ESCI 433/533 POPULATION BIOLOGY

Spatially Structured Populations

Spatial structure affects populations and population processes in diverse ways. These effects are being studied intensively, and several themes have emerged from extensive field, laboratory, and theoretical analyses. First, there are thresholds in habitat area and number of habitat patches below which populations go extinct. Second, persistence depends on asynchrony in the dynamics of local populations. Such asynchrony can result from persistent environmental gradients, or through protection of some patches from deleterious factors. Third, inter-patch dispersal is essential to metapopulation persistence, which requires that colonization rates exceed rates of local population extinction. Fourth, migration couples the dynamics of local populations to create regional systems. Fifth, populations can be impacted by stressors located outside habitat boundaries. Sixth, different population distributions and abundances may result from similar initial conditions, implying that model analysis is vital to proper interpretation of empirical data.

This project will address spatial structure in the form of discrete patches of suitable habitat. The earliest attempts to understand effects of patchy spatial structure employed simple models that sorted habitat patches into those that were occupied by populations of interest and those that were not occupied. Patch-occupancy models are the oldest and simplest metapopulation models, dating to Levins' (1969) original formulation. In these models, patches are either occupied or vacant, and different patches are assumed to be equivalent in all other ways. Patch-occupancy models track the total number or fraction of occupied patches in a system, as determined by rates of colonization and extinction that are identical for all patches. These models can be classified further into two categories: systems with a “mainland” or perpetual source of dispersing individuals, and systems without a permanent source and in which all potential colonizing organisms originate from occupied patches. These models, their assumptions, and analyses of their results are summarized in Gotelli (2008).

Several assumptions of simple patch-occupancy models limit their application to field settings. Models reviewed by Gotelli (2008) assume a very large or infinite number of habitat patches, but all real systems are finite. More problematic is the model assumption that all patches are identical in both individual characteristics and landscape position. In field systems, patches with large populations are likely to provide more dispersing individuals and large or centrally located patches contribute to metapopulation connectivity more than small or peripheral patches. To address these limitations, Hanski (1994) developed the “quantitative incidence function model,” which avoids these assumptions yet remains simple enough that its parameters can be estimated from field population survey data. Hanski et al. (1996) demonstrated the utility of quantitative incidence function model by fitting it to field data on a metapopulation of rare butterflies, and analyzing effects of various land management methods on population persistence.

Hanski and Ovaskainen (2000) developed a model even more accessible to field systems. Their model requires just two variables for each habitat patch: patch area, and distances to other patches. These values can be obtained readily for most systems of discrete habitats. An additional advantage of the model is that it generates quantities of conservation and management interest: the capacity of the system to support a metapopulation and the relative importance of each habitat patch. The model describes patch-specific changes in probability of patch occupancy, $p_i(t)$.

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

If one assumes the following functional forms for colonization and extinction rates,

$$\text{Colonization rate}_\text{i} = c\sum_{j \neq i} \exp(-\alpha d_{ij}) A_j p_j(t)$$

$$\text{Extinction rate}_\text{i} = e / A_i$$

c, e = constants
A_i = area of patch i
d_{ij} = distance betw/ patches i, j
$1/\alpha$ = mean migration distance,

then the system can be described using the following matrix formulation.

Metapopulation matrix **M**, with elements m:

$$m_{ii} = 0$$

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

A non-zero ($\hat{p}_i > 0$) equilibrium solution exists only if

$$\lambda_M > e/c$$

λ_M = leading eigenvalue of **M**.

The relative importance of each patch in the metapopulation is obtained by squaring elements in the leading eigenvector of **M**:

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

The fractional importance of patch i is simply x_i^2.

Study Area Data

We will use wetlands in and adjacent to Chuckanut Community Forest (CCF) as a set of habitat patches for this project (Figure 1). For more information about CCF, see Eissinger (2015). Wetland areas are listed in Tables 1 and 3. Inter-wetland distances are in Tables 2 and 4. To simplify your analysis without much effect on results, you may use Tables 3 and 4.

Data Analysis

1 Construct a metapopulation matrix for CCF wetlands using each wetland as a habitat patch. Use a dispersal distance of 70. meters, a value derived from Pacific chorus frog (*Psuedacris regilla*) dispersal data in Jameson (1956).

2 Construct a second metapopulation for CCF wetlands using a mean dispersal distance of 125 meters for ambystomatid salamanders reported by Semlitsch (1998).

3 Calculate the metapopulation potential, λ_M, for chorus frog and salamander matrices. If large values for λ_M concern you, consider units are m^2. To convert to km^2, divide by 10^6.

4 Calculate the relative importance of each CCF wetland to the metapopulation potential for chorus frogs and salamanders. Calculate leading eigenvectors for each of the four matricies developed in (2). Square each element in each leading eigenvector to obtain relative importance of that patch to the metapopulation, x_i^2.

5 Repeat steps 1-4 for a restoration scenario in which hydrological connectivity between wetlands CC, HH, KK, JJ, and LL are fully restored. For this scenario, treat those wetlands as a single habitat patch with area equal to the sum of the current constituent wetlands. For distances to other wetlands, use the smallest distances from the aggregate wetland to each of the other wetlands.

Questions and Interpretation

1 Compare the magnitude of λ_M for chorus frog and salamander matrices. How sensitive is λ_M to dispersal distance?

2 Compare relative importances (x_i^2) among the wetands. Using CCF wetland map, deduce relationships between relative magnitude of x_i^2 and wetland area or position within the wetland network. Compare x_i^2 values for chorus frog and salamander matrices. Does dispersal distance appear to affect wetland importance? Why or why not?

3 Compare λ_M and x_i^2 values for the current wetland system (steps 1-4) vs. values for the restoration scenario in step 5. How would such restoration affect wetland network connectivity for amphibians?

4 Suppose chorus frogs were a species of conservation concern, and you had a restoration goal of maximally increasing probability that chorus frogs would persist in CCF wetlands. Identify the top restoration priority, defined as the action that would achieve the largest increase in metapopulation potential, λ_M. Explain why that action would increase λ_M most.

References

Eissinger A. 2015. Chuckanut Community Forest Baseline Documentation Report. Prepared for Chuckanut Community Forest Park District, Bellingham, WA. http://www.chuckanutcommunityforest.com/wp-content/uploads/2015/11/CCF_Baseline_Documentation_Report_Public_Draft_V4.pdf

Gotelli NJ. 2008. *A Primer of Ecology, 4th ed.*, Chapter 4: Metapopulation Dynamics. Sinauer Assoc., Sunderland, MA.

Hanski I. 1994. A practical model of metapopulation dynamics. *J.Anim.Ecol.* 63:151-162.

Hanski I, Moilanen A, Pakkala T, Kuussaari M. 1996. The quantitative incidence function model and persistence of an endangered butterfly metapopulation. *Cons. Biol.* 10:578-590.

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

Jameson DL. 1956. Growth, dispersal and survival of the Pacific tree frog. *Copeia* 1956:25-29.

Semlitsch RD. 1998. Biological delineation of terrestrial buffer zones for pond-breeding salamanders. *Cons.Biol.* 12:1113-1119.

Data Tables

Table 1: Area of wetlands within and adjacent to Chuckanut Community Forest. Areas were converted from NES 2005 data reported in Eissinger (2005). Areas of wetlands BB and JJ have not been delineated in entirety. Areas for BB and JJ below were estimated graphically from Eissinger (2015).

Wetland	Area (m^2)
AA	836
AX	12
AY	46
BB	27,240
CC	10,176
DD	550.
EE	85
FF	6070.
GG	31
HH	814
JJ	44,810
KK	6706
LL	152

Table 2: Distances (m) between wetlands within and adjacent to Chuckanut Community Forest.

Wetland	AA	AX	AY	BB	CC	DD	EE	FF	GG	HH	JJ	KK	LL
AA	0	22	22	113	156	277	251	165	216	91	247	156	238
AX		0	82	82	225	342	320	207	290	156	286	221	299
AY			0	173	130	247	221	147	204	61	273	165	255
BB				0	316	372	372	91	381	242	342	303	377
CC					0	35	17	152	52	35	281	69	221
DD						0	18	174	139	147	389	189	307
EE							0	178	113	121	359	173	281
FF								0	251	113	416	277	372
GG									0	117	247	69	165
HH										0	273	126	225
JJ											0	43	74
KK												0	17
LL													0

Table 3: Area of wetlands within and adjacent to Chuckanut Community Forest. This is a reduced version of Table 1, omitting wetlands AX, AY, and GG. Areas were converted from NES 2005 data reported in Eissinger (2005). Areas of wetlands BB and JJ have not been delineated in entirety. Areas for BB and JJ below were estimated graphically from Eissinger (2015).

Wetland	Area (m^2)
AA	836
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AY	46
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CC	10,176
DD	550.
EE	85
FF	6070.
GG	31
HH	814
JJ	44,810
KK	6706
LL	152

Table 4: Distances (m) between wetlands within and adjacent to Chuckanut Community Forest. This is a reduced version of Table 2, omitting wetlands AX, AY, and GG.

Wetland	AA	BB	CC	DD	EE	FF	HH	JJ	KK	LL
AA	0	113	156	277	251	165	91	247	156	238
BB		0	316	372	372	91	242	342	303	377
CC			0	35	17	152	35	281	69	221
DD				0	18	174	147	389	189	307
EE					0	178	121	359	173	281
FF						0	113	416	277	372
HH							0	273	126	225
JJ								0	43	74
KK									0	17
LL										0

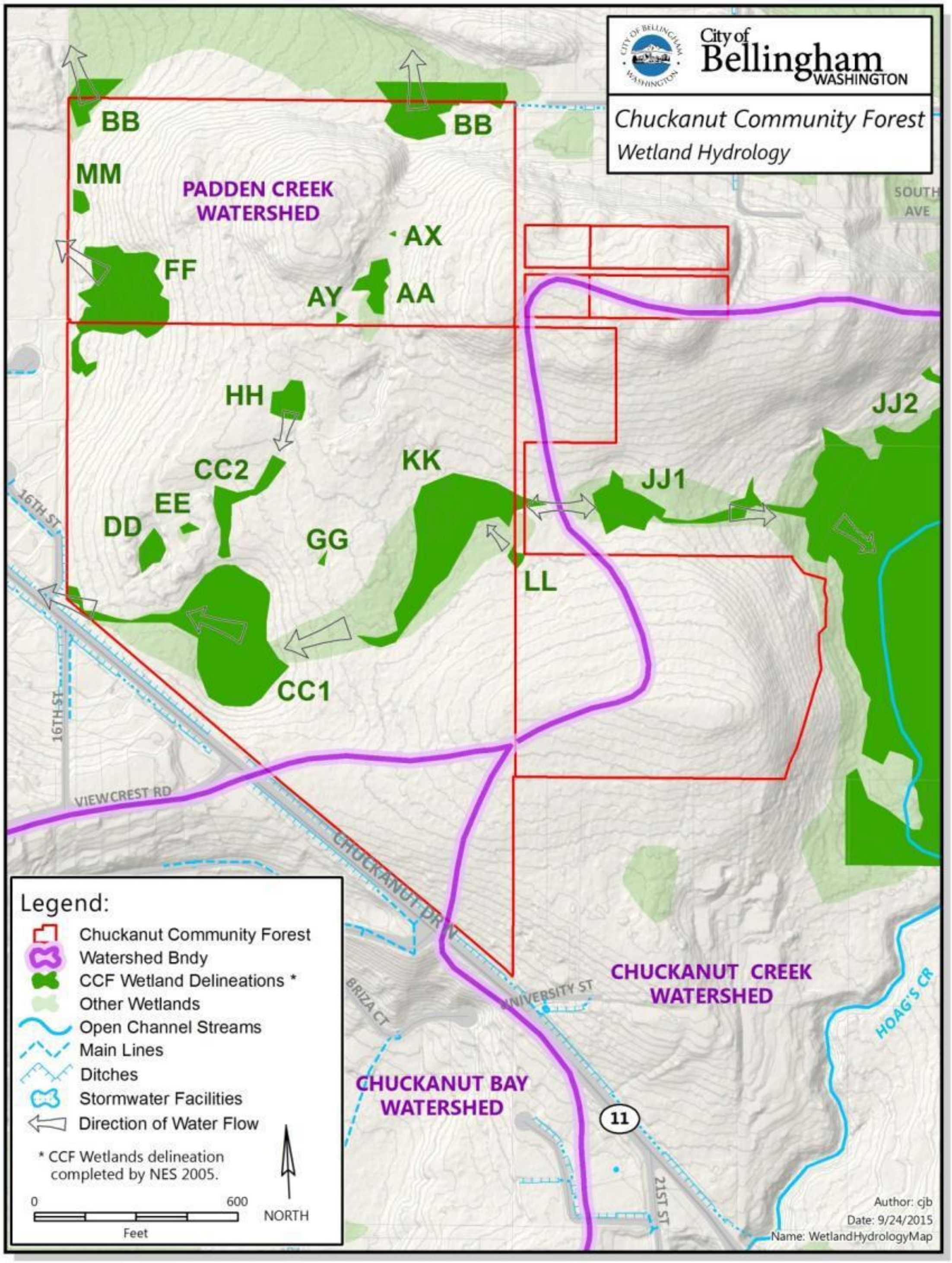

Figure 1: Chuckanut Community Forest map, including delineated wetlands and seasonal hydrologic connections between wetlands. The map contains one obvious delineation error: wetland soils, plants, and habitat extend through CC1 and CC2 without interruption. CC1 and CC2 are a single continuous wetland. Map source: Eissinger (2015).