

**Patch Occupancy Models****I. Isolated populations:**  $P_x = 1 - (p_e)^x$  $x = \# \text{ patches}$  $P = P\{\text{extinction/yr}\} \text{ of all } x \text{ pops}$  $p^e = P\{\text{extinction/patch}\}$ **II. General Patch Occupancy Model**

$$\frac{df}{dt} = I - E$$

**III. Mainland - Island or Reservoir - Satellite (simple case)**

$$I = p_i(1-f) \quad E = p_e f$$

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

$$\hat{f} = \frac{p_i}{p_i + p_e} \quad \hat{f} = \text{steady state fraction occupied patches}$$

- persistence guaranteed

**Assumptions:**

- homogeneous patches
- patches identical
- $p_e$  &  $p_i$  constant
- no time lags

**IV. Internal colonization; no mainland**

$$p_i = if \quad E = p_e f \quad i = \text{effect of occupied patches on } P\{\text{colonization}\}$$

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

$$\hat{f} = 1 - \frac{p_e}{i}$$

- persistence not guaranteed (need balance  $i$  vs.  $e$ )

**V. Mainland - island; w/propagule rain & rescue effect**

$$I = p_i(1-f) \quad E = p_e f \quad p_e = e(1-f) \quad e = p_e \text{ w/out rescue effect}$$

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

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

- persistence guaranteed (mainland-island)

**VI. Internal colonization w/ rescue effect**

$$\frac{df}{dt} = if(1-f) - ef(1-f)$$

set  $df/dt = 0$ ; solve for  $\hat{f} \rightarrow (0,1,f)$ 

$$\hat{f} = 0 \quad i < e;$$

$$\hat{f} = 1 \quad i > e;$$

$$\hat{f} = f_0 \quad i = e$$

**VII. Metapopulation with habitat loss**

Finite number of patches (c.f. infinite number of patches assumed in models above)

Only  $h$  fraction of  $f$  patches are suitable (habitat loss =  $1 - h$ )

$$\frac{df}{dt} = chf(1-f) - ef \quad c, e = \text{colonization, extinction rate parameters}$$

$$\hat{f} = 1 - \frac{e/c}{h} \quad \text{or} \quad \hat{f} = 1 - \frac{\delta}{h}, \quad \delta = e/c$$

$$\hat{f} > 0 \quad \text{only if } \delta < h$$

Note:  $\hat{f}$  is the equilibrium fraction of suitable patches occupied (i.e.,  $\hat{f}$  out of  $h$  possible)

$\delta$  is threshold amount of habitat required for persistence;

If destroy enough habitat so that  $h < \delta$ , then metapopulation (regional) extinction.

**Metapopulation Potential**

Hanski I and O Ovaskainen. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404:755-758.

Finite number of unique patches ( $i$ ); patch-specific probabilities of occupancy:  $p_i(t)$ .

Rate of change in occupancy probability:

$$\frac{dp_i(t)}{dt} = (\text{Colonization rate}_i)[1 - p_i(t)] - (\text{Extinction rate}_i)p_i(t)$$

For example, (particular functional forms)

$$\text{Colonization rate}_i = c \sum_{j \neq i} \exp(-\alpha d_{ij}) A_j p_j(t) \quad c, e = \text{constants}$$

$$\text{Extinction rate}_i = e / A_i$$

$A_i = \text{area of patch } i$

$d_{ij} = \text{distance betw/ patches } i, j$

$1/\alpha = \text{mean migration distance}$

Matrix notation:

Metapopulation matrix  $\mathbf{M}$ , with elements  $m$ :

$$m_{ii} = 0$$

$$m_{ij} = A_i A_j \exp(-\alpha d_{ij}), \quad j \neq i$$

Equilibrium solution, with  $\hat{p}_i > 0$ , iff

$$\lambda_M > \delta$$

$\lambda_M$  is leading eigenvalue of  $\mathbf{M}$

Condition for persistence in given landscape.

Weighted average of occupancy probabilities:

$$\hat{p}_\lambda = 1 - \frac{\delta}{\lambda_M}$$

Note:  $\lambda_M$  same functional role as  $h$  in model VII.

Contribution of patch  $i$  to metapopulation potential ( $\lambda_M$ ):

$$\lambda_i = x_i^2 \lambda_M, \quad \text{where } x_i \text{ is } i^{\text{th}} \text{ element in the leading eigenvector of matrix } \mathbf{M}$$

**Source-Sink Dynamics**

- A. habitat 1 = source;  $\bar{\lambda} > 1$       habitat 2 = sink;  $\bar{\lambda} < 1$       recall:  $\bar{\lambda} = (\lambda_1 \lambda_2 \dots \lambda_t)^{1/t}$
- B. Model population change thru time
  - $n_1$  grows to  $n_1^*$  (= max density supportable in habitat 1)
  - @ max density,  $\bar{\lambda}_1 n_1^* = n_1^* + n_1^*(\bar{\lambda}_1 - 1)$   
 $\Rightarrow$  annual influx of  $n_1^*(\bar{\lambda}_1 - 1)$  from habitat 1
  - habitat 2 reaches equilibrium:  $n_2^* = n_1^* \left( \frac{\lambda_1 - 1}{1 - \lambda_2} \right)$   $\lambda_1 - 1 =$  reproductive surplus in source  
 $1 - \lambda_2 =$  reprod. deficit in sink
- C. Conclusion: higher N in sink than in source, if surplus in source  $>$ . deficit in sink
  - “Most of the individuals in a local population may exist in habitat that cannot maintain the population.” – Pulliam 1988 *Am.Nat*

**Quantitative Incidence Function Model & applications to *Melitaea cinxia***

- A. Incidence of pop in patch “i”:  
 (1)  $J_i = \frac{C_i}{C_i + E_i}$        $J_i = P\{\text{patch i occupied}\}$   
 $C_i = P\{\text{patch i colonized}\}$   
 $E_i = P\{\text{extinction in patch i}\}$
- B. Extinction Probabilities: Assume  $E_i \propto$  Area of patch I (because  $E_i \propto N_i$ )  
 (2)  $E_i = \min \left[ \frac{\mu}{A_i^x}, 1 \right]$        $A_i =$  area of patch I       $\mu, x:$  fitted parameters
- C. Colonization Probabilities = f(patch area & locations of extant populations)  
 (3)  $C_i = \frac{M_i^2}{M_i^2 + y^2}$        $M_i =$  # migrants to patch i per year  
 (4)  $M_i = \beta \sum_{j=1}^n p_j e^{-\alpha d_{ij}} A_j = \beta s_i$        $p_j = 1$  if patch j occupied, 0 if empty  
 $d_{ij} =$  distance between patched i & j  
 $y, \alpha, \beta =$  fitted parameters
- D. Rescue effect: assume patches can be rescued from extinction by immigration:  
 (5)  $J_i = \frac{1}{1 + \frac{\mu'}{s_i^2 A_i^x}}$        $\mu' = \mu y'^2$ ;  $y' = y / \beta$  for patches  $> A_0$ , critical area  
 $(A_i < A_0 \Rightarrow E_i = 1)$

- **Essential point:** incidence function (eq.1) is transformed into parameterized model
  - can be fitted to empirical occupancy data
  - calculation of "metapopulation capacity" & persistence threshold

(Hanski & Ovaskainen 2000. Nature 404:755-758.)