DeAngelis and Gross 1992). The behavior and fate (e.g., dispersal, survival, reproduction) of individuals depend on their location, age, size, sex, physiological stage, social status and other characteristics.

The advantage of individual-based models is that they are even more flexible than structured models, and can incorporate such factors as genetics, social structure, and mating systems more easily than other types of models.

- One disadvantage of individual-based models is that they are very data-intensive. Only a few species have been studied well enough to use all the power of individual-based modeling.
- Another disadvantage is that the structure (as well as the parameters) of the models depend on the ecology and behavior of the particular species modeled. Thus, unlike structured models with a common framework, each individual-based model must be designed and implemented separately, making this approach impractical for most species

DATA NEEDS AND MODEL CHOICE

The types of data that can be used in a PVA include distributions of suitable habitat, local populations or individuals, patterns of occupancy and extinction in habitat patches, abundances, vital rates (fecundity and survival), as well as temporal variation and spatial covariation in these parameters

Aspects that should be considered in determining the appropriate model:

- ✓ Model structure should be detailed enough to use all the relevant data
- ✓ Model results should address the question at hand (e.g., if the question concerns risk of a 50% decline, the model should report such a result).
- ✓ The model should have a parameter related to the question (e.g., if the question involves the effect of timber harvest, the model should include parameters that reflect such an effect realistically).
- ✓ Model assumptions should be realistic with respect to the ecology of the species and the observed spatial structure (e.g., if there is population subdivision, a metapopulation model should be considered).
- ✓ For occupancy modeling, the species must occur as geographically distinct local populations in a landscape or region, and species occurrence or turnover patterns (extinction/colonization) need to correlate significantly with measurable habitat variables

Guidelines for selecting a model

i. Demographic data for building a structured or individual-based model already exist

ii. There are reasons to believe that demographic, behavioral or genetic processes are important for local extinction, or the ecology of the species indicates that internal population dynamics are important

iii. The species occurs in a small number of populations

iv. Suitable but unoccupied habitat patches cannot be easily identified

v. Species occurrence or turnover (extinction/colonization) patterns do not correlate significantly with measurable habitat characteristics (or such data are harder to collect than demographic data)

vi. The management question addressed involves a factor related to within-population dynamics (e.g., questions about impacts on different age classes or questions regarding management and conservation actions that affect different life history stages differently)

vii. The required answer is in terms of abundance rather than occupancy (e.g., risk of a population decline, or expected time until the population falls below a given threshold abundance)

ADVANTAGES

Relevance to conservation of biodiversity: PVA has direct relevance to biodiversity conservation. An increasing number of species are presently threatened or endangered, and PVA results directly relate to the mandates of such laws as the Endangered Species Act. In addition, PVA can be applied to validated focal or umbrella species (Fleishman et al. 2000) to guide conservation efforts for entire nested species groups. Thus, PVAs of selected threatened species and sets of indicative species will be central for efficient conservation planning at local or regional levels, and for measures taken to comply with international treaties such as the UN Convention Biological Diversity

Rigor: Unlike some of the other methods, PVA is rigorous and quantitative. Its results can be replicated by different researchers. The assumptions of a PVA can be (and should be) explicitly stated and enumerated; they can also be validated given sufficient data. Validation of stochastic results (such as risk of decline or extinction) requires data for several independent populations, as well as observed trajectories or extinctions for comparison. t PVA is a valid and sufficiently accurate tool for categorizing and managing endangered species.

ADVANTAGES

Ability to use all available data and multiple data types: A PVA can use various types of data sets, including presence-absence data, habitat relationships, GIS data on landscape characteristics, mark-recapture data, surveys and censuses. Thus, it is possible to incorporate all available data into the assessment. Such an assessment is more reliable than one that ignores part of the available information

Incorporating uncertainty: Uncertainty is a prevalent feature of ecological data that is ignored by most methods of assessment. If data for a PVA are unavailable or uncertain, ranges (lower and upper bounds, instead of point estimates) of parameters are used. In addition, uncertainties in structure of the model can be incorporated by building multiple models (e.g., with different types of density dependence). There are various methods of propagating such uncertainties in calculations and simulations. The uncertainties can also be used in a sensitivity analysis. Results of sensitivity analyses are used to identify important parameters and help guide future fieldwork

ADVANTAGES

Conservation planning with multiple objectives: Conservation and landscape management decisions often involve multiple objectives such as ecological and economic goals. Population viability analyses do not explicitly incorporate economic factors, because it is often counterproductive (and usually impossible) to assign monetary value to the viability or persistence of a species. However, because of the quantitative nature of PVA results, it is possible to jointly consider ecological and economic objectives, for risk-based (and risk-weighted) decision-making. This can be done by keeping ecological and economical values separate, and presenting the results of the analysis in two dimensions, instead of only one (Fig. 2). Thus, the resulting graph has an x-axis in monetary units (e.g., the cost of implementing a certain management or conservation option), and a y-axis in biological units (e.g., reduction in the risk of extinction of the species).

LIMITATIONS

Single species focus: The focus of a PVA is generally a population or multiple populations of a single species. Its focus on single species is a limitation in cases where the goal is the management and conservation of an ecosystem. In other cases, the single species focus is the strength of PVA: the dynamics of single species are much simpler

Data needs: PVAs may need more data than some of the other methods. However, incomplete information does not necessarily preclude meaningful results. First, PVAs can incorporate uncertainties in the data, and in some cases, these uncertainties do not effect the overall conclusion . Second, uncertainties in the data may not affect results when the goal of PVA is comparative, as in ranking management options. Third, there is very significant value in building a model for its own sake. It clarifies assumptions, integrates knowledge from all available sources, and forces us to be explicit and rigorous in our reasoning. It allows us to identify, through sensitivity analyses, which model structures and parameters matter, and which do not

LIMITATIONS

Risk criteria: Some uses of PVA involve determining whether the risk faced by a particular species is acceptable. Such questions require a benchmark for "an acceptable level of risk" for the extinction of species. There are some benchmarks used but none is accepted universally

Identifying causes of decline: Caughley (1994) contrasted two paradigms in conservation biology: "small population" and "declining population". Under the "small population paradigm", factors threatening species with extinction include stochasticity, catastrophes and genetic degradation; under the "declining population paradigm," they include overkill, habitat loss and fragmentation. In this scheme, PVA and modeling are included under the "small population paradigm". This separation is now seen as artificial because PVAs can and do incorporate systemic pressure (i.e., deterministic decline) and overkill (or overharvest)

WHEN PVA IS MOST USEFUL

- A specific question involving focal/target species is addressed
- A case with sufficient data is focused
- All available and relevant data is used including spatial (GIS) data, presence-absence data, habitat relationships, and demographic data from mark-recapture studies, surveys and census
- Model choice should be based on the availability of data, the question addressed and the ecology of the species
- An assessment should explicitly list all the assumptions (even the most obvious ones) related to model structure, parameters and uncertainties
- Model accuracy can be validated by using data from one half of the study system and making predictions for the other half that are compared to observed values
- All parameters should be specified as ranges that reflect uncertainties
- Sensitivity of results to assumptions and parameters must be analyzed
- Results are more reliable and relevant if they are expressed in probabilistic terms (risk of decline) rather than deterministic terms
- For analysis of risk of extinction and risk of decline to an unacceptably small population size relative risks is used instead of absolute risk

References:

A) Akçakaya H.R. and P. Sjögren-Gulve. 2000. Population viability analysis in conservation planning: an overview. Ecological Bulletins 48:9-21

B) MorrisW, Daniel D, Martha G , Kareiva P, Fieberg J, Gerber L, Murphy P. and Thomson D. 1999. A Practical Handbook for Population Viability Analysis. The Nature Conservancy

C) Boyce M. 1992. Population Viability Analysis. Annu. Rev. Ecol. Syst. 1992.23:481-506