Junipers and Stand Dynamics in a Semi-Arid Grassland: Succession, Stand Initiation or Invasion?

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Introduction

Euro-American settlement has brought many changes to the arid southwest. Land uses such as grazing, water development and logging have had a substantial impact on the biological communities in the region. Riparian degradation, widespread soil erosion and forest compositional and structural changes receive much of the attention of the conservationist. Shrub encroachment into semi-arid grasslands is another critical conservation issue which until recently has received less attention.

Woody Encroachment into Semi-Arid Grasslands

Semi-arid grasslands on the Colorado Plateau are typically situated between pinyon-juniper woodlands at higher elevations and semi-arid scrub communities at lower elevations (Grahame and Sisk 2002). Historically, in semi-arid grasslands, junipers (*Juniperus* sp.) were excluded at higher elevations (Johnsen, 1962), while at lower elevations shrub species were kept at bay (Van Auken 2000). However, this all began to change shortly after the arrival of white settlers and their cattle.

Intense livestock grazing during Euro-American settlement had a profound impact on the natural fire regime in the southwest. The overstocking of both cattle and sheep in semi-arid grasslands eliminated the grass fuels required to carry low intensity wildfires (Grahame and Sisk 2002). Aldo Leopold first reported these changes in 1924. Leopold observed both pinyon and juniper trees and shrubs such as manzanita (*Arctostaphylos* sp.), snakeweed (*Gutierrezia* sp.) and sagebrush (*Artemisia* sp.) invading areas which were once grassland. He also noted the dramatic soil erosion associated with this change in cover type.

Later research found that this brush invasion was a continuing process. In the absence of fire, junipers and woody shrubs can out-compete grasses for soil moisture. In addition to fire regime alterations, grazing suppressed grasses, giving shrubs a competitive advantage. Furthermore, once the density of shrubs and trees reaches a certain level, the low fuel loads of these species effectively fireproofs the system, thus preventing reestablishment of grasslands by means of prescribed or natural fire. With fire unable to impact the system and return grass dominance, these ecosystems cross an ecological threshold, becoming increasingly shrub dominated and eventually the grassland is permanently replaced with scrubland or woodland (Fuhlendor et al 1996, Bock and Bock 1997).

As a result of this shrub encroachment, the total area of grassland habitat in the southwestern United States has significantly declined during the last 150 years (Kearney and Peebles, 1960; Lowe, 1964; Dick-Peddie, 1993; Brown, 1994). The increase in shrub and pinyon-juniper tree density across the Southwest has generally had a negative impact on other elements of semi-arid grasslands. Increased shading and competition for resources, most notably water, has lead to a dramatic reduction in grass and forbs diversity and abundance (Arnold, 1958;

Tausch and West, 1994). This loss of grassland habitat has had a significant negative impact on many grassland dependant species such as pronghorn antelope (Neff 1986, Bogan et al. 1998).

Wupatki National Monument: a Juniper Encroachment Case Study

Wupatki National Monument was established in 1924 to protect prehistoric pueblos. The monument encompasses approximately 14,000 hectares (35,000 acres). The western half of park (7,000 hectares or 17,000 acres) is a semi-arid grassland/juniper savanna habitat known as Antelope Prairie. The elevation within Antelope prairie varies, however the mean elevation of this part of the park is 1,675 m (5,500 ft).

The majority of Antelope Prairie is grassland or juniper savanna. This savanna condition is believed to be juniper encroachment resulting from the effects of cattle grazing associated with Euro-American settlement. However, within the grassland/savanna matrix there are isolated patches of juniper woodland. The juniper refugia populations are found on rocky slopes and outcroppings, sites which would be sheltered from the direct impacts of frequent, low intensity fires.

A study of packrat middens and juniper fire scars at Wupatki determined that the historic fire return interval was between 15 and 25 years. (Cinnamon 1988). However, the trees used in this study were on the edge of the grassland environment, and thus were likely exposed to fire less often than would a location within the grassland itself. Therefore, I feel that the actual fire return interval was likely more frequent than reported by Cinnamon. For the purposes of this paper, I will assume a return interval of 5-20 years for the grasslands community in Antelope Prairie.

Wupatki grasslands were impacted by Navajo sheep herding and Anglo cattle ranching as early as the 1860's. For the following 140 years grassland fires in Wupatki were rare and covered only a very small area. Cattle grazing was removed from Wupatki in 1989. Since then, the herbaceous plants in Antelope Prairie have been able to recover from grazing. As a result, approximately 1000 ha (2,600 acres) have burned in four fires in 1995, 2000 and 2002.

Despite the recent upsurge in fire activity, by the 1990's, as much as 1,200 hectares (3,000 acres, or 17%) of the Antelope Prairie area may have succeeded to juniper woodland. Several grassland-dependent vertebrates inhabit the Antelope Prairie, including pronghorn antelope, Gunnison's prairie dog, Burrowing Owl, Ferruginous Hawk, Golden Eagle, and Little-striped Whiptail Lizard. If the entire grassland biome succeeds to juniper woodland, several of these species may eventually be at risk of extirpation from the Monument. In addition, certain herbaceous plant species may also be at risk of local extirpation from the lack of fire disturbance and increased shading by juniper trees.

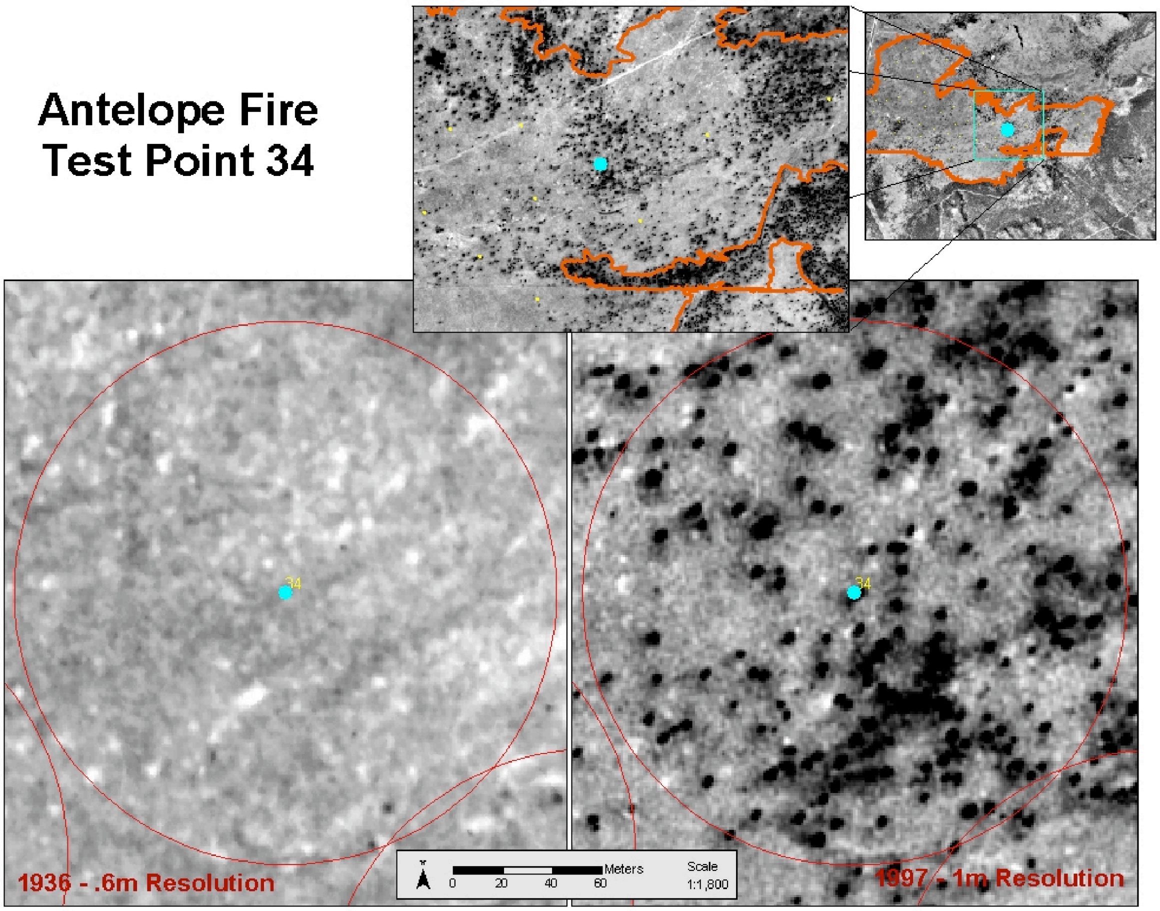

Figure 1: A single research spot as seen from aerial photographs in 1936 (left) and again in 1997 (right). The intensity of encroachment of junipers, which appear in these photos as black dots, is dramatic.

My Research Project

Objectives

As a result of concern regarding juniper encroachment into Antelope Prairie, a research project was developed. The purpose of this study is to assess 140 years of juniper cover and density increase via age/size distribution and stand structure at Wupatki National Monument and examine the pattern of increases in juniper cover relative to key ecosystem properties. Research questions include:

1) What are the age distribution patterns of junipers in Wupatki? Does stand initiation correspond to Euro-American settlement and fire exclusion? Are there peaks in reproduction during years of favorable climatic conditions? What is the rate of increase of juniper density?
2) Is there a correlation between tree age and tree size attributes? If so, are these correlations consistent across stands or is there variation in growth rates among stands?

3) Are there correlations between certain site factors such as elevation, soil type, latitude, land use history or vegetation cover predict juniper invasion, initiation, rate, and patterns?

Research Methods

The study area for this project includes both Wupatki National monument and a portion of the Coconino National Forest to the south of the monument. For the purposes of my research project, stands are defined as areas sharing the same bedrock (either base limestone or one of several basalt shelves) and having a fairly consistent elevation. Within Wupatki, we are limited to removing samples only from dead trees. Therefore, the only juniper stands we are able to study within the monument are savanna stands defined by the outline of several recent wildfires, which resulted in significant juniper mortality (see Map 1). There is no juniper mortality among refugia stands within the monument, hence, these stands cannot be sampled. For the portion of the study area on the Coconino National Forest there are no such restrictions, therefore stands encompass an entire basalt shelf.

A total of approximately 60 plots will be sampled over the course of this project. These plots will be randomly distributed within each stand. The number of plots per stand will vary according to the variability within each stand. A greater number of plots will be assigned to stands with a weaker age/size correlation and greater variance in mean tree age.

In juniper woodland stands, a plot will consist of a .238 ha circular sample area (diameter of 27.5 m) centered around a sample point. In stands considered to be juniper savanna or "grassland with scattered junipers", plots will consist of a 3.80 ha circular sample area (diameter of 110 m). Presampling has determined that there is an average of 6.3 trees/ha in savanna areas and approximately 96 trees/ha in wooded area. Therefore, this change in plot size is necessary to maintain a consistent sample size, and a consistent ratio of trees measured to samples taken per plot, across habitat types.

In each plot, one juniper tree from each of four arbitrary size classes based on height (0-1.5 m, 1.5-3.0 m, 3.0-4.5 m and 4.5 and greater) will be selected and cut with to remove cross sections for analysis. These cross sections will be aged using dendrochronological methods in the lab. In addition, we will be measuring tree heights, crown diameters (drip line), and diameter of the largest stem for all trees within the sample plot. By gathering this information we can correlate size class to tree age, allowing us to make inferences regarding the age distribution of the stand while removing a minimal number of trees. This method is necessary primarily due to the sampling restrictions within Wupatki National Monument requiring that only dead trees be sampled and that no more than 100 trees are cut within the monument.

The ages of all measured trees in each stand will be calculated using age/size correlations determined by the smaller number of trees sampled. Based on these results, rates and patterns of juniper savanna and woodland expansion will be examined. Each stand will be analyzed separately to determine establishment patterns and tree growth rates. Comparisons will be made between stands and stand information will also be pooled to determine if there are any landscape level patterns present. Additionally, we will use site attribute information acquired by previous studies and archival information to analyze juniper establishment patterns in comparison with herbaceous vegetation cover, soils type, cinder depth, elevation, and historic land use patterns. By examining the relationship of these factors to juniper establishment, we can develop a better understanding of which factors are useful predictors of juniper invasion patterns throughout the southwest.

Preliminary Results

By correlating tree size to age, we are able to estimate the age of all trees in the sample plots for each stand. This process has been completed using a limited set of initial data for several stands. These results are highly preliminary and have not been tested for significance using statistical scrutiny. An example of this age/size analysis can be seen in Figure 2 below.

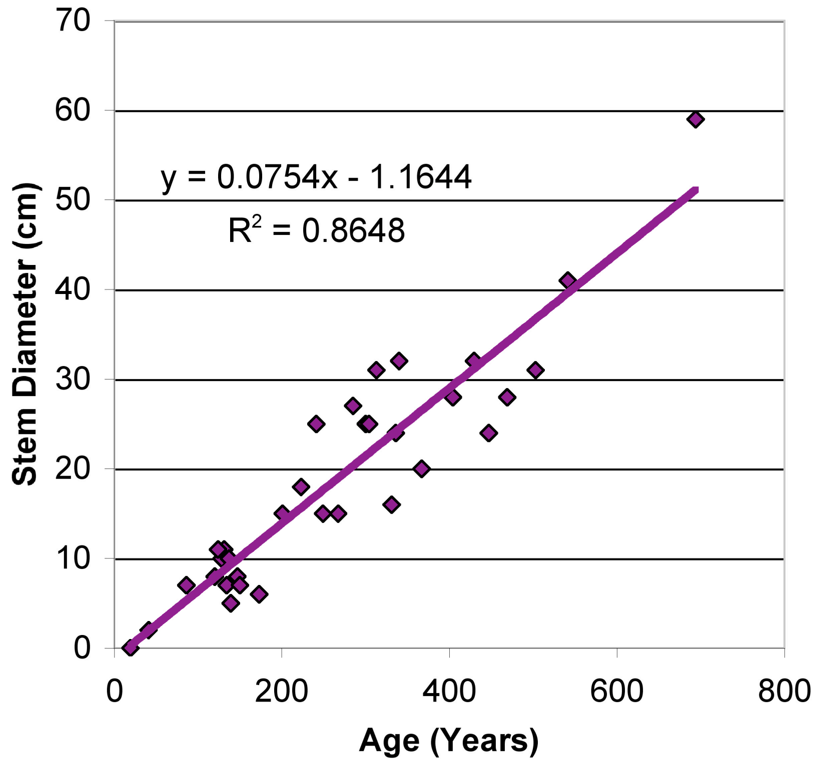

Figure 2: The correlation of stem diameter to tree age for the Antelope Prairie South stand. See Map 1 for stand location.

The results of these allometric projections are displayed on figures 3-5 below. Note distinctive difference in establishment patterns in the Antelope Prairie South stand which is a juniper woodland as compared to the Moon Fire and Antelope-State Fire stands which are juniper savanna environments. Judging by the broad bell shaped curve of the number of trees established per decade woodland encompassing the Antelope Prairie Stand has clearly been an establish woodland since well before Euro-American settlement. Indeed, the oldest trees in this stand date to shortly after the most recent eruption of Sunset Crater, which blanketed this area with volcanic cinder and ash. It is possible that these oldest trees represent the first trees to become established in the area after the Sunset Crater eruption.

The establishment of trees in these savanna stands is clearly quite recent, however the oldest trees predate the initiation of grazing impacts. This can be explained by viewing juniper encroachment as a continuing process. Young junipers are constantly sprouting in the grassland only to be removed by fire before they are able to become large and well established enough to survive a grass fire. However, once frequent fire was removed from the system, junipers which had sprouted before grazing impacts took effect were then able to continue their survival and become large, well established trees.

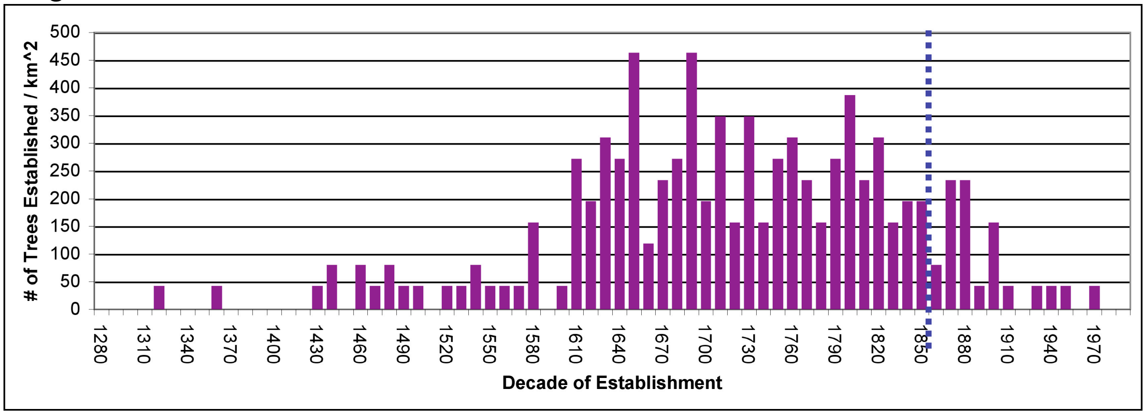

Figure 3: Juniper establishment by decade in the Antelope Prairie South stand. The dotted line represents the approximate date of initial impacts due to grazing.

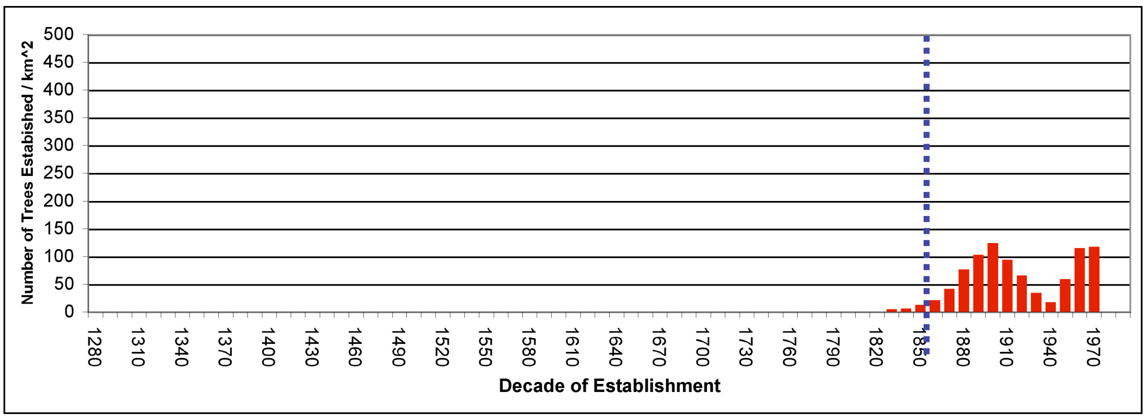

Figure 4: Juniper establishment by decade in theAntelope-State Fire stand. The dotted line represents the approximate date of initial impacts due to grazing.

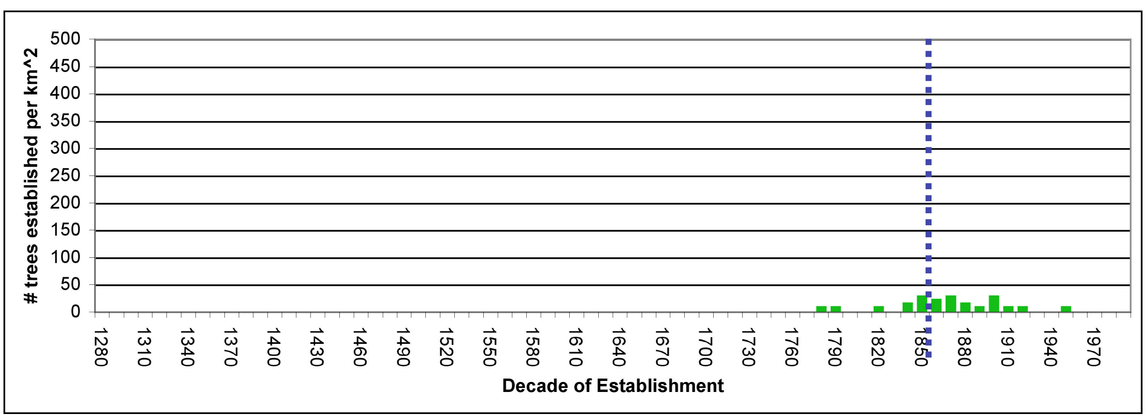

Figure 5: Juniper establishment by decade in the Moon Fire stand. The dotted line represents the approximate date of initial impacts due to grazing.

From these results it seems apparent that juniper encroachment into the Antelope Prairie at Wupatki National Monument is a direct result of human impacts. However, it is equally clear that we should use caution when distinguishing between grasslands which have been impacted by fire suppression and suffered species compositional changes as a result, and a juniper woodlands which are well established and appear to not have been effected much at all by 140 years of cattle grazing. Though prescribed fire and juniper thinning may be appropriate within the juniper savannas within Wupatki, removal of junipers in woodland stands would simply be yet another human impact on a community which is remarkable in the fact that it has been effected little (at least as far as juniper establishment is concerned).

Modeling Encroachment

Due to time and experience limitations results of a modeling exercise will not be included in this draft of my Forest Stand Dynamics paper. Modeling will consist of simple spreadsheet equations utilizing recruitment and mortality rate data from the stands included in this study to project how these stands might develop into the future under several sets of circumstances. These circumstances will include a continued suppression of fire, reinitiating of a natural fire regime and aggressive prescribed fire. Other variables such as climate may also be included in this model, assuming this information appears to be relevant.

What Process is Encroachment?

Now that we have an understanding of the encroachment process at Wupatki, we can analyze this trend. I have chosen to discuss juniper encroachment within the framework of several common ecological models. Is juniper encroachment succession, stand initiation or invasion?

Succession

Succession is one of the founding concepts of ecology. It has been studied in one form or another for hundreds of years, but was finally synthesized by F. E. Clements in 1916. Simply put, "Succession is a directional, cumulative change in the species composition of vegetation at one location over the course of [time]" (Barbour et. al. 1987).

It is stated that the community changes by passing through "seral" communities until a "climax" community is reached. For example, after a disturbance, pioneering, "weedy" species inhabit a site. These early succession species perform services such as soil stabilization which then allow other species to colonize the site. "Late succession" species then continue this process of site alteration and they are in turn replaced by long-lived "climax" species. A list of ecosystem traits which change as succession progresses is included below. These climax species form a stable climax community which then persists until the next disturbance event. (Barbour et. al. 1987).

Table 11-3 Some vegetation and ecosystem traits that often change during progressive succession. The status of each trait is shown for early and late stages of succession (*not* for pioneer and climax stages necessarily, for some trends peak at intermediate seral stages). Each trend is briefly discussed in the text.

Trait	Early stages	Late stages
Biomass	Small	Large
Physiognomy	Simple	Complex
Leaf orientation	Multilayered	Monolayered
Major site of nutrient storage	Soil	Biomass
Role of detritus	Minor	Important
Mineral cycles	Open (leaky), rapid transfer	Closed (tight), slow transfer
Net primary production	High	Low
Site quality	Extreme	Mesic
Importance of the macroenvironment	Great	Moderated and dampened; less
Stability (absence or slowness of change)	Low	High
Plant species diversity	Low	High
Species life-history character	*r*	*K*
Propagule dispersal vector	Wind	Animals
Propagule longevity	Long	Short

Table 1: Reproduced from Barbour et. al 1987

Upon scrutiny, it has been found that succession is too simple a model to accurately represent the trend seen over time within biological communities. For example, some communities such as those found in the Sonoran desert do not experience changes in species composition after disturbances. Other communities, such as tallgrass prairies and ponderosa pine woodlands never reach a classic "climax" community due to frequent disturbances associated with the historical fire regime in these systems. Finally, the broadest criticism of succession is that it promotes the concept of a biological community as a "superorganism". This concept consists of the view that succession is a directional process, with all components of the system working together in a sort of mutualistic relationship to develop a pristine climax community.

Despite these drawbacks, succession is still a useful model for describing natural processes as exhibited by the ubiquitous use of related terms throughout ecological dialogue. Criticism of succession has also lead to refinements in the successional model. For example, there are now three offshoots of the successional: facilitation, tolerance and inhibition.

Facilitation, also know as relay floristics, is a refinement of the traditional model of succession. Early successional species alter site conditions to the benefit of later successional forms. Tolerance, also known as initial floristics, is the idea that all species, from pioneers to climax species, are present on a site throughout the successional process. Weedy species simply compete best immediately after disturbance and thus are more dominant at that time. Late successional species are also always present, but aren't common and don't express dominance until time and stability provide them with a competitive advantage. Inhibition refers to circumstances in which initial species inhibit others and don't relinquish control of a site until they are damaged or destroyed, in effect, quite the opposite of what is traditionally viewed as succession.

These refinements are important enhancements of succession which allow for a broader range of ecological interaction to be described. However, perhaps the single most important revelation for succession is the concept that multiple successional pathways may lead to alternate climax communities. Simply put, there is not a single climax that a community is inherently driven towards. Instead, there are multiple possible outcomes of succession. These outcomes can be reached by multiple pathways depending on conditions and events that occur over the course of the succession process, and the resulting community interactions.

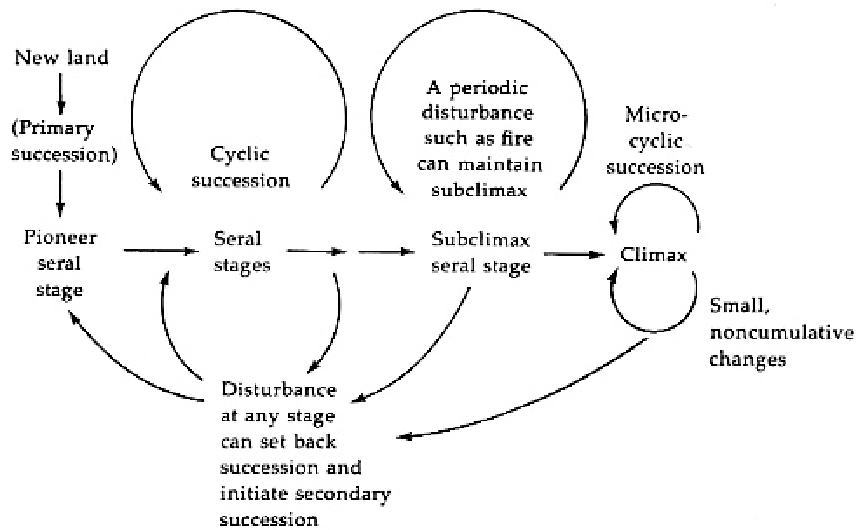

Figure 11-2 Diagrammatic pathway of different types of succession: primary, secondary, and cyclic. The climax stage is in a state of dynamic equilibrium.

Figure 6: Reproduced from Barbour et. al 1987

If we view juniper encroachment in the framing of the traditional succession approach, we can consider the semi-arid grassland to be a sub-climax community maintained by fire. With this mindset, fire cessation allows the community to begin moving towards the climax community, in this case, pinyon-juniper woodland, as seen in Figure 7. It would then take a stand replacing fire to act as a disturbance and return the community to an early successional state. However, this view of a pinyon-juniper woodland as a climax community requires us to accept that human caused changes are, at least in some cases, an important part of the succession process.

However, it seems somewhat false to consider the dominant, pre-settlement community condition as simply a sub-climax community. Could we instead consider the grassland as the climax community? In this mindset we can imagine that fire maintains the stability of the grassland in its climax condition and prevents further change to the system. This line of thinking requires us recognize fire not as a disturbance, but as a regular and integral process within the community. Indeed, in this community, the *absence* of fire is a disturbance.

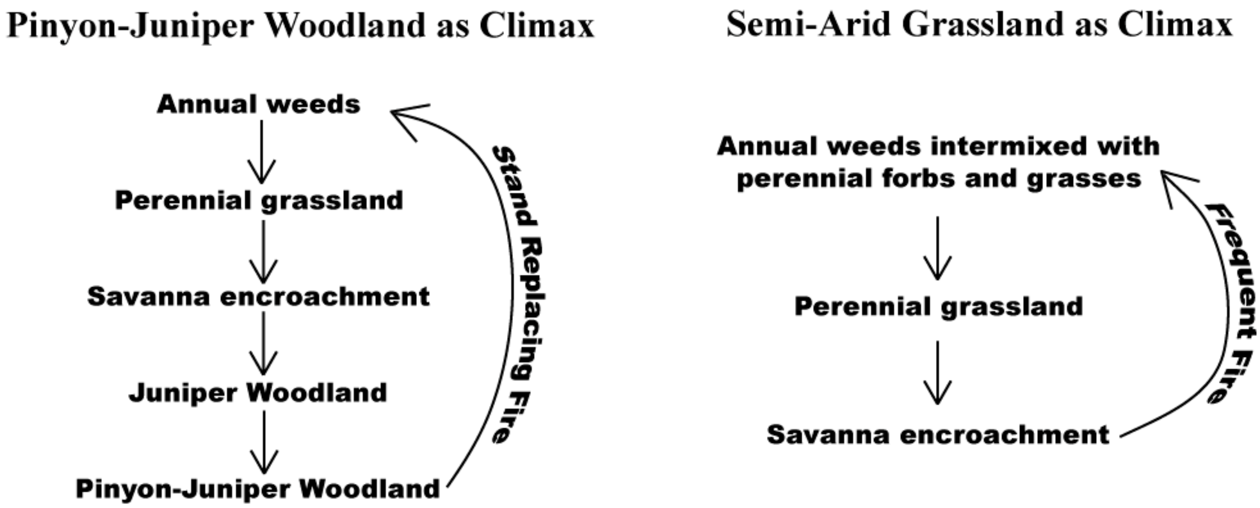

Figure 7: Two models of succession in juniper encroached systems.

It seems apparent that the pinyon-juniper climax model is applicable to many woodlands in the southwest. However, it is arguable that the pinyon-juniper woodland is the climax community at Wupatki, for as long as the historic fire regime is not altered, grassland is the community that will ultimately be achieved following disturbance. The pinyon-juniper climax requires human intervention to alter natural processes to redirect the successional trajectory of this community, and therefore is an inappropriate model with which to view this situation. Instead, we must view succession in the grasslands as a more short term process in which grasses dominate in the climax condition or accept the fact that this community never reaches a climax condition in the traditional sense. If perennial grassland is a "sub-climax seral stage", then we must accept that there are some cases in which, under natural conditions, a community never reaches true climax. Therefore it may be inappropriate to apply the concept of succession in semi-arid grasslands, and many other communities which experience periodic disturbances such as fire.

Stand Dynamics: Stand Initiation

Stand initiation is a fairly simple process to understand. A major disturbance kills all or most of the mature trees in a stand. Reproductive materials such as seeds and stems capable of resprouting are left behind. These propegules then begin to grow and develop into a new stand.

I will not provide a complete summation of stand initiation here, but will instead highlight a few facts which I believe are relevant to juniper encroachment. First, trees are small compared to their environment during the early part of stand initiation and thus are more affected by their environment than adult trees. Therefore, these young trees are more susceptible to desiccation due to heat as well as mortality due to fire. New individuals continue to appear for several years after initial initiation because growing space is still available up until the very end of stand initiation, when stem exclusion begins. The stand environment changes rapidly as these trees grow and dominate the site.

In general, stand dynamics is a robust model and stand initiation can be successfully applied to many situations, including some which do not include tree establishment. Still, stand dynamics does not do an adequate job of describing patterns in some communities, specifically those with high frequency/low intensity disturbance regimes. Ponderosa pine woodlands are a good example of such a regime and it appears semi-arid grasslands may be another.

There are a few changes in perspective necessary when applying stand dynamics to juniper encroachment. For example, instead of stems growing quickly upward, junipers concentrate growth in roots growing outward. High root density is necessary to extract moisture and nutrients from arid, often nutrient poor soils. These roots can have a radius three times that of the crown radius. As a result junipers are typically fairly widely spaced. It is the closure of the “root canopy” which effectively puts an end to the stand initiation phase. Not only does a closed “root canopy” prevent new trees from entering the stand, it also has the effect of greatly reducing the herbaceous ground cover. Stem exclusion is then achieved primarily through attrition where isolated infrequent disturbances such as lightning strikes and insect attacks are the most common cause of death.

Pinyons eventually enter the stand underneath larger juniper nurse trees. They preferentially become established underneath well established junipers with a deep layer of accumulated duff. It is therefore difficult to define pinyons’ role in stand dynamics. Is the influx of pinyons the beginning of the understory reinitiation phase? The association of pinyons with large, old trees and heterogeneous stand conditions would seem to be an attribute of an old-growth obligate species. Yet old-growth will not be achieved until all trees from the stand initiation have been replaced by younger individuals. In the case of a long-lived tree like *Juniperus monosperma*, true old-growth may take over a millennium to achieve.

Clearly, stand dynamics can only be roughly applied to juniper encroachment. We might say that stands initiate after infrequent stand replacing woodland fires. For a while, the stand initiation phase may be put on hold due to frequent low intensity fires setting juniper encroachment back to the initial initiation. In time, either by chance or human caused disturbance, the junipers out-compete the flammable grasses and stand initiation continues. Stand dynamics continue from there until the next catastrophic fire, which has a return interval of perhaps 300-1000 years. For example, in the pinyon-juniper woodlands at Mesa Verde National Park, Romme et al. calculated a mean fire return interval of 400 years (2003).

However, we may also consider the grassland itself in the context of stand dynamics. These stands of grasses and forbs initiate after frequent “low” intensity fires. Some plants are removed by these fires, but survivors reestablish themselves and new propagules quickly recolonize until all available growing space is full. These stands would have a very short life span, ranging from 15-30 years between frequent fires, therefore they may or may note achieve the equivalence of the understory reinitiation and old-growth phases.

Invasion

Biological invasion is the process of a species becoming successfully established outside of its native range. Meffe et. al. considers the exotic status of a species to be a fundamental component of a biological invasion. However, not all exotic species are capable of successfully invading new habitats. Successful invaders are often adept at competing well in human altered environments. In some cases invasive species are capable of altering the physical and biological components of the invaded community to further promote their dominance and permanently alter sucessional trajectories. (D’Antonio and Meyerson 2002). The table below summarizes additional characteristics of invasive species and characteristics of communities which are susceptible to invasion.

Table 8.2
Some Generalized Characteristics of Invasive Species and Invadable Communities

Characteristics of successful invaders
High reproductive rate, pioneer species, short generation time
Long-lived
High dispersal rates
Single-parent reproduction (i.e., gravid or pregnant female can colonize)
Vegetative or clonal reproduction
High genetic variability
Phenotypically plastic
Broad native range
Habitat generalist
Broad diet (polyphagous)
Human commensal
Characteristics of invadable communities
Climatically matched with original habitat of invader
Early successional
Low diversity of native species
Absence of predators on invading species
Absence of native species morphologically or ecologically similar to invader
Absence of predators or grazers in evolutionary history ("naive" prey)
Absence of fire in evolutionary history
Low-connectance food web
Anthropogenically disturbed
Characteristics of communities likely to exhibit large invasion effects
Simple communities
Anthropogenically disturbed communities

Modified from Lodge 1993.
Note: The list is not exhaustive, nor is every characteristic critical in a given situation. These are merely generalized trends, with many exceptions.

Table 2: Reproduced from Meffe et. al

Biological invasion is not an abstract process like succession and stand initiation, but instead is a descriptor of an ecological process. Therefore, it cannot fail to describe occurrences in nature as succession and stand initiation might. However, it may fail to be the best description of juniper encroachment.

The biggest hurdle to applying the concept of biological invasion to the process of juniper encroachment is that juniper is not strictly speaking an exotic species. *Juniperus monosperma* is a common native in the southwest, and in the greater Wupatki landscape matrix. Pre-settlement junipers are not only found in the woodlands to the south of Wupatki, but also interspersed within the grassland community on isolated rocky outcroppings and slopes where they were presumably sheltered from frequent fires (Van Auken 2000, West 1984). However, one may argue that these junipers are locally exotic, alien to the grassland habitat itself. With this perspective, we can examine the ways in which junipers fit the invasion model.

One-seed junipers are not particularly fast growing nor do they reproduce quickly. It takes several years for junipers to reach sexual maturity. However, they are a long-lived, with lifespans approaching 1,000 years (personal observation) and once they do reach maturity, they produce large amounts of seed (Chambers et al. 1999). Though they aren't excessively common or particularly persistent in the seed bank, their perseverance within the landscape matrix allows for quick invasion of grasslands when conditions permit. At Wuptaki and throughout the Southwest, junipers are expanding their populations by taking advantage of human caused disturbances, namely the fire suppression and reduced competition from grasses, a direct result of cattle grazing. Junipers are strong competitors for nutrients and moisture and sequester these resources within their tissue and the soil surrounding the plant (Teidman, 1987). Junipers alter the patterns of nutrient distribution on the soil, leaving few resources available for herbaceous species persistence in the inter-space between the trees (Wilcox & Davenport 1995).

Junipers may not fit the invasion model perfectly. They are native to the landscape, if not the grasslands they invade. They do not display a number of characteristics often associated with invasive species. However, based on the causes and effects of juniper encroachment, I believe this process is very much a biological invasion.

Synthesis

Clearly, when in the right mindset one can view juniper encroachment as an example of any one of these models. Either the rules that define the model can be adjusted to match encroachment, or encroachment can be viewed from a skewed vantage point thus allowing it to fit within the models parameters. What's important is that none of these models fits encroachment precisely.

Obviously, one cannot expect a general concept such as succession or stand initiation to perfectly define all possible community development trajectories. However, it seems that there are serious shortcomings to these models when applied to these semi-arid environments. Furthermore, these faults also expose the fact there are other communities for which these models are inappropriate descriptors. Stand dynamics and succession were created in reference to robust, largely unaltered natural systems, and are broad enough to describe communities which are greatly altered by human impacts.

I believe the key factor in this situation is the alteration of this fragile community as a result of cattle grazing. This human induced impact has far reaching effects on the delicate dynamics of these unique grasslands. These impacts have created artificial forces in this community which cannot easily be accounted for by traditional methods.

All that being said, I believe that invasion is the best model under which to interpret encroachment. If we ignore the fact that *Juniperus monsperma* is not strictly exotic, we find that this species possesses many of the attributes of a successful invader. The fragility of the semi-arid grassland at Wupatki resulted in human impacts which drove junipers into a zone where they became by default successful invaders. It is interesting to note that through indirect means human impacts were able to so greatly alter a species role in an ecosystem. It is a lesson we should learn well to avoid potential ecological calamity in the future.

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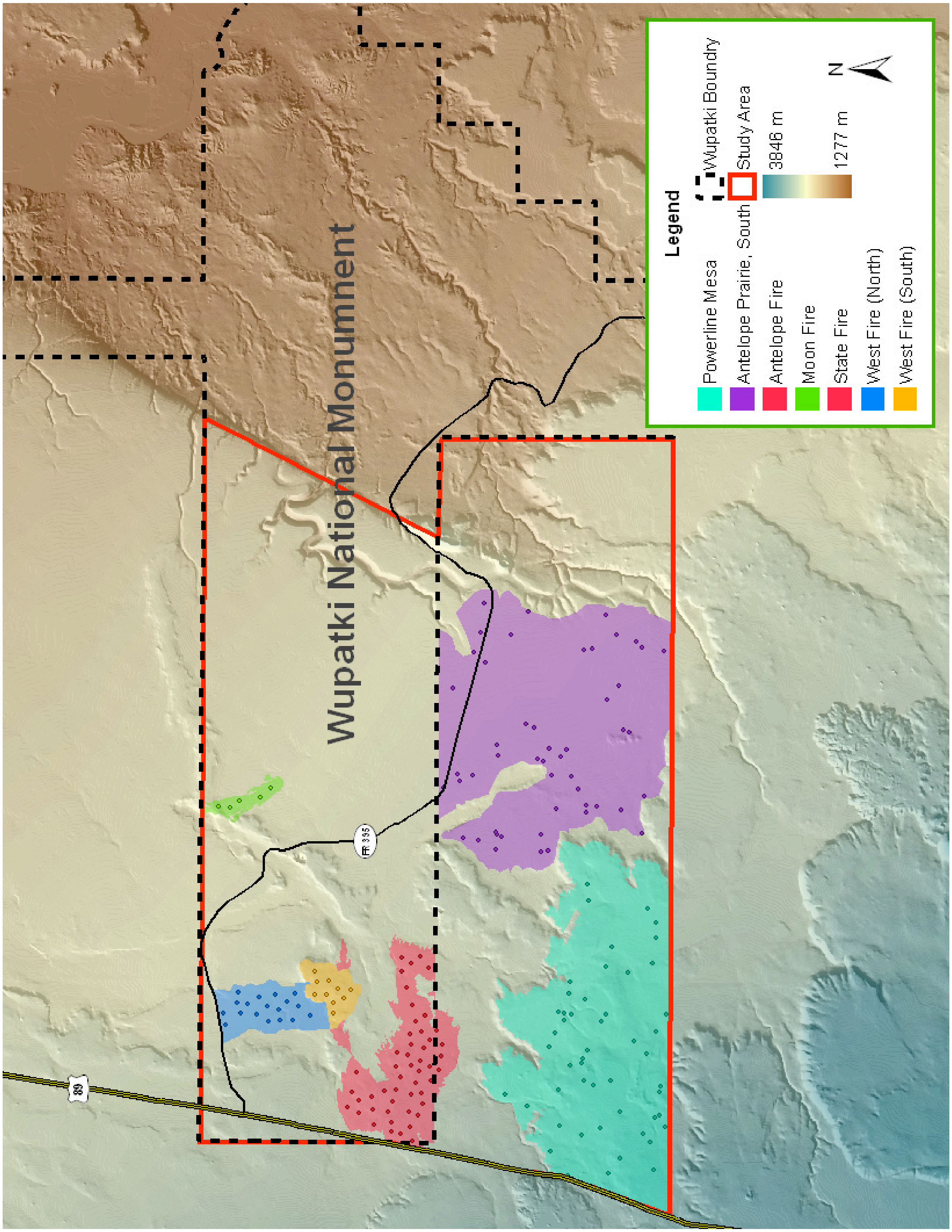
Wupatki National Monument
Legend
Powerline Mesa
Antelope Prairie, South
Antelope Fire
Moon Fire
State Fire
West Fire (North)
West Fire (South)
Wupatki Boundry
Study Area
3846 m
1277 m
N