Analyzing heterogeneous landscapes to reveal ecological processes: the spatial modeling of forest-meadow ecotones using aerial photography

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Abstract

Understanding the mechanisms that create mosaics of communities across broad landscapes is of general interest in ecology. However, in most landscapes, little is known about the mechanisms that drive these patterns, why ecotones form and where they do, and how they have been shaped by human disturbances and topographic patterns. In order to assess the spatial dynamics of forest-meadow ecotones, I conducted a spatial analysis, using GIS, to determine changes in the position of these boundaries, the change in tree cover, and the location and extent of patches of grassland vegetation over time based on historical aerial photos taken in 1938, 1953, 1985, 1990, 1999, 2002, 2004, 2005, 2006, 2008, and 2013. By using aerial imagery and GIS analysis, I will be able to quantify habitat changes for forests and meadows, at the final fine scales needed to better understand the stability or movement of ecotone boundaries. Over this 75 year time slice, there was a 82.3% increase in forest cover for Upper Elk Meadows. The recent encroachment of conifers into montane meadows may constitute one phase of a cyclical process that includes periods of forest expansion, retraction, or statis. However, this rapid conversion of meadow to forest, as seen in Elk Meadows, may signal a shift to an alternative stable state. Regardless of the causes of encroachment discussed above, it is important to maintain open meadow habitats, for both species biodiversity and other resource values.

Key Words

Aerial photographs, ecotone, encroachment, forest, Geographic Information Systems (GIS), meadow, montane ecosystem, Rocky Mountains

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Preface

My interest in this topic stemmed from a background in environmental studies, ecology, and GIS applications.

Acknowledgements

This research and honors thesis would not have been possible without the knowledge and resources of the following individuals: Daniel Doak, Suzanne Anderson, Dale Miller, Teresa Chapman, and Eric Winchell. Also I would also like to thank the University of Colorado at Boulder Geography Department on awarding me the von Dreden fellowship, which allowed me to fund this research during the summer of 2015.

Introduction

Understanding the mechanisms that create mosaics of communities across broad landscapes is of general interest in ecology. However, in most landscapes, little is known about the mechanisms that drive these patterns, why ecotones form and where they do, and how they have been shaped by human disturbances and topographic patterns. In order to investigate ecotone dynamics, I studied forest-grassland ecotones of Colorado's Front Range. The study focuses on the upper montane meadows embedded within dense pine forests in the Colorado Front range. In particular, I concentrate on patterns of tree establishment along forest-grassland ecotones in the northern Colorado Front Range over the last 75 years, the period where repeated aerial photography makes quantitative analysis possible.

To address these questions, I use a pixel-based image analysis approach, which uses image classification, to compare change in tree cover delineated from historical and current imagery. By using aerial imagery, I will be able to quantify habitat changes for forests and meadows at the final fine scale of 1 meter, to better understand the stability or movement of ecotone boundaries.

The questions I am looking to answer are:

- Are forests encroaching into meadows, or are these habitat boundaries stable across time?
- What is the pattern of forest encroachment? Are the meadows being filled by patches of trees inside the meadows through infilling or are the forest boundaries moving into the meadows?

- Based on these answers, what is the natural landscape configuration of montane landscapes in Colorado’s Front Range?

It is the consensus among scientists that forest encroachment into meadows and other grasslands in montane and subalpine zones is occurring through North America, including the Rocky Mountains. These interactions are of importance for anticipating the medium and long-term effects of climate change, and in particular how forest systems will recover after disturbances.

By using image processing and GIS techniques, this study can provide improved understanding of these processes, and hence inform management programs for the Colorado Front Range. These techniques can visually and analytically show changes in vegetation over time at far finer scales than has previously been analyzed, including forest invasion into meadows. As such, these fine-scale analyses of historical and current imagery, can show areas where management techniques, such as prescribed burning, might best be used as well as to understand what natural patterns of ecological communities are most likely (Mast et al. 1997).

Background

The close proximity of strikingly different community types is of long-standing interest to ecologists, for both theoretical and practical reasons. Practically, these sharp ecotones and other features of spatially complex ecological landscapes are known to have substantial effects on a range of ecological functioning, including the maintenance of species diversity (Neilsen, 1993). The tendency for the increased species biodiversity to exist at ecotones is referred to as the edge effect. More theoretically, sharp community boundaries that occur in the absence of obvious abiotic thresholds may provide examples of ecologically driven pattern formation, as well as the existence of alternative stable states (D'Odorico et al.. 2013; Beisner et al., 2003) and evidence for critical state transitions (Sheffer et al., 2009; Dakos et al., 2010). These different perspectives all suggest that understanding the mechanisms that create mosaics of communities is of general interest to ecologists. When boundaries occur in the absence of clear abiotic forcing, researchers have historically resorted to one of two classes of explanations. First are highly system-specific, mechanistic explanations. For example, sharp boundaries at natural forest edges are often created by fire dynamics, although a diversity of other mechanisms have also been discussed. A second class of explanations invokes general principles of hysteresis or reaction-diffusion dynamics to explain why sharply contrasting communities can exist in the same abiotic context. Finally, these interactions are of importance for anticipating the medium and long-term effects of climate change (D'odorico et al., 2013), and in particular how forest systems will recover following increased frequencies of fires and bark beetle epidemics.

Ecotones are generally defined as areas of transition between two different ecosystems, such as between forest and meadows, which is the focus of this paper. In 1988, Di Castri et al.

used a more complex definition of ecotones as “zones of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems” (Di Castri et al, 1988). Depending on the study, the transition can be gradual or abrupt and local or regional scale.

Ecotones are of fundamental importance to the functioning of entire systems (Farina, 2008). Multiple studies suggest that terrestrial ecotones are possibly the most dynamic regions of the world, and in particular that they are where global change impacts will first become evident because they often occur at the extreme limits of tolerance for certain plant species. It has been therefore suggested that ecotones could be considered indicators of global changes and that monitoring efforts should be primarily directed to these regions (di Castri et al. 1988; Nielson 1991; Mast et al., 1998). A basic assumption for this is that at ecotones, small changes in some (limiting) condition -- either bottom up resources or top down controlling processes -- can produce rapid and abrupt responses such as shifts in the distribution of dominant species and associated communities or patches (Kitzberger, 2012).

Grasslands within forest landscapes are important because they are home to unique communities of plants and animals that cannot survive under the forest canopy. Still, non-forested ecosystems, such as grasslands, have generally received much less research than forested systems. Land managers are now realizing that forest encroachment in these open areas could be detrimental for the functioning of ecological landscapes. However, understanding these dynamics is more difficult than previously thought. This is predominantly because many types of grasslands can exist within a landscape, created or maintained by different processes. For example, grasslands can occur where soils are too thin and dry to support trees, such as along ridges at high elevations, or, where soils are permanently saturated such as in poorly drained depressions, such as those found on landslide deposits and glacial landforms. These two types of grasslands are at low risk to conifer encroachment. Grasslands can also occur in less extreme environments, such as on mesic or moist slopes, where soils are productive and well drained—conditions that typically support an abundance of trees, which is the type of grassland where I conducted my study. Understanding the processes that have maintained these types of grasslands, and hence how they will respond to natural and anthropocentric perturbations, is thus a challenge for land managers and ecologists (Swanson, 2007).

Encroachment of trees and shrubs into montane and subalpine grasslands has been documented across the globe (Platt, Mast, etc.), including in the Rocky Mountain region. This encroachment can either occur as advancement of a clear ecotone edges or as establishment of isolated trees within grassland areas through the process of infilling. The rate of and pattern of invasion is variable across different forest-grassland ecotones and especially across opposing sides in a particular forest-grassland system. I will further address the patterns of encroachment in question two of my study.

These shifts in forest-grassland ecotones associated with tree invasions in the western United States have long been the source of interest among ecologists and land managers. During the last 10,000 years in the Rocky Mountains (post-glacial), climatic variations affected the ecotone from the plains grasslands to the coniferous forest (Daubenmire, 1943; MacDonald, 1989). On a shorter temporal scale, many forest-grassland ecotones in the western United States appear unstable, experiencing tree invasion since the mid-1800s i.e. since the peak of the Little Ice Age. In Colorado, these shifts in forest-grassland ecotones often appear to be affected by changes in disturbance regimes such as altered fire frequency and herbivory (i.e. pocket gophers) (League & Veblen, 2006). In addition to climatic factors, disturbances such as fire and grazing also play critical roles in the development of structure, composition and function in the forest-grassland ecotone in this region. Some researchers believe that frequent fires previously maintained grasslands in areas where forests are potentially favored by climate (Mast et al, 1998). Also, wild mammalian herbivores may directly weaken or kill trees by over browsing, twig cutting, partial bark stripping, or girdling of trees. The same dynamics between herbivores and trees are likely to occur in many other habitats across North America, and with other, ecologically similar, fossorial rodents that occur on other continents. Another alternative for why forest encroachment is occurring relates climate change. Recuded snowpacks, longer growing seasons, and other factors allow trees to invade these unique ecosystems that once were carpeted with grasses, shrubs and wildflowers (Swanson, 2007).

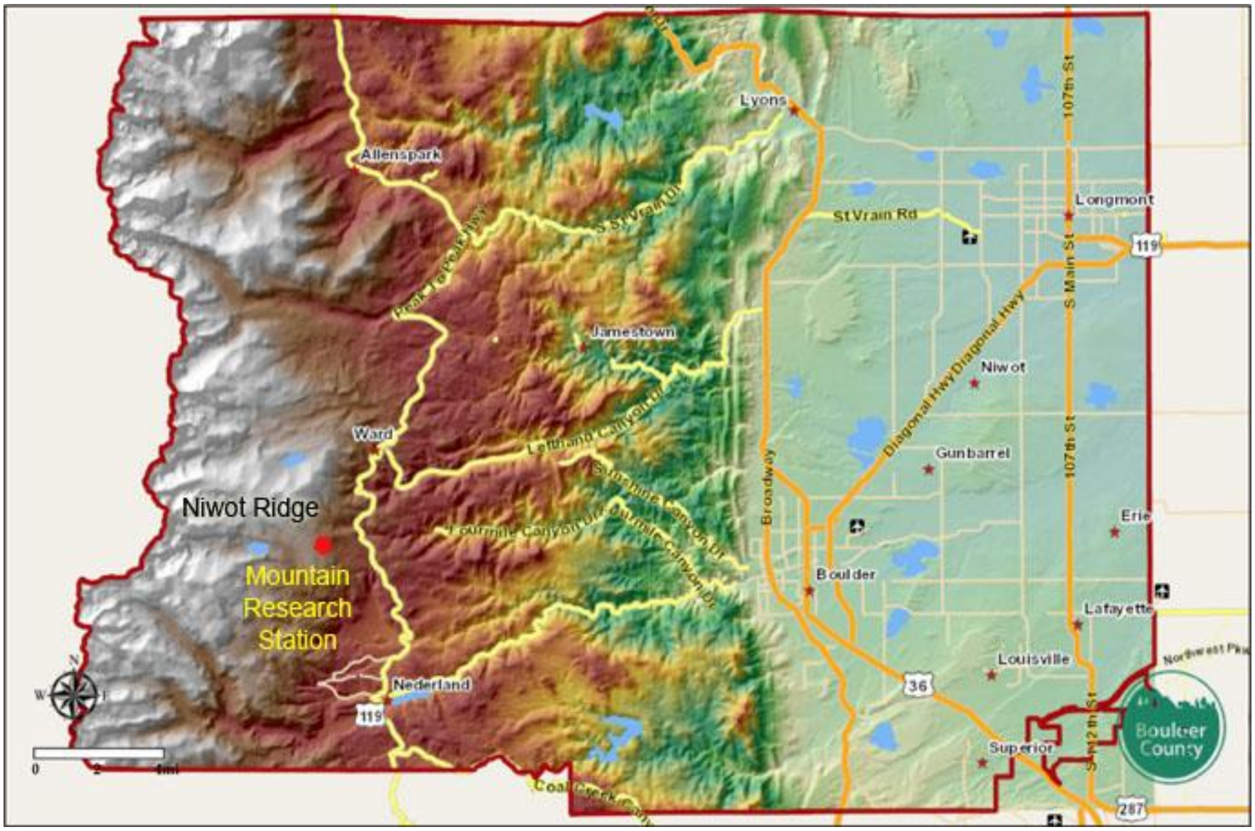
Methods

In order to assess the spatial dynamics of forest-meadow ecotones, I conducted a spatial analysis, using GIS, to determine changes in the position of these boundaries, the change in tree cover, and the location and extent of patches of grassland vegetation over time based on aerial photos taken in 1938, 1953, 1985, 1990, 1999, 2002, 2004, 2005, 2006, 2008, and 2013.

Study area and data

The study area is in the south-facing Upper Elk Meadows in the upper montane zone near the Mountain Research Station located north of Nederland, CO in Boulder County. The Mountain Research Station headquarters are located at 9,500 feet and the Upper Elk Meadows is approximately at 10,000 feet in elevation. So, Elk Meadows is at the upper limit of the montane zone, which ranges from 8,000 to 10,000 feet. The montane zone at upper elevation is typically dominated by ponderosa pine (*Pinus ponderosa*), Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), and Aspen (*Populus tremuloides*). The total study area encompasses 442,140 square meters. I chose this area for the focus of this work because the imagery was easily accessible, the resolution was extremely fine, and there has been extensive research in this area and the surrounding areas.

Figure 1: location of the University of Colorado's Mountain Research Station. Upper Elk Meadows is located adjacent to the station.



To quantify changes in forest-meadow boundaries, I used pixel-based image analysis to compare change in tree cover delineated from historical and modern imagery. The time scale ranges from 1938 to 2013. For each image, I performed the following steps:

1. Pre-processing: this includes re-projecting all of the imagery into the same coordinate system and clipping each set of images to the same extent, every image in the same 1mx1m resolution
2. Training samples: "teach" the software how to classify the pixels in an image. Separate training samples were made for each image.

3. Signature file: created in order to record the spectrum signatures of the two classes across a series of band(s), which contains means and covariances
4. Classification: assigns each pixel in the image to one of the two classes based on the means and covariances of the class signatures
5. Post-processing: removing the noise and improving the quality of the classified output, using Majority Filter tool.
6. Fishnet: creates a grid overlay with 10x10 meter zones
7. Zonal statistics: calculate percent forest cover for each grid

The ten "time-slices" of orthophoto mosaics have a resolution of 0.3 m to 1.0 m and encompass the past seven decades. Previously orthorectified imagery was obtained from various sources for years 2008, 2006, 2005, 2004, 2002, and 1999. Imagery was also orthorectified from historic aerial photography for years 1990, 1985, 1972, 1953, 1946, and 1938. Each high-resolution image has the qualities of a photograph and the functionality of a map layer for use in Geographic Information Systems (ArcGIS). Digital scans of the historic photography were fully orthorectified in Leica Photogrammetry Suite (LPS) at INSTAAR, University of Colorado, using air-photo camera models, a 2 m DEM, information from calibration reports, and image-to-image control points linked to the 2008 reference imagery. Horizontal errors (RMSE) average 2.1 m, relative to the 2008 mosaic. The images are provided in georeferenced .tif (GeoTIFF) format, accompanied by pyramid files (.rrd) generated by ArcGIS. The orthophoto mosaics carry a resolution and accuracy as good or better than satellite imagery; they provide a time series for detailed analysis of environmental change through time. All datasets share a common rectangular extent, encompassing Niwot Ridge, the Green Lakes Valley, and surrounding areas. All map layers share a common projection and datum (UTM zone 13, NAD83).

Since this imagery stopped in 2008, I used Digital Orthophoto Quadrangles (DOQs) for more recent imagery, and included the year 2013. A (DOQ) is a computer-generated image of an aerial photograph in which the image displacement caused by terrain relief and camera tilt has been removed. The DOQ combines the image characteristics of the original photograph with the georeferenced qualities of a map. DOQs are natural color, or color-infrared (CIR) images with 1-meter ground resolution.

A total of two images were rejected due to image limitations. The 1972 imagery only encompasses a portion of the study area. The 1999 image was blurry. The selected image pairs are of relatively high quality, though in some cases the images have deep topographic shadows in parts of the image.

Pre-processing

In all GIS analyses, preprocessing of the imagery must occur in order to view and analyze the data. First, I re-projected each image using the Project Raster tool in ArcGIS. This tool allows all of the images to be projected into the same coordinate system and datum, in this case the coordinate system was NAD83_UTM_zone_13N and the datum was D_North_American_1983. Importantly, this tool guarantees that the re-projection error after the projection is less than one half of a pixel. In this case, all of the error from the re-projection is less than one-half of a meter for each image. This tool also has an option for output cell size that allows the user to set the cell size of the new raster image using an existing raster data set. In this case, I selected the 2013 imagery as the existing raster data set, which has a resolution of 1m x

1m; this was the coarsest resolution of all the ten “time-slices”. I left the other parameters of the tool as the default values. The defaulted nearest option, which performs a nearest neighbor assignment, is best for land-use classification, because it will not change the cell values. The output of this step resulted in all ten images projected into the same coordinate system and datum along with the the same 1 m x 1 m resolution.

Next, I used the Clip Data Management tool to extract the Elk Meadows study area out of each year of imagery. The extent of the study area is a rectangle with an area of approximately 442,141 square meters, which is a relatively small meadow in comparison to the average meadow size in Colorado’s Front Range. After this process, each image had 761 columns of 1 meter pixels and 581 rows of 1 meter pixels. Again, all other parameters of this tool were left as the default values.

Pixel-based image analysis

I used the Image Classification toolbar to classify all l0 of the images. This toolbar can extract information classes from single and multiband raster images, such as the aerial photographs used in this case study. For this analysis, I used a supervised classification, which is an image classification approach that is based on the training samples collected by the analyst. The training samples "teach" the software how to classify the rest of the pixels in the image, such as forest or meadow. Each class is a group of pixels in an image that represent the same object on the surface of the earth. In this case, only two classes were used – forest or meadow. To create these training samples, I used the Training Sample Manager tool in order to identify either forest or meadow classes. The quality of the training samples was analyzed using sample evaluations tools such as histograms and scatterplots. For example, the histograms of different classes should not overlap. If they do overlap, you need to remove or merge some of the classes. Using the Image Classification toolbar and Training Sample Manager, it was determined the training samples were representative for the area and each class was statistically separate.

Once the training samples are created, signature files were created in order to record the spectrum signatures of the two classes across a series of bands. The number of bands in each image varied; some images had 1 band while others have 4 bands. For each class, the signature contains means and covariances calculated from its training sample.

Next, the Interactive Supervised Classification tool allowed me to perform a supervised classification using the Maximum Likelihood Classification tool. This tool is based on the maximum likelihood probability theory. It assigns each pixel in the image to one of the two classes based on the means and covariances of the class signatures, assuming that the distribution of a class sample is normal. By default, all cells in the image are classified, with each class having equal probability weights attached to their signature files. During the classification, it makes use of all the bands available in the selected image layer.

Post-Processing

In these classified outputs, it is inevitable that some misclassified isolated pixels or small regions of pixels may exist. To improve the classification, I used a post-classification processing technique called Majority Filter. Post-classification processing refers to the process of removing the noise and improving the quality of the classified output. The Majority Filter tool replaces the cells in a raster image based on the majority of their contiguous neighboring cells. I specified two parameters for this tool - number of neighbors and the majority definition. The number of neighbors was set to eight, which means the kernel of the filter will be the eight nearest neighbors (a 3-by-3 window) to the present cell. The second parameter, the majority definition, was set to half. This means that half of the cells must have the same value and be contiguous. Two out of four or four out of eight connected cells must have the same value. Using the HALF option will have a more smoothing effect. The output raster will be stabilized (will no longer change) after a few runs of Majority Filter. In this case, I ran the tool a total of three times to reach stabilization; there was no change in the output after the fourth time running the tool.

Typically, the next step for generalization is to use the Boundary Clean tool in ArcGIS. This tool smoothes the boundary between zones by expanding and shrinking the edge. I decided to not use this tool for the following reason: the default sort type for this tool specifies that zones with larger values have a higher priority to expand into zones with smaller values. For my analysis, forested areas are typically larger areas than meadows, so the tool will always result in forest zones expanding into meadow zones. This is problematic because I am looking to examine the ecotone edge between these two ecosystems, but if they are too generalized or favor the classification of one ecosystem over another, the results will be skewed. Thus, I did not use this tool.

Statistical analysis

The goal of the statistical analysis was to determine the rate of tree encroachment and the pattern of this movement by summarizing the percentage of cells as forest or meadow within grids. Further along in the analysis, histograms are created to summarize the percentage of tree cover across space for each of the ten images. The structure of the histograms will show evidence of either forest edge movement or tree infilling.

In order to begin extracting information from the imagery, the forest and meadow classes were reclassified to binary classes. The forest pixels were reclassified to 1 and the non-forest (meadow) pixels were reclassified to 0. This reclassification to binary values was a crucial step for statistical analysis, as discussed further below.

I then overlaid a grid to sample each year of imagery. The grid was created using the Create Fishnet tool in ArcGIS. The tool creates a fishnet of rectangular cells that are polygon features. In addition to creating the output fishnet, a new point feature class is created with label points at the center of each fishnet cell. I specified the cell width and height of the fishnet to be 10 meters x 10 meters. For each image, there are 76 cells in the Y-direction and 58 cells in the X-direction for a total of 4,408 grid cells for each image in the time slice.

In order to sample each grid in the fishnet for the values of each image in the time slice, I used the Zonal Statistics as a Table tool in ArcGIS. This tool summarizes the values of a raster within the zones of another data set and reports the statistical results in a table. In this case, the tool summarized the values of each time slice classification within the fishnet grid zones. The statistics that I collected for each grid included the sum, mean, and standard deviation. The mean for each grid cell ranges from 0 (100% meadow) to 1 (100% forest). Thus, for each image there are 4408 grid cells of 100 meters squared, so the sum for each image ranges from 0 (100% meadow) to 440,800 (100% forest). The standard deviation is derived from the mean values.

Results

Over this 75-year time slice, there was a 82.3% increase in forest cover for Upper Elk Meadows. Figure 2 below shows a representative set of years from the time series of images; these include 1938, 1985, 2002, and 2011. In 1938, approximately 50.6% of the study site was classified as forest. In 1985, approximately 69.0% of the study site was classified as forest. In 2002, approximately 86.1% of the study site was classified as forest. In 2011, approximately 92.3% of the study site was classified as forest. Figure 3 below shows the rate of forest cover over the time period of 75 years including all 10 of the years of imagery in the analysis. The greatest increase during this 75 year time period was between 1985 and 1990, when the percent of forest cover grew by 12.8% over a 5 year period, a 2.36% annual increase.

Figure 2: Output for the maximum likelihood classification for years 1938 (upper left), 1985 (upper right), 2002 (lower left), and 2013 (lower right). The pixels classified as meadow are colored tan and the pixels classified as forest are colored green.

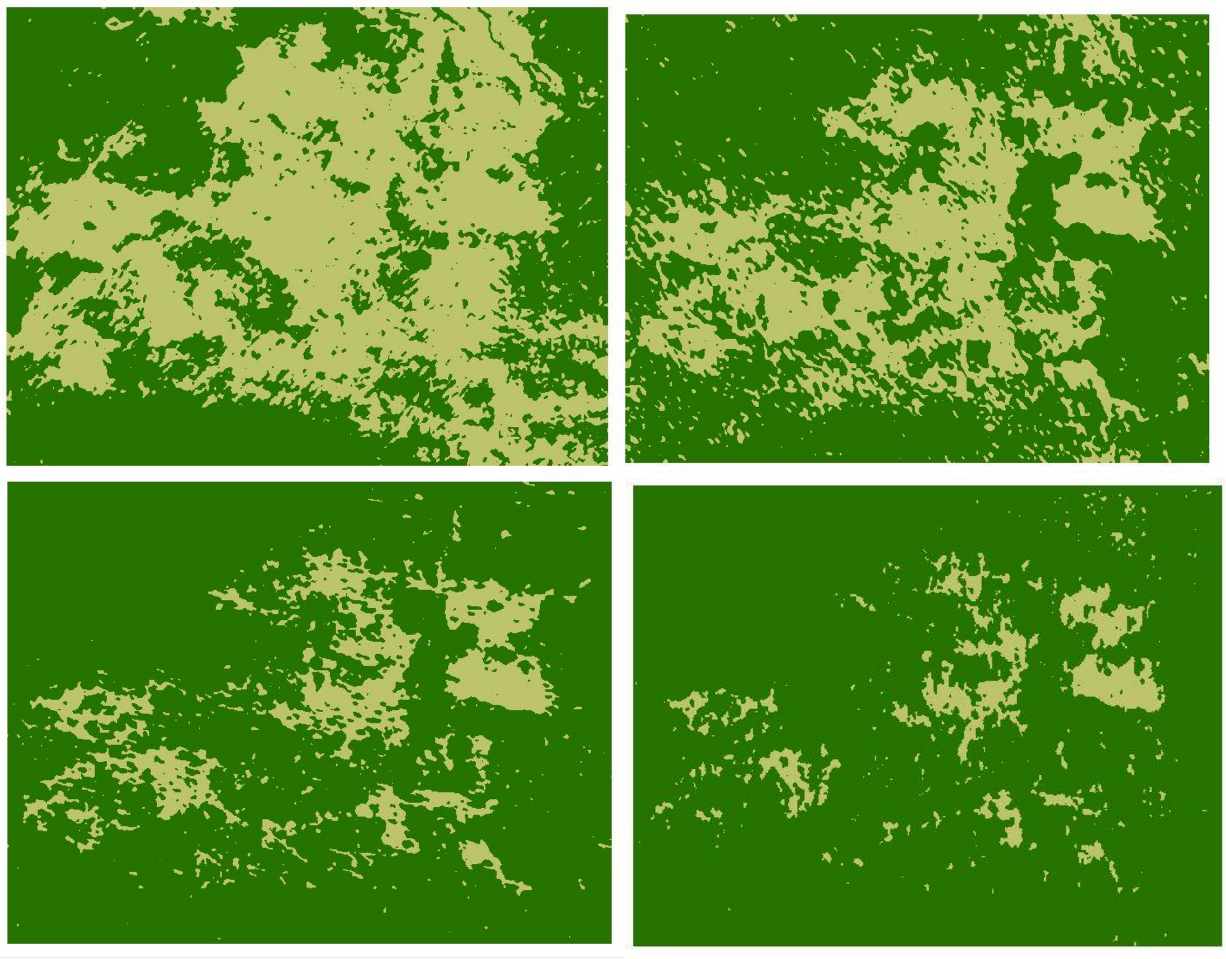


Figure 3: shows the average forest cover per year as a percentage over the 75-year time slice as the blue line. In order to see the general trend, I included a line of best fit, which is in red.

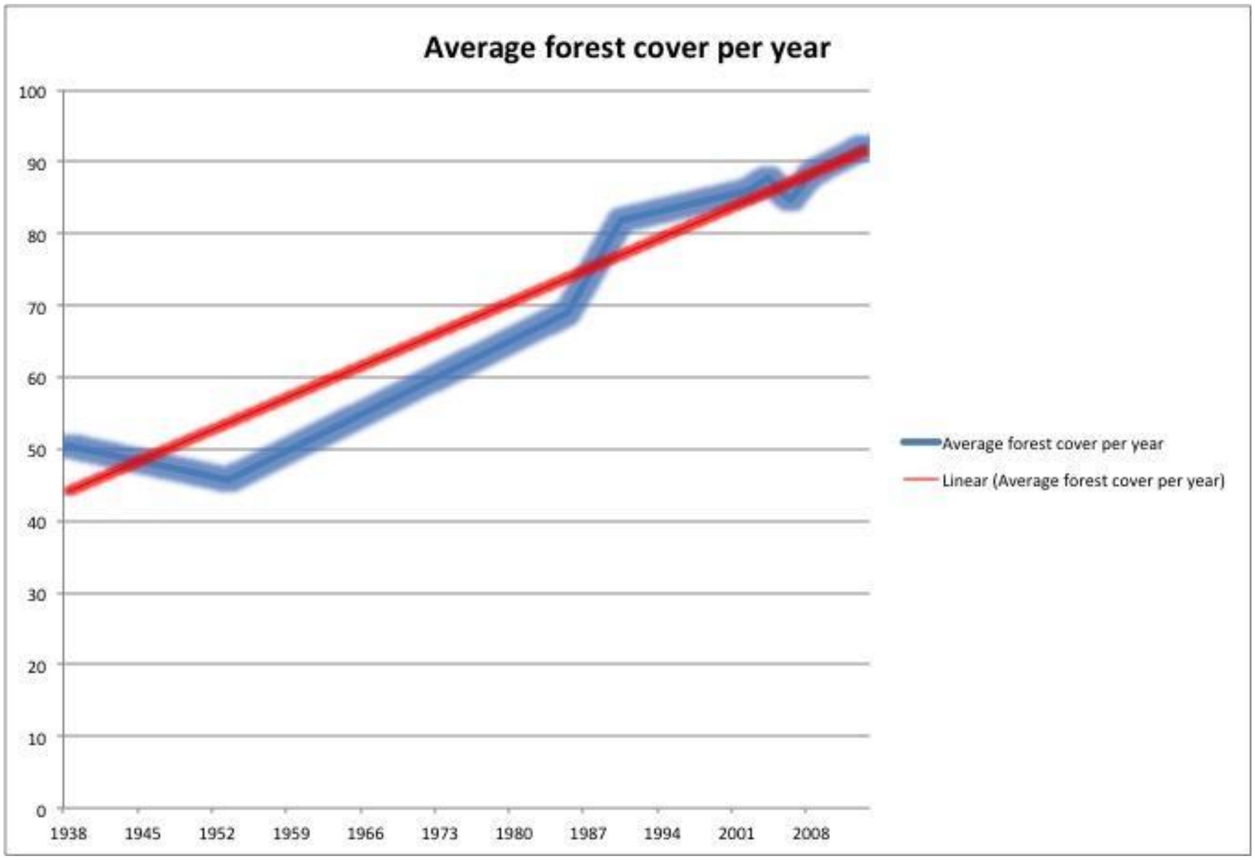
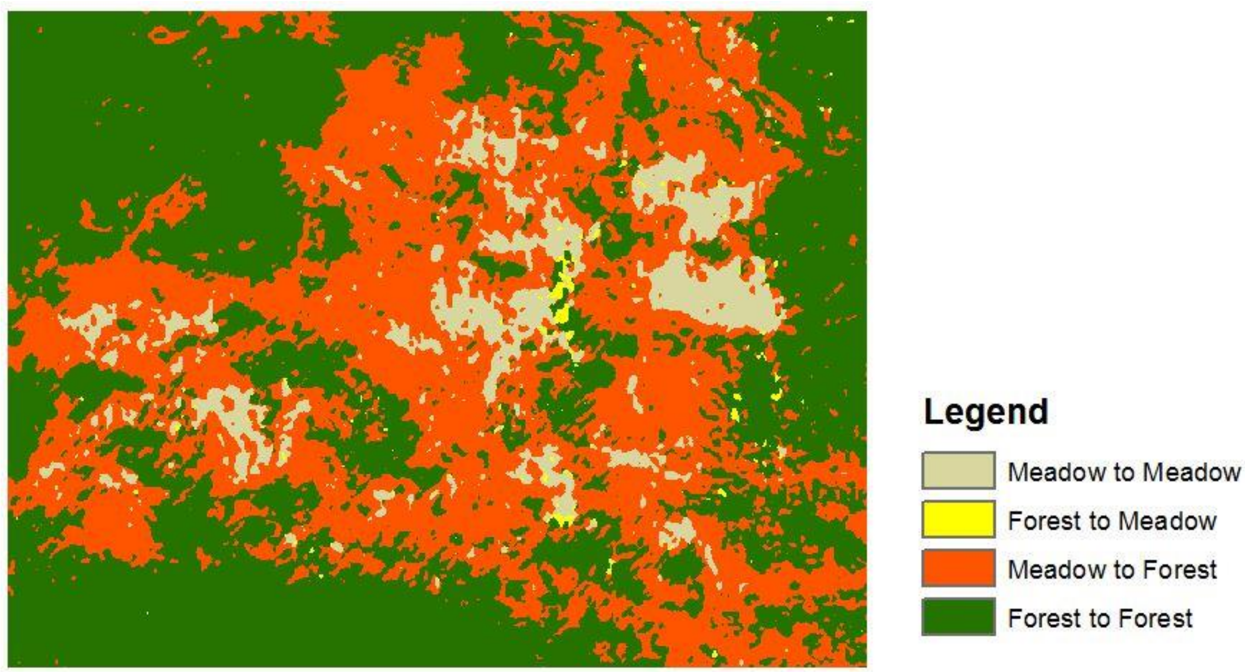


Figure 4: areas of stationary and of changing land cover class over the study period. Tan represents areas that were classified as meadow in 1938 and in 2013. Green represents areas that were classified as forest in 1938 and in 2013. Orange represents areas that were classified as meadow in 1938 and as forest in 2013. Yellow represents areas that were classified as forest in 1938 and meadow in 2013.



In order to look at the pattern of transition from forest to meadow, histograms were made for each image in the time series, showing the frequency of percent forest cover in each image. There are a total of 10 bins for each histogram, which are represented in increments of 10%, starting at 0% forest cover on the left to 100% forest cover on the right. Figure 5 and Figure 6 shows these trends for 1938 and 2013. Figure 7 shows this trend for every year in the analysis.

Figure 5: histogram of forest cover value for each 10 m x 10 m grid in 1938. The sum of all the bars is equal to 4408, which is the total number of grid cells in the image.

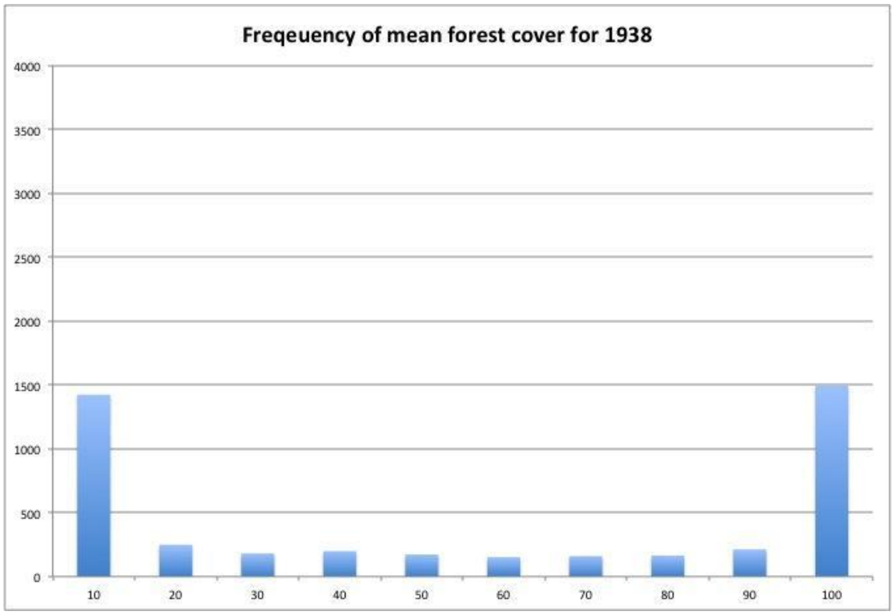


Figure 6: histogram of forest cover value for each 10 m x 10 m grid in 2013. The sum of all the bars is equal to 4408, which is the total number of grid cells in each image.

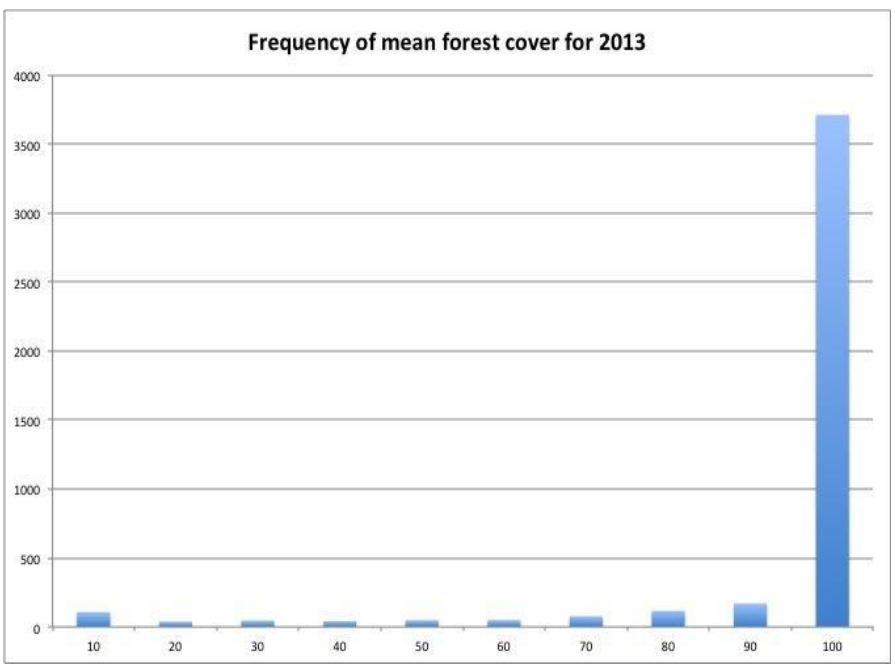


Figure 7: the shift from forest to meadow from 1938 to 2013, by summarizing the number of grids in the fishnet (y-axis), that are greater than 80% forest, in red, or less than 20% forest, in blue, over time (X-axis). Each point represents one year. Linear trend lines were also created to visualize the pattern over time.

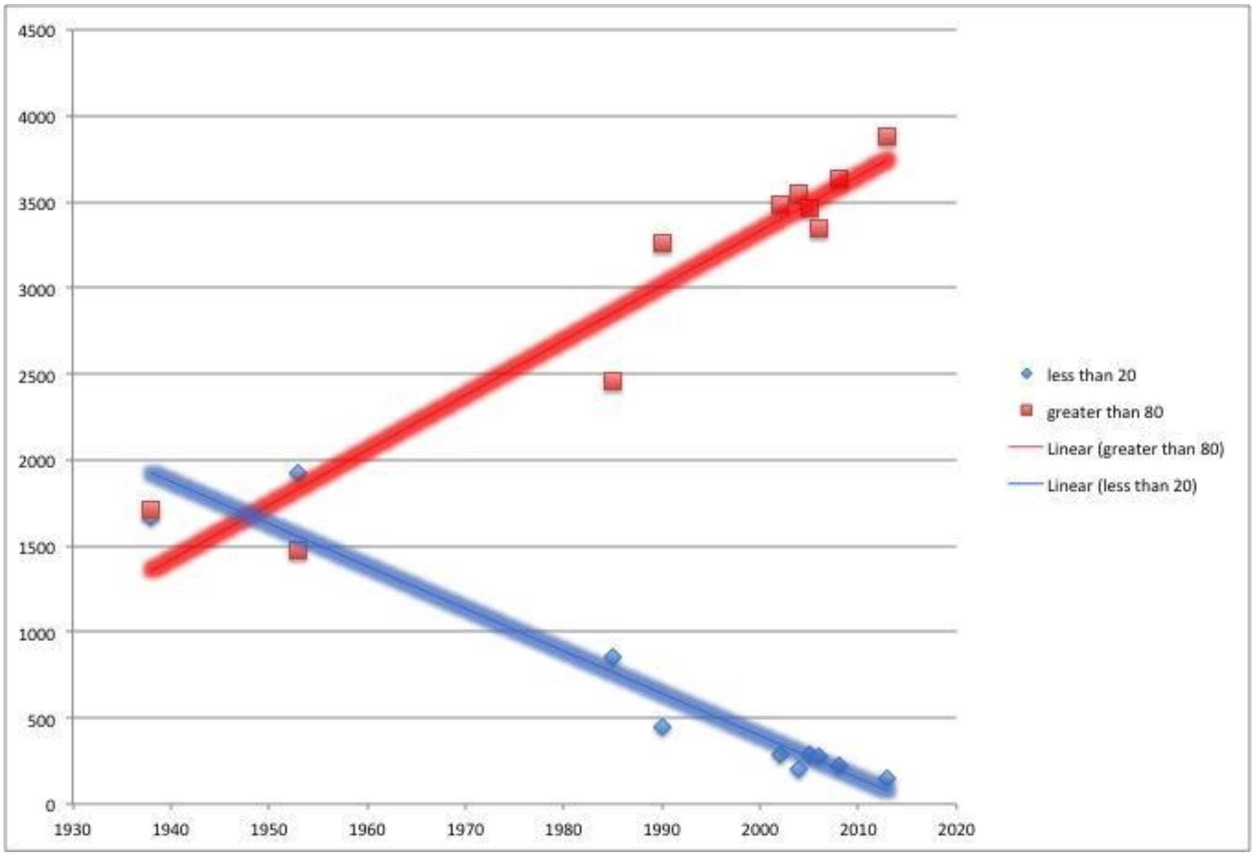
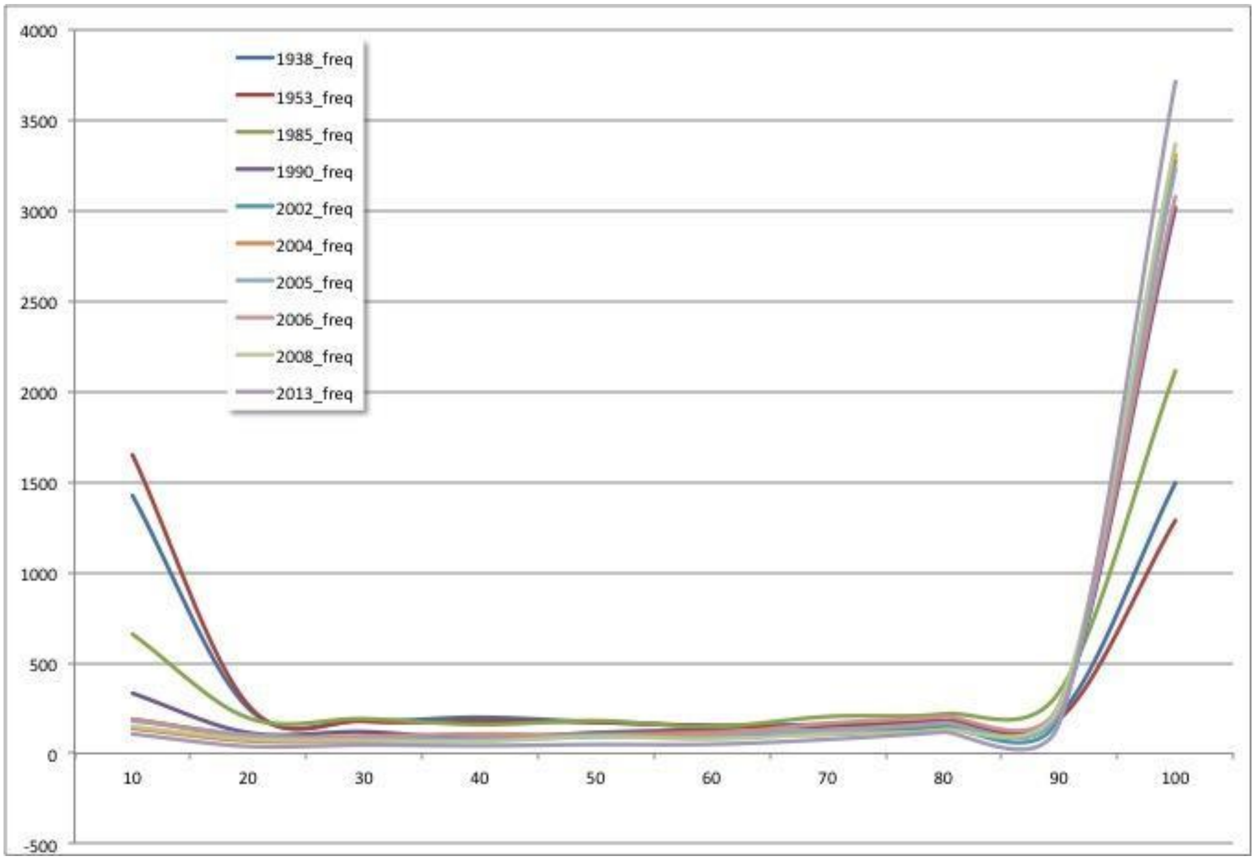


Figure 8: frequency of percent forest cover for every year in the time series that occur within a range of values in increments of 10 percent. The dark blue line corresponds to the year 1938 and the gray line corresponds to the year 2013.



Discussion

My results indicate that there was rapid encroachment of forests into meadows in the Upper Elk Meadows from 1938 to 2013. This rapid rate of forest encroachment is aided by the small size of Elk Meadow. In this region, montane meadows typically occur as small, isolated habitats with floras that are distinctly different from those of the surrounding forested landscape (Halpern et al., 2010; Franklin and Halpern, 1999). Thus, in small meadows, there is more forest edge relative to the size of the meadow opening, and the distance to seed-bearing trees is less than in larger meadows (Zier and Baker, 2006). Once the invasions are initiated, facilitation and positive feedbacks promote rapid conversion of meadow to forest, as seen in Elk Meadows (Halpern, 2010).

Figures 5-8 shows evidence of a pattern of tree encroachment into meadow from the ecotone edge. The histograms are evidence of the ecotone edge moving in because there is a very low fraction of the mixed neighborhoods (i.e., any value greater than 20% forest and less than 80% forest). This means that the increasing forest is spatially confined to meadow margins, for the most part so that there continues to be distinct habitats between forests and meadows. These patterns do not support the alternative hypothesis of a dynamically stable ecotone edge or the pattern of tree infilling. If there was a stable ecotone edge over time, we would not see this rapid increase in forest cover over time, particularly along the ecotone edge. If infilling were to occur at this site, I would have see an increasing number of mixed forest and meadow neighborhoods (i.e., any value greater than 20% forest and less than 80% forest). This would have resulted in patches of trees inside the meadows establishing randomly, which I did not observe.

Although there is ample data that shows forest encroachment into meadows is occurring across the United States (Platt 2009; Mast, 1997; Mast, 1998, etc.), there is a lack of consensus among ecologists for *why* this encroachment is occurring. The causes of encroachment have been considered from many diverse perspectives, including responses to changes in climate, land use, or disturbance regimes (Haugo and Halpern, 2007). Although I will examine each of these in turn, they are not mutually exclusive.

Changes in climate

Forest-meadow ecotones are extremely sensitive to changes in climate (Thompson, 2007). The Mountain Research Station's Long-Term Ecological Research (LTER) meteorological site (C1) located at 10,000 feet, which is the same elevation as Elk Meadows, documents that temperatures have been increasing over the last four decades, particularly in the spring (Barry, 1973). This trend of warmer weather results in wetter conditions that positively correlate with tree establishment. However, climate is unlikely to be the sole factor for forest encroachment.

Disturbance regimes

The historical trends of fire suppression across the United States in the last century have resulted in montane ecosystems experiencing long fire-free intervals. This has resulted in a change in forest stand structure, where forest stands are denser and more mature. Over time, this has also allowed forests boundaries to encroach into surrounding meadows. If this trend continues to occur across the Front Range as a whole, it will result in hundreds and thousands of contiguous acres of ponderosa and lodegepole pine in densely stocked, mature stand conditions.

Fire often maintains the open structure of grasslands; without fire, trees outcompete herbaceous vegetation.

Conclusion

The progressive advance of trees into meadows, as seen in Elk Meadows, is often attributed to changes in climate or disturbance regimes that alter the competitive balance between tree seedlings and herbaceous vegetation (Halpern, 2010). Although tree encroachment into grassland may be triggered by one or more of the three factors above, more proximally they may reflect changes in the strength or direction of biotic interactions that allow for successful establishment and growth of woody plants (Halpern, 2010). The recent encroachment of conifers into montane meadows may constitute one phase of a cyclical process that includes periods of forest expansion, retraction, or statis. However, this rapid conversion of meadow to forest, as seen in Elk Meadows, may signal a shift to an alternative stable state. Regardless of the causes of encroachment discussed above, it is important to maintain open meadow habitats, for both species biodiversity and other resource values. For example, a meadow opening will generate up to four or five times the herbaceous production and plant richness of the nearby forest interior (Moore and Huffman, 2004). The consequences of such dramatic landscape change have cascading effects on meadow populations leading to reduced overall species diversity and smaller individual species populations due to fragmentation and isolation (Haugo and Halpern, 2007). This has caused land managers to experiment with tree removal and prescribed fire in order to reverse this encroachment and the effects of it (Haugo and Halpern, 2007). These results are also of importance for anticipating the medium and long-term effects of climate change, and in particular how forest systems will recover after disturbances, and the impacts of land use change. Understanding the role of biotic interactions is critical to modeling future changes, and to maintaining or restoring the natural dynamics of these and other forest-grassland mosaics.

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