Integrated approach to PVA: Plan

• Demographic Stochasticity
  – Extinction: fragmentation & patch size effects
  – Connectivity & dispersal
• Island biogeography -> Metapopulation
  – Levins: colonisation versus local extinction
    • Example: iberian wolf in Portugal
  – From Levins to Hanski metapopulation
    • Variance in patch-size & dispersal, rescue effect
  – Spotted owl PVA
• PVA in a nutshell
• Example: Blue Crane
• Example: Iberian Lynx & quasistationary distribution
• TD: Doñana Iberian Lynx metapopulation management
Island biogeography theory

• Developed originally in 1963 by MacArthur & Wilson
• Influenced understanding of spatial influences on organisms
• For a while, it was the principle design paradigm for conservation reserves
• “The number of species on an island will reach an equilibrium that is positively related to island size & negatively related to distance from mainland”
• Hence, large islands have more species
• Islands distant from the mainland have fewer species (far from the source of new colonists)
Island biogeography

- Originally applied to islands, but works for any population in a fragmented landscape.
- In this case, a fragment is the “island”, & the mainland is the nearest large contiguous source.
- Species richness in the island is related to immigration rate to the island & extinction rate on the island.
- Immigration rate is a linear function of distance from mainland & is related to size of mainland population.
- Extinction rate is dependent on available resources on island. Should be proportional to island size if all islands are similar.
Colonisation & extinction
Figure 25.14  Occurrence of 10 species of mammals on islands in the Thousand Islands region of the St. Lawrence River in New York as a function of island size and isolation. Many species occur only on islands above a certain critical size (horizontal lines). Other species, such as the deer mouse, are affected by both island size and distance from the mainland.

Source: Data from M.F. Lamont, "Mammalian Community Structure in Islands" in Biological Journal of the Linnean Society, 28:1-21, 1986.
Figure 25.15  Island biogeography applied to mountaintops.  
(A) Map of the Great Basin region of the western United States showing the isolated mountain ranges between the Rocky Mountains on the east and the Sierra Nevada on the west.  (B) Species-area relationship for the boreal mammal species. Numbers refer to sample areas on the map.  
Table 2. Mammalian species richness in four Paraguayan national parks and in the area near each park (potential species). Percent present was calculated by dividing the species recorded by the total potential species. The final column refers to the number of species found in only one park.

<table>
<thead>
<tr>
<th>Species</th>
<th>Potential</th>
<th>Percent</th>
<th>Unique</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ybucú'i</td>
<td>59</td>
<td>90</td>
<td>65.6</td>
</tr>
<tr>
<td>Cerro Cora</td>
<td>46</td>
<td>66</td>
<td>69.7</td>
</tr>
<tr>
<td>Defensores del Chaco</td>
<td>67</td>
<td>71</td>
<td>94.4</td>
</tr>
<tr>
<td>Teniente Enciso</td>
<td>54</td>
<td>62</td>
<td>87.1</td>
</tr>
</tbody>
</table>

Fig. 2. The logarithmic relationship between the percent of available mammalian species protected in parks and park area.

Fragmented Forest in Kenya
Why did metapopulations begin to interest ecologists in the 1980s?

Some habitats are naturally patchy. Some have become fragmented.
Forest fragmentation in Finland over 200 years
• Suitable habitat for many species is naturally patchy.

• Suitable habitat for other species is relatively more continuous but has been fragmented by human land uses.

**Habitat alteration:**

1. Habitat loss

2. Habitat fragmentation

• Reduced patch size
• Increased isolation of patches
• Increased amount of edge
Metapopulations

• A metapopulation is made up of a group of subpopulations living on patches of habitat connected by an exchange of individuals.
Classic metapopulation assumptions

- Every subpopulation has an equal chance of extinction
- Every subpopulation has an equal chance of being colonized (all dispersal connections are equivalent)
- And the model result: Metapopulations will persist as long as colonization probability > extinction probability
Classic metapopulation

- Subpopulations have independent dynamics and are connected by dispersal
Metapopulation Concept

- Assemblage of local populations that interact via dispersal of individuals among patches
  - We no longer assume populations are closed. A set of local populations (subpopulations) are open and dispersal among these is critical to persistence of metapopulation.
- Metapopulation persists despite local extinctions due to recolonization
  - Emphasizes dynamics of local extinctions and patch recolonizations
    - Suitable habitat patches can be unoccupied
    - Can model with snapshot of patch occupancy
Levins’ model: classic metapopulation dynamics

\[
\frac{dp}{dt} = cp(1-p)-ep
\]

- \( p \) = proportion of occupied patches
- \( 1-p \) = proportion of empty patches
- \( c \) = colonization rate
- \( e \) = extinction rate

- Differential equation predicting rate of change in proportion of patches occupied.

- Analogous to population models: rate of change depends on ‘birth” of patches (colonization) minus “death” of patches (local extinction).

- Equilbrial solution to number of patches occupied:

\[
p = 1 - \frac{e}{c}
\]

- Metapopulation persists if colonization rate exceeds extinction rate
Metapopulation model

- Most populations have a finite probability of extinction \( m \) which is greater than 0
- This implies that all populations will go extinct on a large enough time frame
- Fragmentation can therefore benefit a species, allowing recolonization from neighbouring populations
- This creates a locally dynamic, but regionally stable population
- This regional population, or collection of local populations, was termed a metapopulation by Levins (1969)
- This depends on the ability to maintain an exchange of species
La distribution du loup d’après le RNA

- 5 nuclei: Gerês, Alvão, Bragança, Lapa, Sabugal
- Fragmentation associé aux rivières le plus importants
« Turnover Rate » : les extinctions locales
### « Turnover Rate » : les extinctions locales

<table>
<thead>
<tr>
<th>Region</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
<th>Year 4</th>
</tr>
</thead>
<tbody>
<tr>
<td>North</td>
<td>Extinction</td>
<td>0.26 (0.05)</td>
<td>0.33 (0.25)</td>
<td>0.30 (0.00)</td>
</tr>
<tr>
<td></td>
<td>Colonisation</td>
<td>0.28 (0.13)</td>
<td>0.33 (0.00)</td>
<td>0.33 (0.31)</td>
</tr>
<tr>
<td>South</td>
<td>Extinction</td>
<td>0.52 (1.00)</td>
<td>0.44 (0.00)</td>
<td>0.54 (1.00)</td>
</tr>
<tr>
<td></td>
<td>Colonisation</td>
<td>0.44 (0.00)</td>
<td>0.50 (1.00)</td>
<td>0.48 (0.00)</td>
</tr>
<tr>
<td>Total</td>
<td>Extinction</td>
<td>0.33 (0.09)</td>
<td>0.36 (0.25)</td>
<td>0.37 (0.05)</td>
</tr>
<tr>
<td></td>
<td>Colonisation</td>
<td>0.32 (0.13)</td>
<td>0.38 (0.05)</td>
<td>0.37 (0.31)</td>
</tr>
</tbody>
</table>
Levins’ model is simplistic:

• Spatially implicit approach—does not consider actual locations of habitat patches.
• Dispersal is global and colonization is equally likely no matter where a patch is located
• Patches are homogeneous—ignores any variation in patch size (and habitat quality).
  – Smaller patches have smaller population sizes and thus are more prone to extinction due to stochastic processes.
  – Distant patches are less likely to be colonized
Figure 6.6. Proportion of dispersing California gnatcatcher (*Polioptila c. californica*) juveniles as a function of distance (after Akçakaya and Atwood 1997; data from Atwood et al. 1996).
Metapopulation predictions: patch occupancy patterns

Masked shrew

Nuthatch

Silver-spotted skipper

Pika

Checkered blue butterfly

Common shrew
Colonization & extinction processes

- Silver spotted skipper
- Bush cricket
- Bush cricket
- Bay checkerspot
- Spiders
- Spiders
Mainland-Island metapopulation

- 1 area persists indefinitely and provides colonists to other areas that go extinct
Patchy population

• Migration among patches is sufficient to eliminate interpatch differences in population dynamics
Non-equilibrium
“meta” population

- Persistent population relics without dispersal among patches
Intermediate/ combination/ mixed
Spatial Population Structures

(figure 2) Relationships among different types of metapopulation.

(from Harrison and Taylor 1997)
Source-Sink metapopulation

- In sources, populations grow
- In sinks, populations shrink
- Sinks persist because they are resupplied with individuals from sources
Source-sink model

• A special-case model was proposed (Pulliam, 1988) in which local populations have unique demographics in response to local variation in habitat quality
• This naturally gives rise to the source-sink concept (Dias, 1996)
• Areas with greater reproductive success than death rates must have a net excess of individuals, making the areas sources
• Other areas, where local mortality is greater than birth rates, have a net deficit in individuals, making them a sink
Source-sink model

• Individuals will tend to move from sources to sinks to avoid overpopulation of their areas, despite the poorer quality of sinks.
• Patch quality is often related to size – the source effect is greater for large patches with increased per capita production.
• Long-term studies needed to determine whether a patch is source or sink:
  – Stochastic events (high rainfall) in a generally unfavourable site (desert) may give a false impression that it is a source
• There are a number of observable special cases of the source-sink model that can lead to erroneous assumptions of carrying capacity of the area.
Source-sink: Pseudo-sinks

- Occurs where two adjacent areas are favourable, but one has a better carrying capacity
- The poorer site becomes overpopulated because the net immigration rate is higher than the birth/death rate
- This site may falsely be identified as a sink
- In a true sink the population becomes extinct if immigration is removed
- In a pseudo-sink, reduced immigration will reduce the population to a more sustainable level
- This effectively increases the viability of individuals in the population, due to better resource availability
Source-sink: Traps

- Some habitats may appear extremely favourable to a species, but lack the resources to ensure a full reproductive cycle.
- Effectively, a trap is a sink that looks like a source (Pulliam, 1996).
- Typified in many human-influenced regions, particularly due to agriculture.

Grasshopper sparrows (*Ammodramus savannarum*) are attracted by hayfields in early spring due to high food levels.
- In summer, the fields are mowed before the sparrows have completed their breeding cycle, and the absence of food means that chicks may starve.
Source-sink: Stable maladaptation

- Exemplified by bluetit (*Parus caerulus*) populations breeding in deciduous and evergreen oak (Blondel *et al*, 1992)
- Birds synchronise laying dates with food availability in deciduous forest
- In evergreen forest, the food availability is 3 weeks later, giving lower bird fertility
- Birds adapted to deciduous forest, but emigrate to evergreen forest in a patchy landscape
- In Corsica (all evergreen), the same species of bird is adapted to the altered timing, because it is an island population (gradual speciation through evolutionary adaptation)
Perspective of Hanski and Gaggiotti:

- The metapopulation approach has become the dominant paradigm for understanding and conserving wildlife species in highly fragmented habitat.

- Forces conservation to focus on broader spatial scales.

Practical metapopulation models

- Developed by Ilka Hanski and others
- Spatially explicit — locations of patches matter
- Patches differ in size

**Priority variables:**

<table>
<thead>
<tr>
<th>Patch area</th>
<th>Extinction risk</th>
</tr>
</thead>
<tbody>
<tr>
<td>Patch isolation</td>
<td>Colonization rate</td>
</tr>
</tbody>
</table>
Hanski’s Conditions for Metapopulations

1. Local breeding populations occur in discrete habitat patches.

2. No local population is so large that its expected lifetime is long compared to that of the whole metapopulation. If not, it is a called a mainland-island system.

3. Dynamics of local populations are relatively asynchronous.

4. Habitat patches are not so isolated that recolonization is impossible. If not, system is a non-equilibrium metapopulation that is headed toward extinction.
<table>
<thead>
<tr>
<th>Correlation</th>
<th>Movement</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>None</td>
</tr>
<tr>
<td>-</td>
<td>Sep. pops., contrasting env. drivers; mult. pops.</td>
</tr>
<tr>
<td>0</td>
<td>Sep. pops., uncorrelated fates; mult. pops.</td>
</tr>
<tr>
<td>+</td>
<td>Sep. pops., correlated fates; mult. pops.</td>
</tr>
</tbody>
</table>
Which type of metapopulation?

- All juvenile ground squirrels disperse to new areas
- When completely isolated from other patches, one butterfly subpopulation continued to persist
- Smaller butterfly subpopulations with less genetic variation are more likely to go extinct

Spotted owl dynamics have been modeled as metapopulations – adult pairs are fairly sedentary in forest patches that contain preferred food, and some juveniles disperse (dangerous if across unforested areas).
Figure 6.5. California Spotted Owl metapopulation (after LaHaye et al. 1994).
“Spreading the risk”

Figure 4.1 The relationship between the probability of regional persistence ($P_r$), the probability of local extinction ($p_e$), and the number of populations ($x$). Note that as the number of populations is increased, the probability of regional persistence is substantially higher, for a given probability of local extinction.
The Rescue Effect

• Immigration into patches with small populations could increase chance of persistence and rescue population from local extinction.

• Idea originally developed in context of Island Biogeography but also can occur in classical metapopulation.

• Hence, less isolated patches should not only be recolonized more easily following extinction event, they could be less likely to go extinct in first place.

• For instance, pool frog populations isolated by >1 km often went extinct, whereas less isolated tended to persist.
Habitat loss
Habitat isolation
Small habitat patches

Extinction
Connectivity
Demography

Landscape management
Organism requirement
Habitat fragmentation
Population-based strategy

Population-based strategy
Figure 1 Three approaches to spatial ecology. Theoretical ecologists typically assume homogeneous continuous or discrete (lattice) space. Landscape ecologists tend to analyse the structure of complex real landscapes, with less emphasis on modelling population dynamics. Metapopulation ecology, in the middle, makes the simplifying assumption that suitable habitat for the focal species occurs as a network of idealized habitat patches, varying in area, degree of isolation and quality (the latter is not shown or discussed here, but see ref. 77), and submerged in the midst of uniformly unsuitable habitat.

Approche populationnelle

Biologie des métapopulations  Ecologie du paysage

Métapopulation  Paysage

Population locale  Tache d’habitat
Principe

• Modélisation de la dynamique du système de populations dans un paysage spatialement explicite
  – 1. Démographie des populations locales
    • stochasticité démographique
    • stochasticité environnementale
  – 2. Fréquence de la dispersion entre taches d’habitat
  – 3. Evolution du paysage

⇒ Outils de modélisation: Modèles matricielles (ULM), IBM
⇒ Vortex, RAMAS/GIS
From dispersal to connectivity

Euclidian distance
Isotropic matrix

Least cost distance
Complex matrix
Approche réseau Natura 2000

- Directive européenne Faune-Flore-Habitats (92/43/CEE)
- “Habitat”: zones naturelles ou semi-naturelles ayant des caractéristiques biogéographiques et géologiques particulières et uniques
  → protection des habitats sensibles: zones de conservation
  → création d’un réseau: liaison par des éléments linéaires, des mares, étangs, bosquets et des zones en friches
Approche Natura 2000

- Principes généraux: politico-socio-économiques
- Définition floue de l’habitat
- Utilisation abusive du terme réseau
  → le “réseau écologique” est une utopie, il y a des réseaux écologiques
Take-home messages

“The world is patchy, has always been so, and is sadly becoming, for many species, ever more patchy”
Ilkka Hanski 1999

The conservation framework based on both metaclimax dynamics equilibrium and metapopulation management is the only way to provide guidelines for landscape planning aiming at the (re)conciliation of biodiversity with human activities
Gestion de populations

Analyse de viabilité de populations

Réseaux d’habitats favorables

Augmentation de l’effectif des populations (réintroduction)

Dispersion
Demographic PVA in a nutshell

- Create life-cycle graph
- Convert it to a transition matrix
- Estimate parameters for year-specific (if available) and average matrices
- For average matrix:
  - Calculate $\lambda_1$
  - Calculate CI of $\lambda_1$
  - Calculate sensitivities of $\lambda_1$ to vital rates
- If multiple years of data:
  - Calculate log $\lambda_S$
  - Use simulations to estimate extinction risk
  - Use sensitivity analysis of $\lambda_1$ to guide explorations of the effects of changing various vital rates on extinction risk
- If population is small:
  - Create models with demographic stochasticity (with or without ES)
Terminology for spatial PVA

- **Site:** discrete patch of habitat that has some potential to maintain the species
- **Local Population:** group of individuals living at a site
- **Global (Multi-Site) Population:** individuals living at all sites
- **Metapopulation:** multi-site population characterized by frequent local extinction and recolonization
Endpoints

- Probability of global extinction
- Importance of given population for global persistence
- Value of increasing or maintaining dispersal between sites (e.g. through corridors)
Scenarios

• Independent populations
• Mainland-island
  – One highly viable site
  – Other sites depend on immigration from “mainland” site
• Archipelago
  – All sites with moderate viability, some dispersal
• Metapopulation
  – Local extinction frequent
  – Recolonization by dispersers frequent
No dispersal

• If populations are *independent* then total extinction probability is product of local extinction probabilities

• Positive spatial correlation in environmental variables will increase overall extinction risk
Low dispersal

- Local population dynamics qualitatively unchanged
- Extinct sites can be recolonized
- Inbreeding effects reduced
High dispersal

- Substantial effect on local population dynamics
- Small local populations can be “rescued”
- Otherwise unviable local populations can be maintained ("source-sink" dynamics)
- Leads to spatial correlation in population size
Data requirements

• Population size or demography at each site
  – What do we assume for sites where we don’t have data?

• Spatial correlations in environmental variables
  – Negative correlations: different habitat types?
  – Positive correlations: environmental drivers, tend to decline with distance

• Dispersal rates among sites
  – Factors influencing emigration and immigration
  – Dispersal mortality
  – Behavior in “matrix” (non-habitat)
  – Connection probability tends to decline with distance
Quantifying environmental correlation

• Correlation in population growth rates
• Correlation in vital rates
• Correlation in weather variables
• Spatial extent of catastrophic events
Clapper rail in SF Bay

**Figure 10.3** Annual population growth rates for populations of California clapper rails inhabiting three different marshes on the perimeter of San Francisco Bay.
Rainfall correlations

Figure 10.6 The correlation between annual rainfall for four weather stations near spotted owl populations in Southern California, plotted against distance between stations (after Lahaye et al. 1994).
Clapper rail viability – no dispersal

### TABLE 10.1 Log population growth rates and extinction risk for three populations of the California clapper rail \(^e\)

<table>
<thead>
<tr>
<th>Population</th>
<th>Numbers in 1996</th>
<th>(\mu)</th>
<th>(\sigma^2)</th>
<th>Probability of quasi-extinction by 50 yrs</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mowry</td>
<td>70</td>
<td>0.043</td>
<td>0.051</td>
<td>0.06</td>
</tr>
<tr>
<td>Faber</td>
<td>29</td>
<td>-0.002</td>
<td>0.041</td>
<td>0.79</td>
</tr>
<tr>
<td>Laumeister</td>
<td>33</td>
<td>0</td>
<td>0.051</td>
<td>0.72</td>
</tr>
</tbody>
</table>

\(\text{Data from Harding et al. 2001b.}

\(\text{Extinction risk calculated for a 50-year time horizon, using an extinction threshold of 20 and four estimates of annual growth for Laumeiser and five for Mowry and Faber.}

\[
\begin{bmatrix}
    n_M(t+1) \\
    n_J(t+1) \\
    n_L(t+1)
\end{bmatrix} =
\begin{bmatrix}
    \lambda_{M,J} & 0 & 0 \\
    0 & \lambda_{J,J} & 0 \\
    0 & 0 & \lambda_{L,J}
\end{bmatrix}
\begin{bmatrix}
    n_M(t) \\
    n_J(t) \\
    n_L(t)
\end{bmatrix}
\] (11.11)
Global viability depends on Mowry

Figure 11.2  Extinction time cumulative distribution functions for count-based simulations of the California clapper rail. (A) Extinction probabilities with and without the estimated correlation structure in population-specific growth rates (Tables 10.1 and 10.2). (B) Extinction results based on all three populations and on simulations that eliminated the Mowry Marsh population from consideration. Note the different scales of the y-axes.
Quantifying dispersal

• Mark-recapture data
  – Examine distribution of distance moved

• Behavioral observations
  – Movement models (e.g. random walk) allow extrapolation from short-term measurements

• Genetic data
  – Decline in genetic similarity with distance
California gnatcatcher dispersal

Figure 10.7 The number of resighted California gnatcatchers found at different distances from their original location (redrawn from Bailey and Mock 1998).
Which grizzly pops are most important for persistence?

Table 11.1 Single population viability estimates for five grizzly bear populations*

<table>
<thead>
<tr>
<th>Population</th>
<th>Population size</th>
<th>Probability of quasi-extinction (500 years)**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Divide</td>
<td>306</td>
<td>$7.1 \times 10^{-8}$</td>
</tr>
<tr>
<td>Greater Yellowstone Ecosystem</td>
<td>226</td>
<td>$1.66 \times 10^{-7}$</td>
</tr>
<tr>
<td>Selkirk Mountains</td>
<td>25</td>
<td>0.000258</td>
</tr>
<tr>
<td>Cabinet/Yaak Mountains</td>
<td>15</td>
<td>0.001374</td>
</tr>
<tr>
<td>North Cascade Mountains</td>
<td>5</td>
<td>0.04995</td>
</tr>
</tbody>
</table>

*Population size estimates are from the United States Fish and Wildlife Service (1993).

**The estimated quasi-extinction risk shown for the Yellowstone population differs from that estimated in Chapter 3 because here we use total population numbers and, more importantly, we use a quasi-extinction threshold of 2 rather than 20.

Figure 11.4 Extinction risk for sets of grizzly bear populations over 500 years. From left to right, each bar plots the overall extinction probability obtained by adding sequentially smaller populations to a collection of protected areas.
Multi-site demographic PVA (no dispersal)

\[ G = \begin{pmatrix}
0 & 0 & 0 & a_{1,4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & a_{2,1} & a_{2,2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & a_{3,2} & a_{3,3} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & a_{4,3} & a_{4,4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & b_{2,1} & b_{2,2} & 0 & b_{1,4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & b_{3,2} & b_{3,3} & 0 & b_{1,4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & b_{3,2} & b_{3,3} & b_{4,3} & b_{4,4} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{1,4} & c_{1,4} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{2,1} & c_{2,2} & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{3,2} & c_{3,3} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{4,3} & c_{4,4} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{4,4} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{4,4} & 0 \\
\end{pmatrix} \]
Multi-site demographic PVA
(juvenile dispersal)

\[
G = \begin{pmatrix}
0 & 0 & 0 & a_{1,4}(1 - m_{ba} - m_{ca}) & 0 & 0 & 0 & b_{1,4}m_{eb} & 0 & 0 & 0 & c_{1,4}m_{ac} \\
a_{2,1} & a_{2,2} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & a_{3,2} & a_{3,3} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & a_{4,3} & a_{4,4} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & a_{1,4}m_{ba} & b_{2,1} & b_{2,2} & 0 & b_{1,4}(1 - m_{eb} - m_{eb}) & 0 & 0 & 0 & c_{1,4}m_{bc} \\
0 & 0 & 0 & 0 & b_{3,2} & b_{3,3} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & b_{4,3} & b_{4,4} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & a_{1,4}m_{ca} & 0 & 0 & b_{1,4}m_{cb} & 0 & 0 & 0 & c_{1,4}(1 - m_{bc} - m_{bc}) \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{2,3} & c_{2,2} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{3,3} & c_{3,2} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & c_{4,3} & c_{4,4} & 0 \\
\end{pmatrix}
\]

(11.15)