METAPOPULATION RESPONSE TO HABITAT DESTRUCTION BY MOTH SPECIES IN THE SUBALPINE MEADOWS OF THE HJ ANDREWS EXPERIMENTAL FOREST

ABSTRACT

Subalpine meadows in the H.J. Andrews Experimental Forest are being encroached upon by the surrounding forest. This process threatens the biodiversity in these highly heterogeneous habitats. We employed metapopulation theory to analyze how meadow dwelling moth species would respond to the habitat shrinkage caused by encroachment. Model parameters were derived from GIS data detailing the area and location of each meadow, as well as presence/absence data from moth trapping. Using digitized aerial photographs, and satellite images, meadow area and location data were gathered for the years 1946, 2000 and 2005 in GIS. Stochastic spatial simulations of metapopulations were carried out using this data. From these analyzes we hope to develop an understanding of metapopulation response to habitat destruction in different settings of meadow geography. Such an understanding would inform meadow habitat management choices.

INTRODUCTION

As a result of the ever expanding impact which humans have on the environment, habitat loss and fragmentation threaten many of the world's species. In order to make decisions about conservation and management of these species it is important to understand how partially isolated groups of populations in small habitat patches behave. Metapopulation theory provides a framework to aid in this understanding. The most basic features of metapopulations can be addressed with simple deterministic models.

The simplest metapopulation models describe the rate of change in the number of occupied patches. In these models patches are homogenous and non-spatial. Each patch is has the same probability of extinction and colonization between patches does not depend upon any kind of distance measure. The Levin's model describes the behavior of a large number of metapopulations on these patches with one simple differential equation:

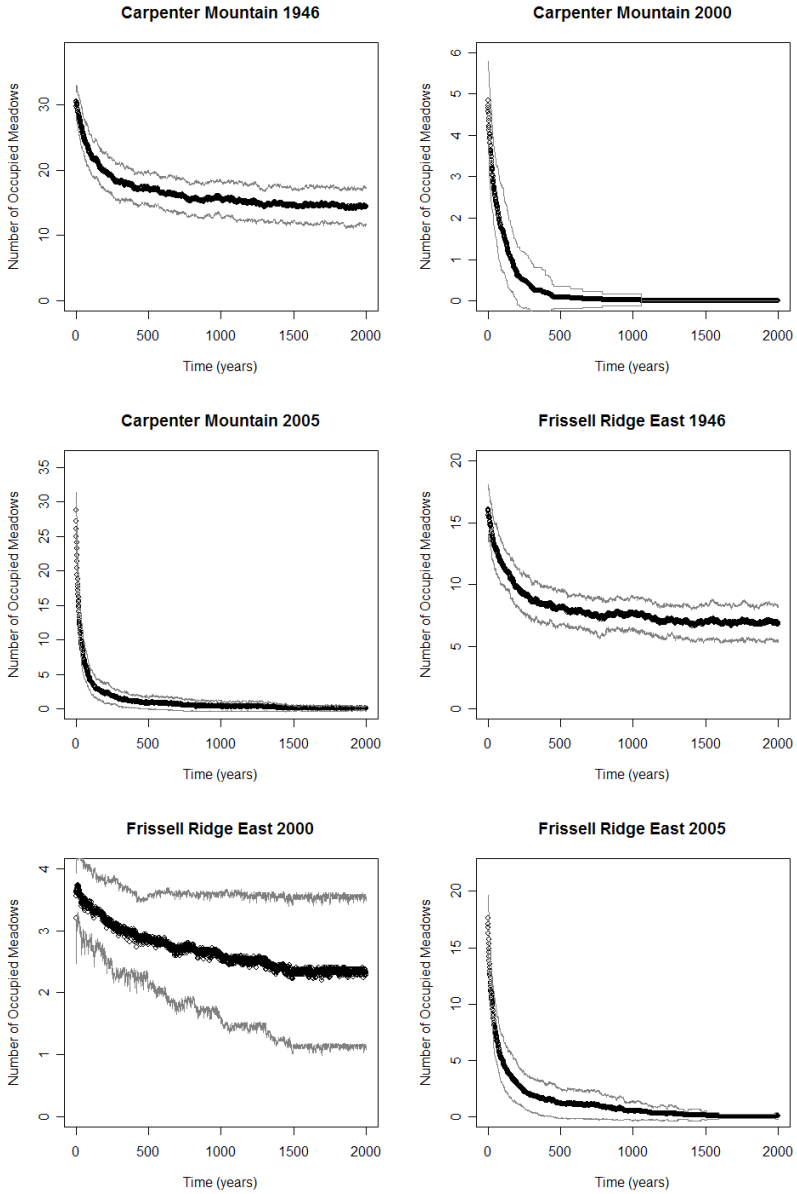
$$dx / dt = c (1 – x) – e (x)$$

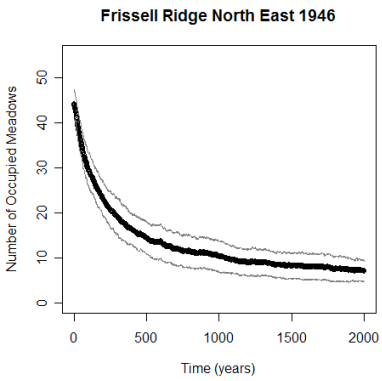
where c is the colonization rate, e is the extinction rate and x is the current patch occupancy.

Simple models like Levin's model have the advantage of being simple to understand and general, but in applications to real world scenarios they have several shortcomings. In applications to conservations, trying to incorporate spatial data results in arbitrary averaging (in order to determine extinction parameters) that often throws out important information about the spatial arrangements of meadows. The Levin's model is non-spatial (does not incorporate spatial arrangements of patches) and patch homogenous (all patches are equal). Such models can't be used to analyze spatial processes like non-random habitat destruction (which is extremely significant in cost-benefit decisions in conservation). For instance the highly central and large patches are very important to the health of a metapopulation, only a spatially explicit, patch heterogeneous model can be used to identify such patches of conservation interest.

SUPLEMENTARY MATERIALS

A. Plots for all Meadow regions for all three years of time steps vs. meadow occupancy, with standard deviation lines.

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20
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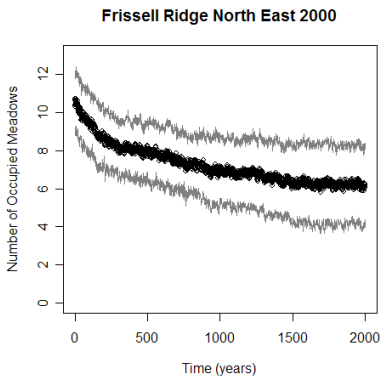
50
0
500
1000
1500
2000
Time (years)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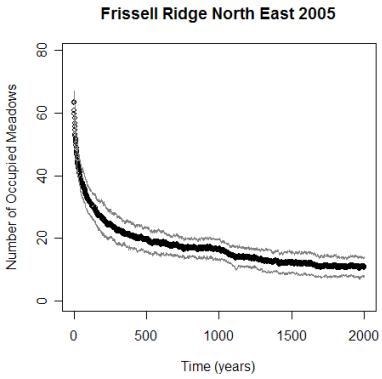
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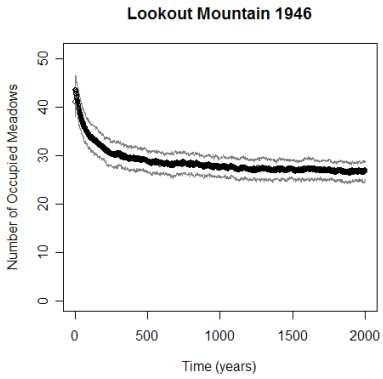
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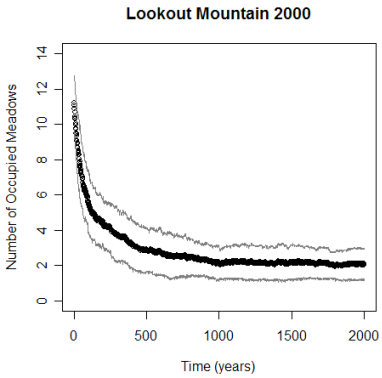
Time (years)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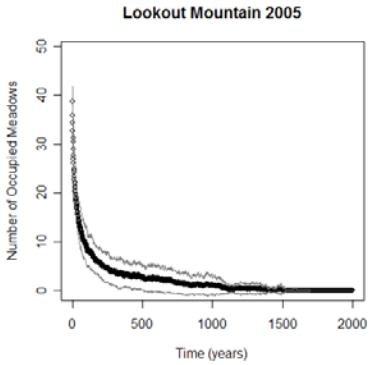
Time (years)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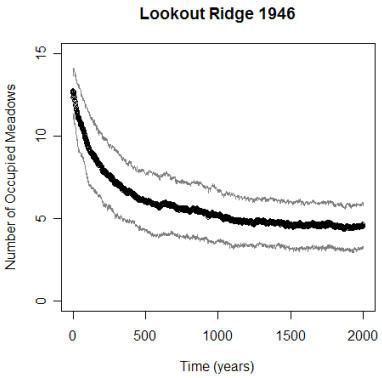
Time (years)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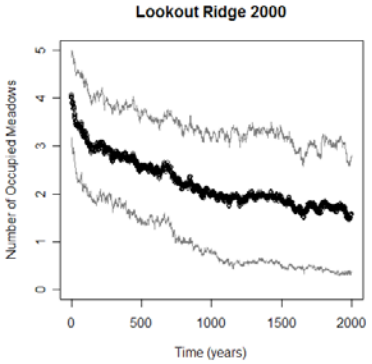
2000
Time (years)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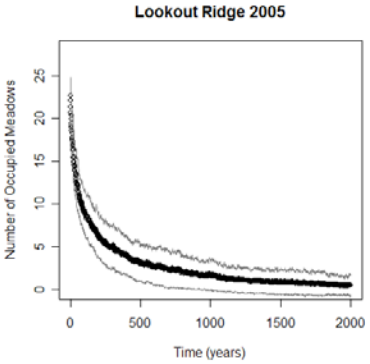
Time (years)


Lookout Ridge 2005
Number of Occupied Meadows
0
5
10
15
20
25
0
500
1000
1500
2000
Time (years)

[Here I would have liked to include a section on the importance of the biodiversity of the moths at Andrew's and some general information about moths pertaining to metapopulations; specifically why we conjecture that these moths are likely to be structured as metapopulations. Unfortunately, time is short and Amanda, who would have been the one to write such a section, has not been in touch since the program ended. Anyway, the section explaining why we think moths populations are structured as metapopulations is crucial to this paper so I'll mention what the argument would have involved. Ecological factors such as flight distance, and specialization on meadow host plants would necessarily limits some moth populations to meadows. Furthermore, the increasing fragmentation and shrinkage of the meadows would make it much more likely for a moth to remain in a meadow for its entire life meaning that each meadow would have a semi-isolated moth population. It would also be important to cite some studies showing evidence of metapopulation structure in other lepidopterans.]

METHODS

Data for Model Parameters

Spatial data was obtained from three GIS layers that detailed the locations shapes and sizes of every meadow at the HJ Andrews in three separate years, 1946, 2000, and 2005 (figure 1). Due to the subjectivity involved in creating these layers (due to factors like: forest shadows, discrimination between meadows and shrub fields, minimum size of clearing required for catalog, etc.) there are inconsistencies between the maps. This is specially apparent between the maps for 2000 and 2005 because they were created by different researchers (Stephen Highland, unpublished) [REFERENCE NEEDED the creator of the 1946 and 2000 meadow layers].

The meadows at the HJ Andres were split into independent patch groups based on distances between clusters that were so large as to make colonization between patch groups extremely unlikely. This splitting proved to make sense for all three years that were studied.

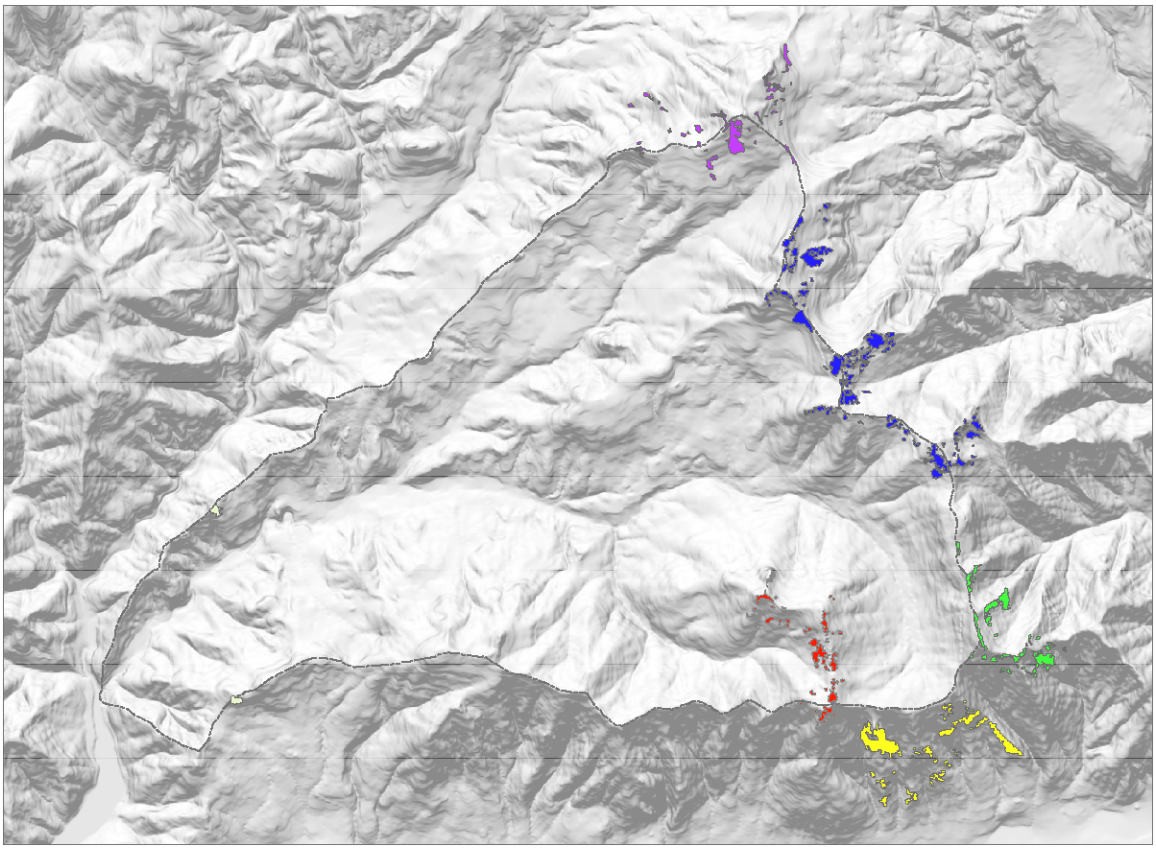


Figure 1: 2005 Meadow Layer

Color coded by meadow region. Red, Lookout Mountain; yellow, Lookout Ridge; green, Frissell Ridge East; blue, Frissell Ridge North East; purple, Carpenter Mountain.

The Model

The GIS data is input into the model as a vector of the areas of each meadow and a matrix of the distance between one meadow to another (the entry at row *i* and column *j* in this distance matrix is the distance between meadow *i* and meadow *j*). The model uses these and a randomly chosen starting state (a vector of 0's and 1's representing unoccupied or occupied for each meadow) to generate vectors for extinction and colonization probabilities for each patch.

The equation:

$$E_j = p_j \frac{A_0}{A_j}$$

Where A_j is the area of meadow *j* (the jth entry of the area vector)
A_0 is a constant
p_j is 1 for occupied *j* and 0 for unoccupied *j*

describes the extinction probability of patch *j*. This is simply a function of the area of each patch. During each time step this probability is calculated and used to switch a patch in the occupied state (1) to the unoccupied state (0).
The equation:

$$C_j = \sum_{i=1}^{n} p_i \frac{A_i}{P_0} e^{-d_{ij}/d_0}$$

Where A_i is the area of meadow i
P_0 is a constant
d_{ij} is the distance between meadow i and meadow j
d_0 is a constant

describes the colonization probability of patch *j*. It's a summation of the probabilities that propagules form the occupied patches will reach patch *j*. This is a function the area of each occupied patch and the distance between that patch and patch *j*. During each time step this probability is calculated and used to switch a patch in the unoccupied state (0) to the occupied state (1).

The model proceeds in this way storing the occupancy information at each time step for later analysis.

The values for the constants P_0, d_0, and A_0, were chosen based on the ecological properties of moths. Since P_0 and A_0 both represent ecologically similar constants (the meadow area at which a population of moths will produce migrants and the meadow area at which a population of moths will go extinct) we chose $100m^2$ for both of these parameters. This area is based on observations by Steven Highland (private communication) who has conducted numerous field studies on moth populations in the Andrews meadows. According to Steven at this area, meadows lose much of the diversity necessary for moth populations, they become dominated by a single plant species. Thus inability to produce migrants and extinction are likely occur around this area. Collaboration with Steven also provided valuable estimates for d_0 (about 1/3 the maximum flight distance of a moth), which was chosen to be 15m. Figure 2 depicts some parameter exploration simulations that demonstrate that the model is fairly stable with changing P_0.

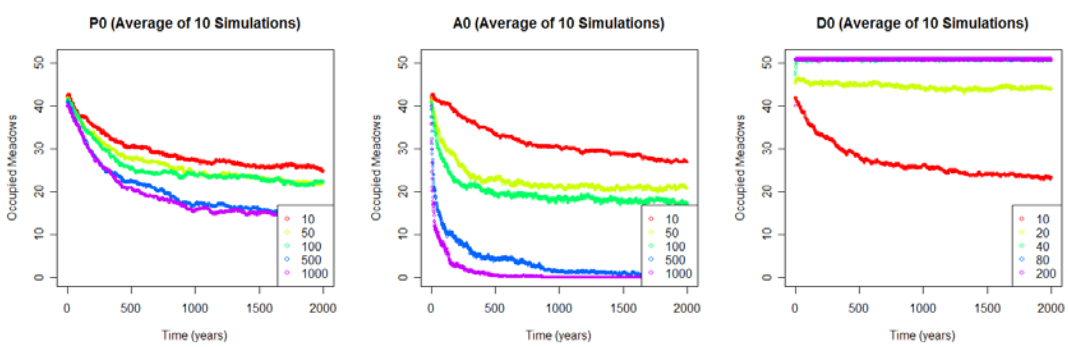


Figure 2 Parameter Exploration

RESULTS

Table 1 summarizes the results of the model simulations. 100 simulations are averaged for each meadow region for each year to yield a statistic of fraction of meadows occupied at equilibrium. The graphs in figure 2 illustrate the output of the model for one particular meadow region over the three studied years. Time is on the x-axis and on the y-axis is the averaged number of meadows occupied at that time step. The grey lines above and below the points indicate 2 standard deviations from the mean, giving a 95% confidence interval.

As can be seen in the graphs the metapopulations settle to semi-stable equilibrium states. After a brief period of time, during which non-equilibrial meadows go extinct, a group of meadows seems to remain occupied for the rest of the simulation. It is this group, measured at the 1000th time step that is recorded in the "Fraction Occupied at Equilibrium" column of table 1.

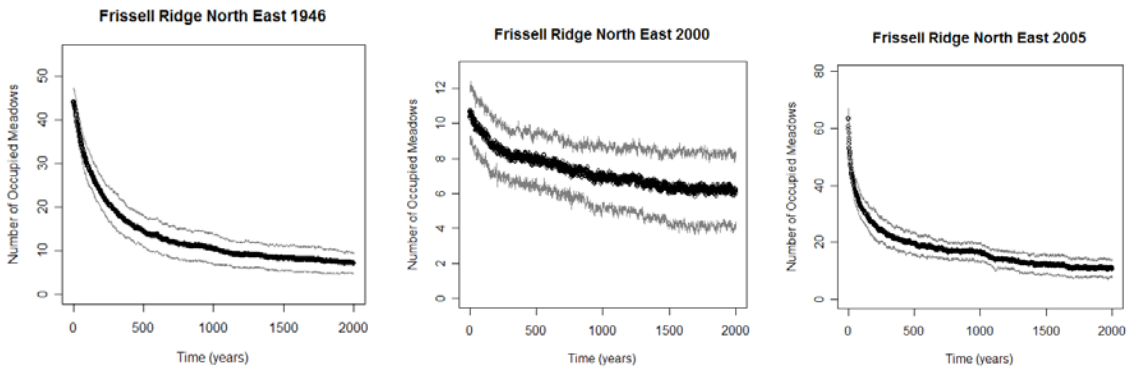


Figure 3 Model output for Frissell Ridge North East

Region	Year	Number of Meadows	Mean Area (m^2)	Mean Distance (m)	Fraction Occupied at Equilibrium
Carpenter Mountain	1946	38	22200	1560	0.42
Frissell Ridge E	1946	20	18000	850	0.37
Frissell Ridge NE	1946	55	17200	2030	0.20
Lookout Mountain	1946	51	19900	990	0.54
Lookout Ridge	1946	15	35800	870	0.37
Carpenter Mountain	2000	6	11200	540	0
Frissell Ridge E	2000	4	14500	330	0.65
Frissell Ridge NE	2000	13	11500	1130	0.54
Lookout Mountain	2000	14	13600	760	0.17
Lookout Ridge	2000	5	31100	330	0.46
Carpenter Mountain	2005	36	5600	1070	0.01
Frissell Ridge E	2005	22	9700	690	0.01
Frissell Ridge NE	2005	79	7500	1610	0.21
Lookout Mountain	2005	49	3900	900	0.01
Lookout Ridge	2005	28	13000	760	0.07

Table 1 Summary of Results

The fraction of meadows occupied at equilibrium is a good measure of the stability of the system. Since extinction is a probabilistic process, in any given time step any occupied meadow might go extinct. But if the fraction of occupied meadows is high then there is likely

to be a non-extinct meadow that will be able to colonize the recently extinct meadow in the next time step. Since the numbers in the table are averages of 100 simulations, the fraction of occupied meadows at Carpenter Mountain, 0.01, means that only one of the simulations had a meadow occupied after 1000 time steps.

A high fraction of occupied meadows in the 1946 simulations indicates that the meadows during these years, which supported such healthy digital populations of moths, were abundant, large, and closely associated. The 2000 simulations tell a slightly different story. The number of meadows is so low that even a 65% occupancy in Frissell Ridge East means that less than 3 meadows on average were occupied. If one looks at the occupancy over time plots however (see Supplementary Materials A), it is evident that this arrangement of 3 occupied meadows is actually quite stable due to the arrangement of these meadows. Meaning that the habitat destruction which took place between 1946 and 2000, was not enough to make our model populations unsustainable. This is likely a product of the fact that habitat destruction is non-random in that small meadows (which are less important to metapopulation stability) are affected disproportionately. (Small meadows are encroached upon faster simply because the ratio of meadow area to perimeter is lower for smaller meadows). Finally, the 2005 simulations predict that only the Frissell Ridge North East meadow region can sustain a stable population.

DISCUSSION

The model behaves as one would expect given a conceptual understanding of metapopulation theory. Meadow populations in tight clusters, as well as populations in large meadows, are present consistently throughout simulations.

What the model tells us is clear, that the meadow regions now, are less suited for supporting a metapopulation behaving as theory would predict, because current meadows are fewer, smaller and more fragmented. The model can also inform management decisions as it can pinpoint meadows that have constantly high occupancies at stable configurations (see Supplementary Materials B). These meadows would clearly be important targets in conservation decisions.

Future Work

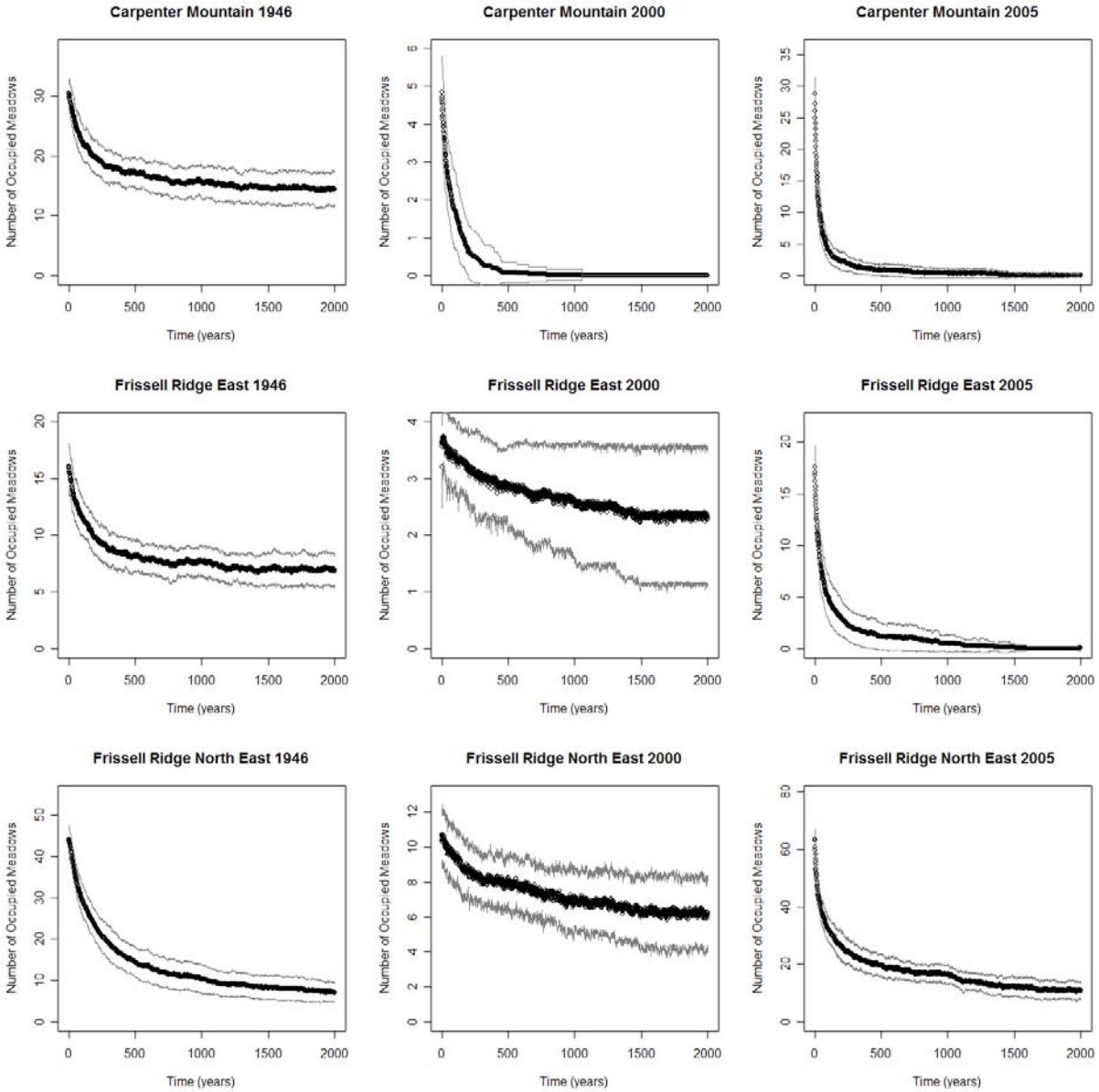
Having completed our analysis of the theoretical possibilities for metapopulations on the HJ Andrews meadows, several things come to mind that could be improved. Simulations need to be more extensive and more varied in their parameter choice in order to better predict real world scenarios. Also, a detailed study of aerial photographs with the goal of identifying meadows specifically for metapopulation modeling would greatly increase our understanding of the meadows at the Andrews.

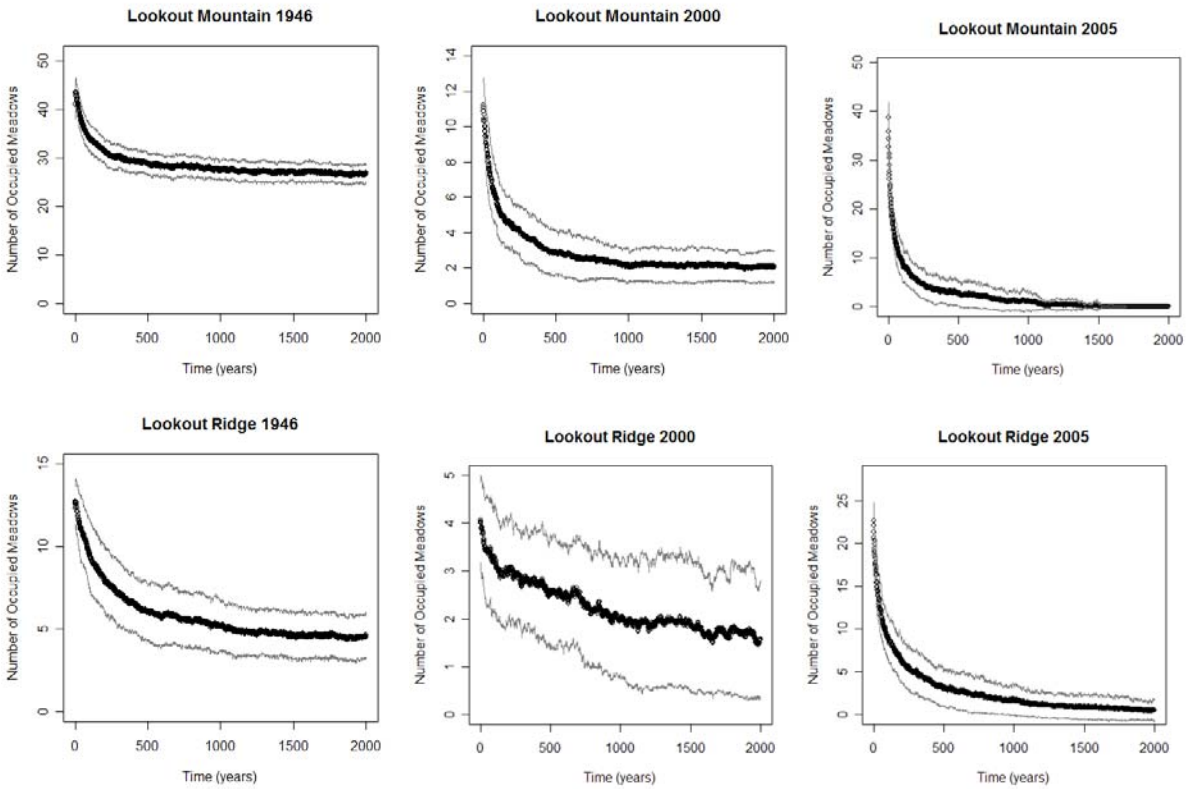
Future work will also need to address the very important aspects of empirical evidence for metapopulation structure in the moth species at the Andrews. Comparing current sample data to the model reveals no correlation between meadows predicted to have high occupancy and meadows with high numbers of meadow specialists. More sampling at meadows of interested (identified by the model) might reveal patterns now invisible due to extra variables. These variables include time of year for sample, different battery lives of the traps used, and slightly different trap locations. What would be needed would be a thorough, though not necessarily

long term program of trapping at a few meadows predicted to have high occupancy and a few predicted to have low occupancy. The trapping would have to take place in a short span of time with several traps in each meadow in order to eliminate as many extraneous variables as possible and to collect a good sample of the species present at each meadow.

SUPLEMENTARY MATERIALS

A. Plots for all Meadow regions for all three years of time steps vs. meadow occupancy, with standard deviation lines.

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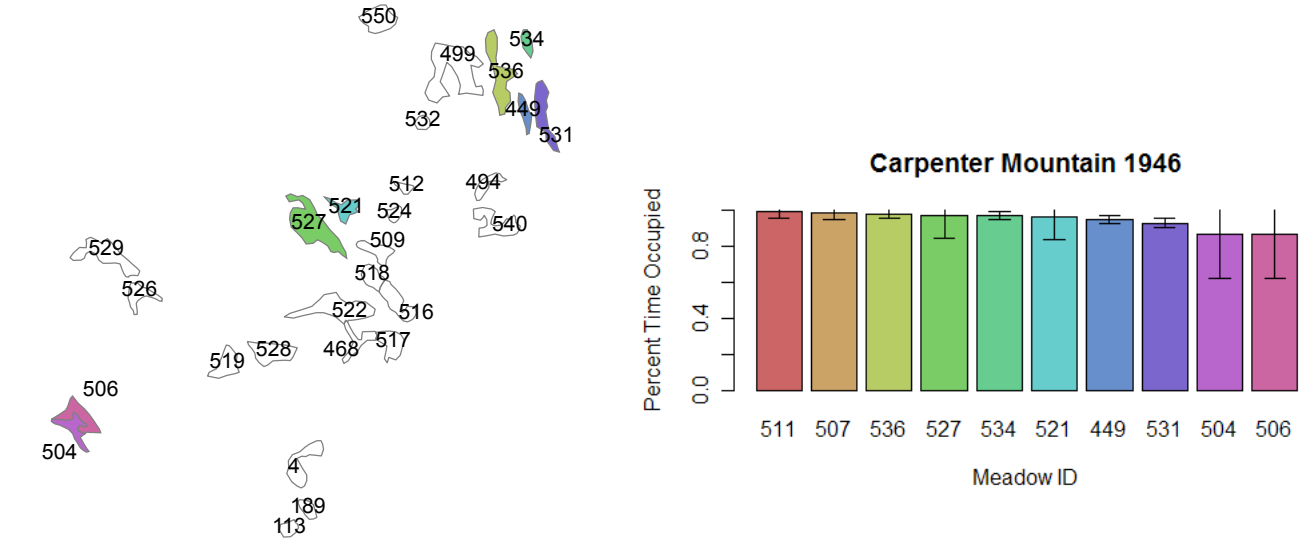
Lookout Mountain 2000
Lookout Mountain 2005
Lookout Ridge 1946
Lookout Ridge 2000
Lookout Ridge 2005
Number of Occupied Meadows
Time (years)

B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468
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Carpenter Mountain 1946
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0.4
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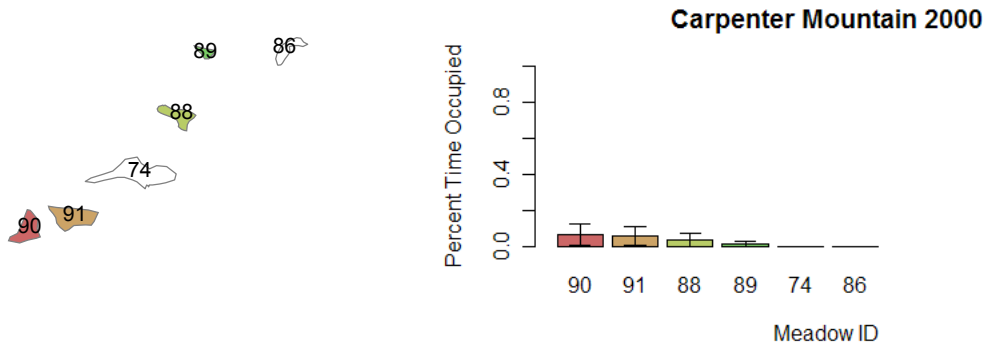
Meadow ID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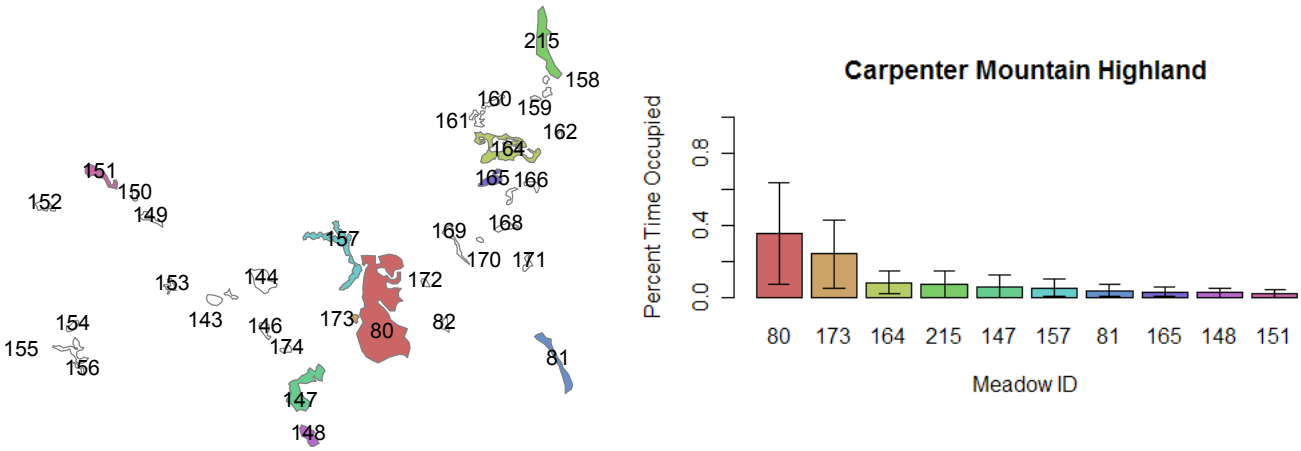
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Carpenter Mountain Highland
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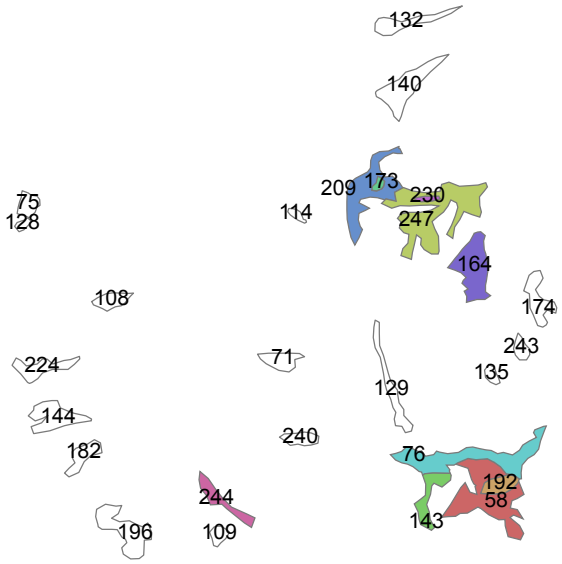
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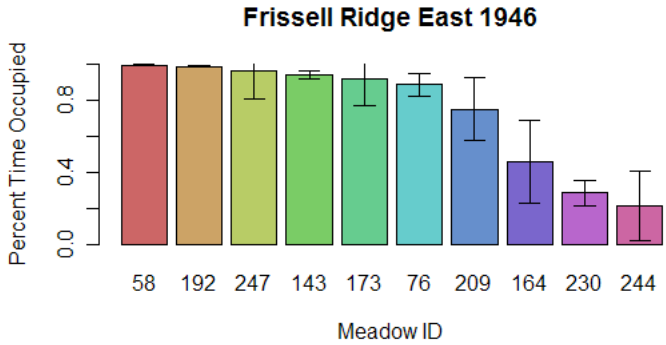
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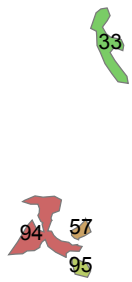
Meadow ID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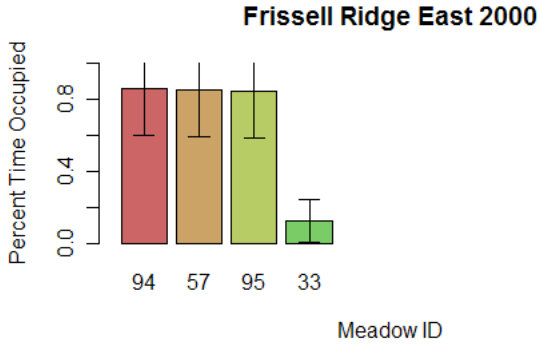
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Percent Time Occupied
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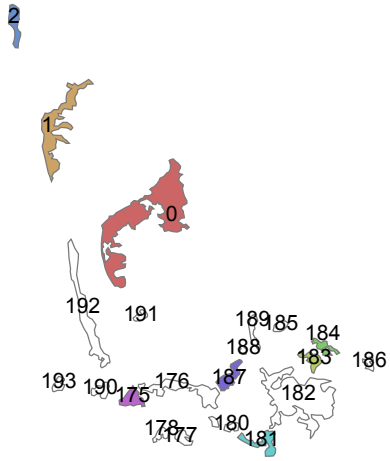
Meadow ID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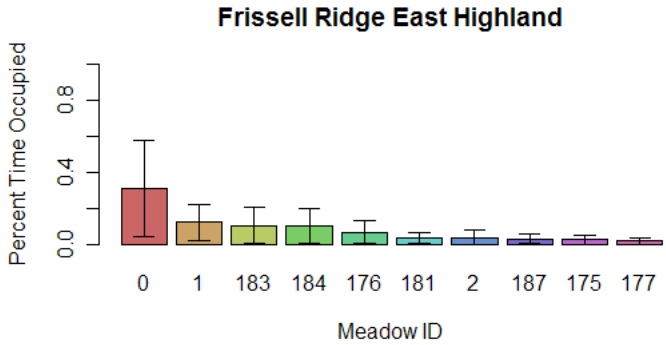
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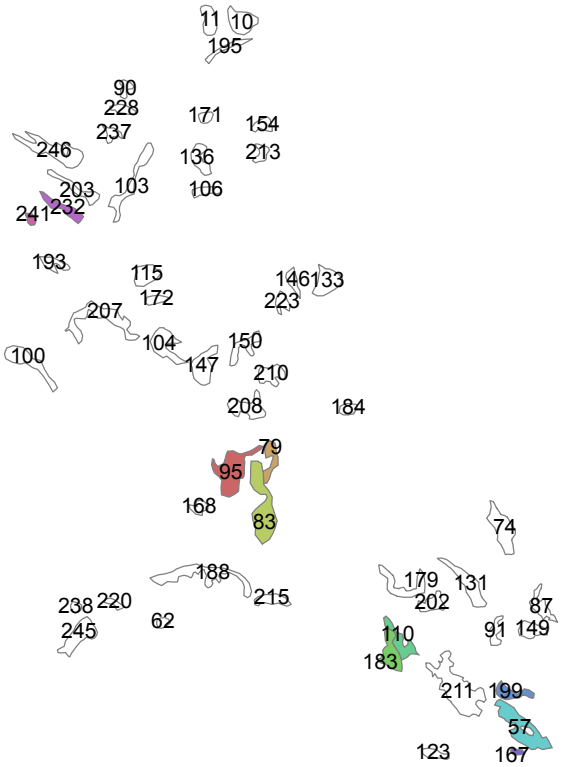
Meadow ID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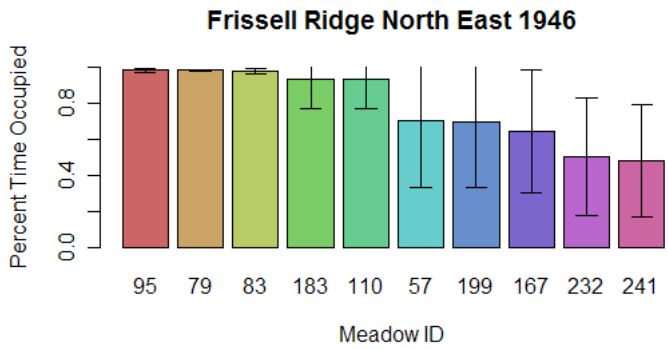
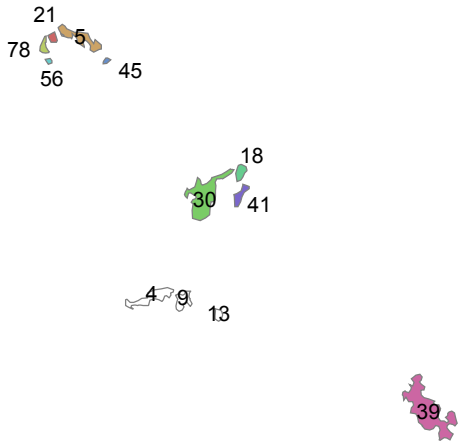

Frissell Ridge North East 1946
Percent Time Occupied
0.0
0.4
0.8
95 79 83 183 110 57 199 167 232 241
Meadow ID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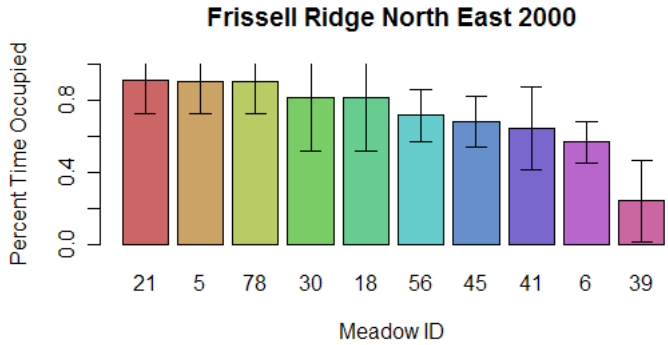
Frissell Ridge North East 2000
Percent Time Occupied
0.0
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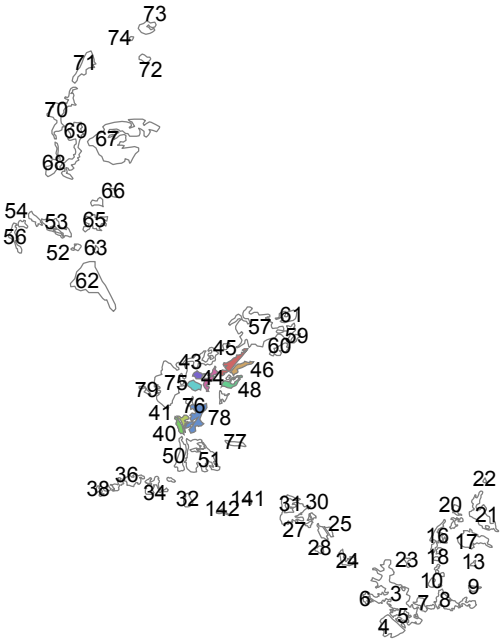
0.8
21 5 78 30 18 56 45 41 6 39
Meadow ID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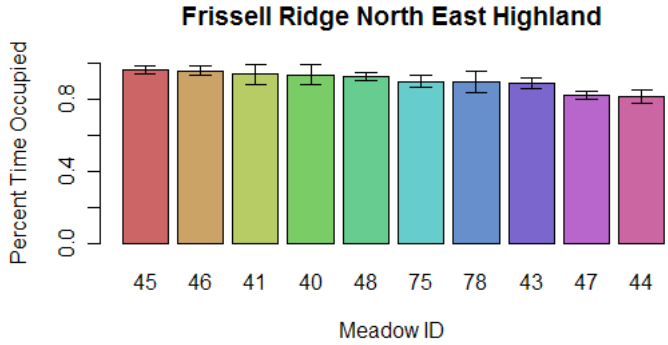
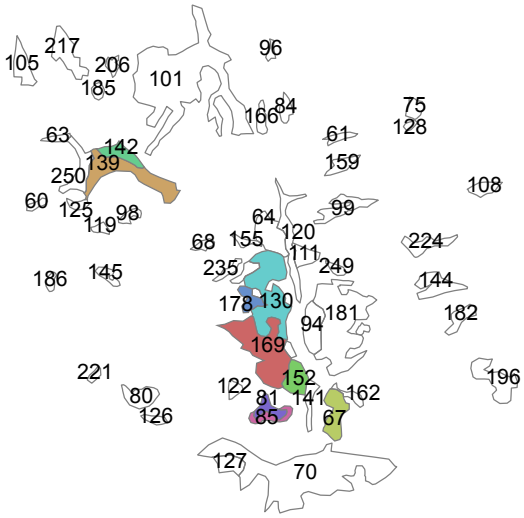

Frissell Ridge North East Highland
Percent Time Occupied
0.0
0.4
0.8
45 46 41 40 48 75 78 43 47 44
Meadow ID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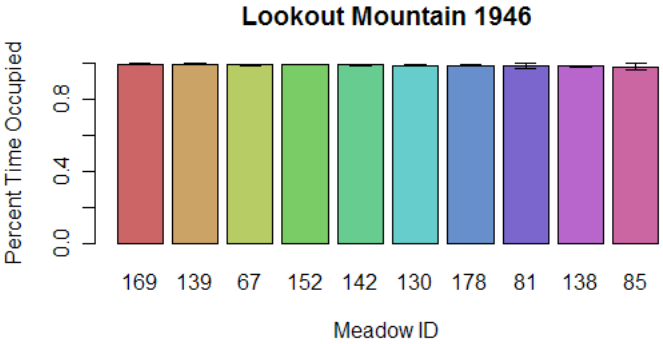
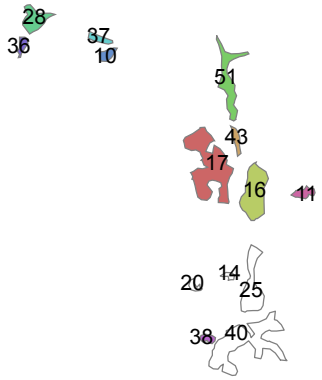

Lookout Mountain 1946
Percent Time Occupied
0.0
0.4
0.8
169
139
67
152
142
130
178
81
138
85
Meadow ID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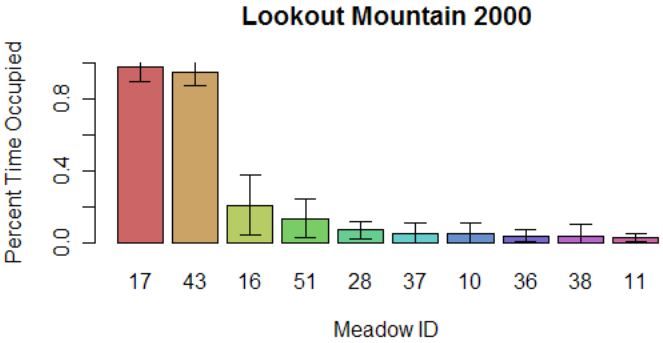
Lookout Mountain 2000
Percent Time Occupied
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0.4
0.8
17
43
16
51
28
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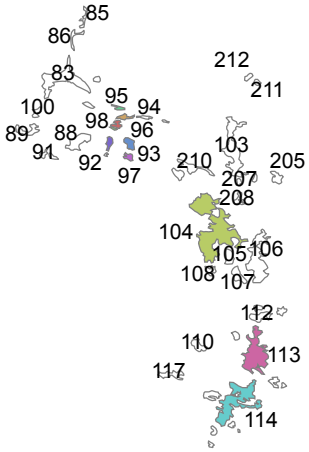
10
36
38
11
Meadow ID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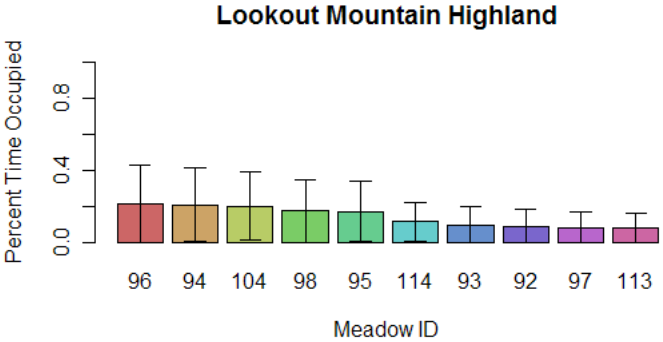
Lookout Mountain Highland
Percent Time Occupied
0.0
0.4
0.8
96
94
104
98
95
114
93
92
97
113
Meadow ID

214
239
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225
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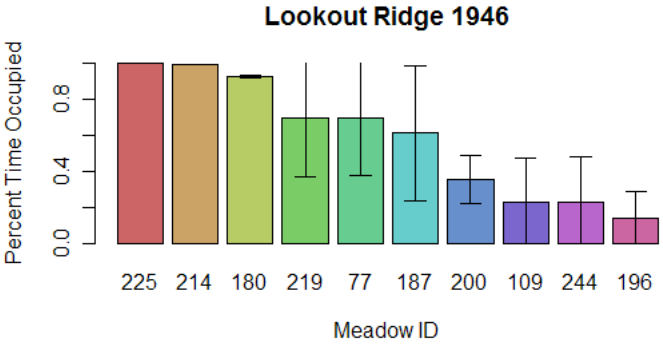
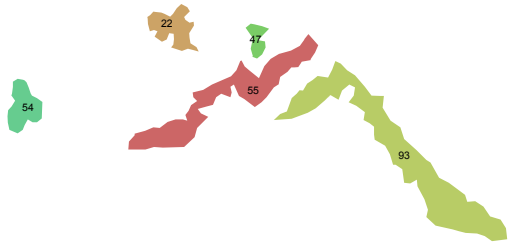
212


Lookout Ridge 1946
Percent Time Occupied
0.0
0.4
0.8
225 214 180 219 77 187 200 109 244 196
Meadow ID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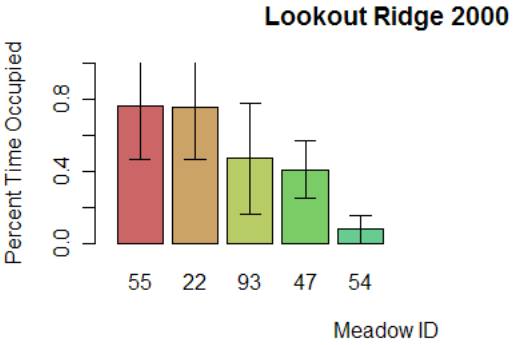
Lookout Ridge 2000
Percent Time Occupied
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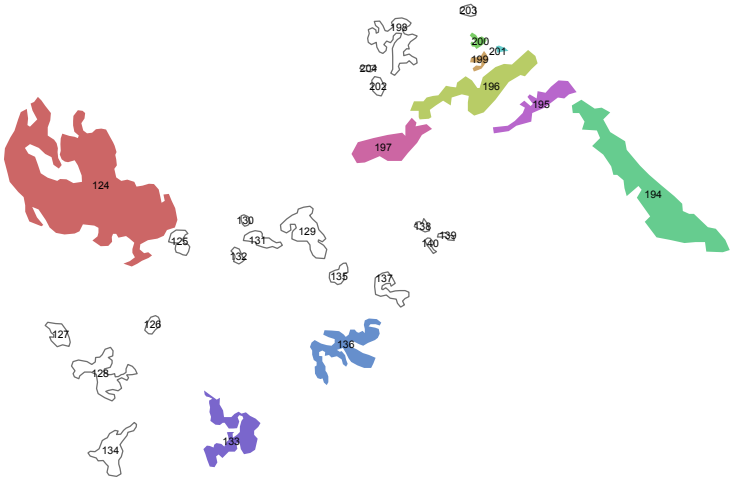
0.4
0.8
55 22 93 47 54
Meadow ID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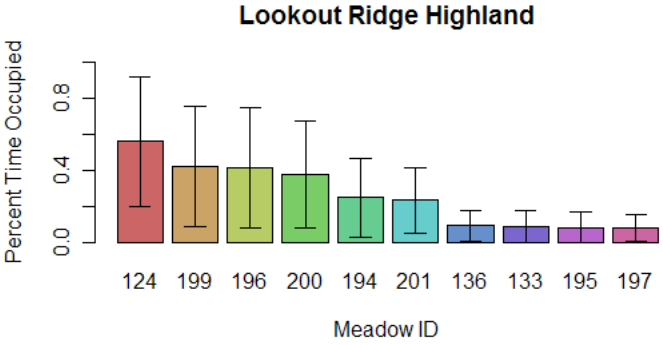
Lookout Ridge Highland
Percent Time Occupied
0.0
0.4
0.8
124 199 196 200 194 201 136 133 195 197
Meadow ID