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# Exploring A Stable Aspen Niche Within Aspen-Conifer Forests of Utah

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# EXPLORING A STABLE ASPEN NICHE WITHIN ASPEN-CONIFER FORESTS OF UTAH

by

Cody M. Mittanck

A thesis submitted in partial fulfillment
of the requirement for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

| | |
|---|---|
| Ronald J. Ryel<br>Major Professor | Paul C. Rogers<br>Committee Member |
| R. Douglas Ramsey<br>Committee Member | Mark R. McLellan<br>Vice President for Research and Dean of the School of Graduate Studies |

UTAH STATE UNIVERSITY
Logan, Utah

2012

# ABSTRACT

## Exploring a Stable Aspen Niche Within Aspen-Conifer Forests of Utah

by

Cody M. Mittanck, Master of Science

Utah State University, 2012

Major Professor: Dr. Ronald J. Ryel
Department: Wildland Resources

Quaking aspen (*Populus tremuloides Michx.*) is the most widespread broadleaf tree species of North America. Increasing evidence shows that aspen has diverging ecological roles across its range as both "seral" and "stable" aspen community types. This leads us to believe that the successional pathway of aspen may not always lead to a climax conifer sere, but may in some cases consist of persisting stands of pure aspen. This study is an attempt to understand the relationship of aspen community types to climatic, physical, and biophysical variables by modeling patterns of aspen and conifer distribution using remote sensing and GIS technology. Study methodologies and results were specifically designed to aid land managers in identifying extent and status of aspen populations as well as prioritizing aspen restoration projects. Four study sites were chosen in order to capture the geographic and climatic range of aspen. Photointerpretation of NAIP color infrared imagery and linear unmixing of Landsat Thematic Mapper imagery were used to classify dominant forest cover. A Kappa analysis indicates photointerpretation methods to be more accurate (Khat=92.07%, N=85) than linear unmixing (Khat=51.05%, N=85). At each plot, variables were calculated and derived from DAYMET data, digital elevation models, and soil surveys, then assessed for precision and ability to model aspen and conifer distributions. A generalized linear model and discriminant analysis were used to assess habitat overlap between aspen and conifer and to predict areas where “stable” aspen communities are likely to occur. Results do not provide definitive evidence for a “stable” aspen niche. However, the model indicates 60 to 90 cm of total annual precipitation and topographic positions receiving greater than 4,500 Wh m$^{-2}$ d$^{-1}$ of solar radiation have a higher potential for “stable” aspen communities. Model predictions were depicted spatially within GIS as probability of conifer encroachment. In addition, prediction-conditioned fallout rates and receiver operating characteristic curves were used to partition the continuous model output. Categorical maps were then produced for each study site delineating potential “stable” and “seral” aspen community types using an overlay analysis with landcover maps of aspen-conifer forests.

(143 pages)

# PUBLIC ABSTRACT

## Exploring a Stable Aspen Niche Within Aspen-Conifer Forests of Utah

by

Cody Mittanck, Master of Science

This study addresses a critical issue faced by resource managers confronting aspen restoration projects in the Intermountain West. Quaking aspen (*Populus tremuloides Michx.*) forests have received a large amount of popular and academic attention over the last decade due to concerns over decline. As a result, both private and public forest resource managers have focused attention on actively restoring aspen communities through treatments such as prescribed burning, logging, and grazing exclosures to name a few. There is increasing evidence suggesting the existence of "stable" aspen communities. This community type undergoes processes entirely different from successional aspen communities and therefore may require entirely different restoration treatments. Classifying "stable" aspen communities has traditionally been done in the field according to community composition. However, there is evidence that suggests "stable" aspen communities may be related to biophysical variables that can be attained through remote sensing and GIS methods. This suggests the potential for a habitat modeling approach to classify "stable" and "seral" aspen communities, providing an extremely useful tool for planning aspen restoration projects across landscape scales. This study aims to produce such a model.

# DEDICATION

This work would never have been possible without the inexorable patience, belief, and support of my partner, Lindsey.  And to my parents for providing everything I needed in life to be successful.

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I am appreciative for the thoughtful reviews of drafts from Dr. Paul Rogers, Dr. Doug Ramsey, Dr. Dale Bartos, and Dr. Helga Van Miegroet, as well as the integral role you have all played in advising and guiding this project towards completion. To my major professor, Dr. Ron Ryel, I am extremely thankful for the opportunity. Your tireless efforts and dedication to my education, even while facing the most difficult times of your own life, will never be forgotten.

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There are many others that provided support. Karen Mock and Josh Leffler were always there to bounce ideas off of. My friends and colleagues that I shared classes and offices with throughout the project provided advice countless times. Thank you all.

Cody Mittanck

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# CHAPTER 1

# INTRODUCTION

Quaking aspen (*Populus tremuloides Michx.)* is the most widespread broadleaf tree species of North America (Little, 1971) ranging from the Boreal Forests of Northern Canada to the mountains of Mexico. In the Intermountain West aspen often co-occurs with conifer in mixed stands as well as in adjacent pure communities (Mueggler, 1988). Despite these observations, aspen is widely assumed to be seral to conifer species throughout much of this landscape (Baker, 1918, 1925; Bartos et al., 1983). Traditional views of aspen-to-conifer successional pathways describe aspen requiring disturbance, whereas it dominates the site for a period of 40-80 years, but eventually succumbs to encroaching conifer species (Debyle et al., 1985). Though this pattern has been observed across the landscape and is well documented in the literature, many studies suggest the existence of aspen communities operating outside of this deterministic successional pathway (Langenheim, 1962; Betters and Woods, 1981; Mueggler, 1988; Romme et al., 2000; Shepperd et al., 2006; Rogers et al., 2010). Such studies suggest that we have both “seral” and “stable” aspen types on the landscape. While these studies have documented aspen communities that remain free of conifer encroachment, the environmental factors describing this niche space have not been thoroughly explored on a landscape scale. With aspen cover potentially decreasing (Bartos and Campbell, 1998), there is an immediate need to characterize seral and stable aspen sites in order to prioritize aspen treatment projects.

## 1.1 Study Background

This study stems from an observation of aspen and conifer forests at the Deseret study site which was first brought to my attention by my advisor, Dr. Ron Ryel. This observation was that aspen and conifer's geographic distributions seem to follow non-random patterns across the landscape. In particular, the distributions seem to follow patterns relating to topographic position, where conifer species seem to dominate steep north-facing slopes, and aspen dominate gently sloping plateau tops and moderately steep south slopes, while mixed aspen/conifer stands inhabit the transition from plateau to steep north-facing slopes. This observation suggested that conifer encroachment may be related to biophysical variables and raised the question as to whether stable aspen communities exhibit a niche space that can be defined by these variables. I created a conceptual model to explore this question further and to provide a framework to form a research hypothesis (Fig. 1.1).

The conceptual model shown in Figure 1.1, defines a stable aspen community by its separation from the deterministic successional processes involved in seral aspen communities. We would expect the processes within these two communities to be different. For example, in stable aspen communities fire may not play a primary role in regeneration as it does in seral stands. Stable aspen, consisting of a compositionally pure aspen overstory, is not considered to be a flammable forest type (Debyle et al., 1985; Fechner and Barrows, 1976). In place of stand-replacing disturbance through severe and frequent fire, stable aspen has been shown to sufficiently regenerate via gap dynamics and episodic suckering (Kurzel et al., 2007). This self-regeneration leads to multiple aspen age-cohorts within the stand structure, which is often observed in pure aspen communities (Mueggler, 1988).

However, self-regeneration may not ultimately indicate a stable aspen community at a particular site; instead, using a logical definition, the persistence of a stable aspen community hinges on its ability to remain free of conifer encroachment. Ecological mechanisms that maintain a stable aspen community may be as simple as conifer seed dispersal limitations. Conifer seeds are primarily wind-borne with nearly 50% of the seeds falling within 30 meters of the parent tree, the directions determined by prevailing winds and thermals moving up slopes (Noble, 1978). Due to distance or geographic barriers, stable aspen stands may remain un-encroached for lack of conifer "seed-rain." For those pure aspen stands that abut mature seed-producing conifer forests, understory characteristics may help to explain inhibition of conifer establishment at both the germination and seedling stages of development. Pure aspen stands have been shown to have productive herbaceous understory communities (Mueggler, 1988), in combination with the aspen overstory, this results in thick litter layers that may prevent contact of conifer seeds with the preferred mineral soil seedbed (Coates et al., 1991). Other potential mechanisms that may be responsible for preventing conifer encroachment may involve generally poor performance of conifer species within the soil, light, and temperature environments that are conducive for aspen growth. In this case, while we may see very sparse conifer in the overstory it never reaches the required percentage of canopy cover that would promote stand-replacing fires. This case also points to the importance of the rate of conifer encroachment influencing our definition of stable aspen communities. While some aspen stands never reach enough conifer canopy cover to allow-stand replacing fire and/or conversion to a pure conifer community, others may eventually reach this point over timescales along the lines of hundreds to thousands of years. For management intents and purposes, these stands are often classified as stable aspen communities (Mueggler, 1988).

It is difficult to design experiments around mechanisms that prevent conifer encroachment and can even be difficult to target them with well-designed sample surveys. However, some studies suggest that it may be possible to indirectly account for these mechanisms by using biophysical variables that define distinct environmental conditions. On the Owyhee Plateau in southwestern Idaho, Strand et al., (2009b) found that 14% of their pure aspen plots occupied south-facing slopes above 1900 m. Over a 30-year period, Crawford et al. (1998, p. 201) did not notice any appreciable conifer encroachment into pure aspen stands in a study performed in the montane and subalpine forests of Gunnison County, Colorado. Where conifer establishment did occur in aspen stands, it was on the "cooler, moister N-facing slopes," noting that this was "consistent with the observation that in the Crested Butte area aspen on northern slopes are more commonly seral to coniferous forests." These studies suggest topographic position, as a surrogate for distinct environmental conditions, may influence conifer encroachment. While this does not pinpoint any particular mechanisms, it provides a starting point from which to search for mechanisms that prevent conifer encroachment and provides justification for treating seral and stable aspen stands differently.

I suggest that using a habitat approach based on biophysical variables to model a realized niche of aspen within aspen-conifer forests will provide insight into the potential mechanisms that would allow a stable aspen community to persist on the landscape. We would expect that if biophysical variables act as surrogates for these potential mechanisms, stable aspen communities will inhabit an environmental space, i.e. niche space, which is distinctly separate from conifer species. This stable aspen niche space is similar to the concept of a realized niche introduced by Hutchinson (Hutchinson and Evelyn, 1965). According to this theory, a species realized niche is that portion of its fundamental niche that does not overlap in environmental space with competing species. Many niche-based analyses are founded on this concept and use static modeling approaches to attain distributions already acted on by interspecific competition and abiotic factors, and thus thought to represent a realized niche. This same concept and modeling approach can be applied to aspen-conifer systems with a certain caveat. With a static modeling approach we are viewing a current “snapshot” of distributions of aspen and conifer at a single point in time. Since this system is considered to be influenced by succession, we cannot assume that forest compositions are stable; we must therefore assume that if there is aspen environmental space that does not currently overlap with conifer, it does not mean that it will not overlap in the future, if all other factors remain constant. However, with that said, a century of fire suppression policies and a moist climate (Bartos et al., 1983; Gruell, 1983; Kay, 2003; Kulakowski et al., 2004; Kusbach, 2010; Rogers et al. 2011) suggest aspen-conifer distributions are generally in the late stages of succession. This implies that if conifer has not encroached by now, it will likely not encroach within a reasonable forest management timeframe. These assumptions and model limitations are considered when interpreting the results of the analysis.

### 1.2 Management Applications

Understanding the relationship between the successional status of aspen stands and habitat variables may prove to be an important factor in deciding when and how to restore aspen at a particular site. Recently the Utah Forest Restoration Working Group (UFRWG) was formed with the purpose of reaching a consensus on critical forest issues facing Utah’s National Forests. The current issues of aspen decline (Bartos and Campbell, 1998; Rogers, 2002; Di Orio et al., 2005) are at the forefront of their agenda. Before aspen restoration projects can be implemented, UFRWG recommends following a decision making framework to facilitate desired outcomes using a four step process: 1) Assess the condition of aspen, 2) Identify problematic aspen conditions and their agents/causes, 3) Select from appropriate response options that address the potential problematic conditions, 4) Monitor to assess aspen stand conditions and management/restoration (O’Brien et al., 2010).

This framework is informed by tomes of scientific research addressing aspen. In addition to exploring and contributing to the ecological knowledge of aspen ecosystems, this thesis project is designed to specifically address needs proposed by the UFRWG, such as:

- The need to find cost effective methods of assessing extent of pure upland aspen and upland aspen/conifer forest across a large landscape.
- And to provide additional criteria for determining potential climax vegetation for treatment site in question, in order to prioritize restoration efforts.

I addressed the first need by comparing remote sensing sampling methodologies using publicly available imagery to produce an accurate and cost-effective way to assess the extent of upland aspen forest types. For the second need I developed a spatially explicit and parsimonious predictive model that delineates geographic locations of potential stable and seral aspen community types. If successful, this would provide managers with an initial filter, or additional criteria, in order to prioritize aspen treatment projects.

### 1.3 Objectives

In the present study I explore the distributional patterns of aspen and conifer forests across Utah with the aim of determining whether aspen forest types are related to habitat variables. In the process we looked at the ability to use remote sensing sampling methods to acquire samples of upland aspen forest types including: dominant aspen, dominant conifer, and mixed aspen/conifer forest plots. In order to extend our modeling efforts across four large study sites within Utah, as well as producing an accessible and spatially explicit model for management application purposes, remote sensing and GIS methods were used. The primary motive driving this research is based on the needs outlined by the Utah Forest Restoration Working Group. The objectives in this study are:

**Objective 1.** Determine the ability to use remote sensing and GIS methodologies to sample and model the distributions of upland aspen, conifer, and mixed aspen/conifer forest types.

**Objective 2.** Use data obtained from remote sensing and GIS methodologies to model and explore the possibility of a stable aspen niche across four study sites in Utah.

My research hypothesis is derived from the conceptual model shown in Figure 1.1. Explicitly stated my hypothesis is:

**Hypothesis 1.** If biophysical variables used within the model are representative of mechanisms that allow stable aspen communities to resist encroachment, then a stable aspen niche will be indicated by no overlap with conifer in environmental space. If overlap exists, then either biophysical variables used in the model are incomplete, i.e. not entirely representative of important mechanisms, or a stable aspen niche does not exist within the research area.

## 1.4 Literature Review

### 1.4.1 Aspen Physiology and Distributional Requirements

In the Intermountain region aspen can take on a variety of growth forms, have multiple plant associations, and inhabit disparate environmental conditions. Aspen has an elevation range of approximately 1,580-3,200 m, with general physiological requirements of at least 38 cm of precipitation (more commonly 51 cm), deep snow packs, and longer growing seasons (Mueggler, 1988). The distribution of aspen can be considered water-limited, however, it can be observed occupying sites outside its limits of precipitation and elevation, occurring in stringers along riparian zones, or when subsurface moisture, topography, and soils help to alleviate its evapotranspirational demands (Debyle et al., 1985). Aspen is the only plant that is able to grow in all mountain vegetational zones (Daubenmire, 1943), though it may not be a significant component of the community.  It is often found in a stunted and "shrubby" growth form, sparsely distributed, on dry slopes and in gaps and edges of pure conifer communities.  In previous vegetation classification studies done at Franklin Basin, Utah, it was found that aspen did not occur on extremely wet sites or extremely dry sites.  However, there exists "a reasonable environmental difference" among the extremes, between the poor alkaline/calcareous aspen sites and wet riparian aspen sites (Kusbach, 2010).

The wide distribution and ecological amplitude of aspen has much to do with its plastic response to environmental stressors.  Aspen reproduces extensively by vegetative expansion by way of suckering.  Above and below-ground aspen forest clonal structures may provide explanations for the ability of upland aspen forests to withstand drought stress.  Contiguous stands buffer individual ramets against harsh environmental conditions at the edge of the stand (Landhäusser et al., 2006).  Large interconnected root systems of aspen stands have been recorded up to 41 tons/ha (Peterson and Peterson, 1992).  After a disturbance, or dieback of the canopy, this would put the suckers at high root:shoot ratio and give the juvenile ramets an initial growth advantage.

Another physiological adaption that allows upland aspen to deal with drought stress lies in its ability to "react conservatively to low soil moisture and high vapor pressure deficits" (Lieffers et al., 2001).  Amazingly aspen can regulate its stomatal conductance on days with high evaporational demand, resulting in daytime transpiration rates that are constant over a wide range of vapor pressure deficits (Hogg and Hurdle, 1997), while at the same time withstanding leaf water potentials of -2 to -3 MPa without "any apparent impact on photosynthesis rates" (Hogg et al., 2000).  This is compared to other poplar species in riparian sites that seem to have very little control over stomatal conductance and therefore vulnerable to drought stress (Blake et al., 1984).  When aspen stomata are reduced in aperture under drought conditions, overheating of the leaves is ameliorated by fluttering, or “quaking,” in a slight breeze. This breaks down the boundary layer and more readily allows heat transfer and $CO_2$ uptake on hot days. This is possible due to an evolutionary adaptation of flattened petioles and relatively small leaf size. This is thought to decrease temperatures upwards of 2-4°C (Roden and Pearcy, 1993).

Despite its large ecological amplitude, upland aspen sites classified as climax or stable aspen communities seem to express preference for sites fulfilling certain physiological requirements for light, water, and nutrients. In a distributional study of aspen performed in the Book Cliffs of eastern central Utah, aspen stands exhibited a tradeoff between water and light, being strongly constrained by the low incidence of photosynthetically active radiation at the beginning and end of the growing season. However, low water availability may have a stronger, or overriding influence on aspen distribution (Sexton et al., 2006).

The soils of aspen dominated forests tend to be within a few soil suborders: Lithic, Pachic, and Argic Pachic Cryoborolls (Cryer and Murray, 1992; Debyle et al., 1985 ). These suborders are characterized by thick mollic (41-61 cm) A horizons which contain high concentrations of soil organic matter (SOM). The enriched SOM A horizon may be responsible for promoting stable aspen communities above ground. Soil organic matter has been shown to increase cation exchange capacity and therefore the ability of a soil to hold nutrients (Stoeckeler, 1961). It also acts to increase soil water holding capacity by altering pore space distributions through aggregate formation bound by organic matter compounds (Van Miegroet and Boettinger, 2005). Although soil texture is also a big factor in the ability to hold water, improving soil structure with SOM has shown to be more effective (Hudson, 1994) and may be a particularly important discerning factor for stable aspen communities, as similar soil textures have been found under both seral and stable aspen (Debyle et al., 1985).

Although stable aspen communities are highly correlated with certain soil characteristics, the dynamics of plant-soil interactions do not necessarily lead to a causal relationship. In other words, though stable aspen communities seem to thrive in the seasonally warm, moist, nutrient rich soils of Cryoborolls, they also help to create this solum after occupying the site for several generations—this is done primarily by addition of SOM derived from aspen and understory litter. We can then assume that aspen has been the dominant tree species at the site for multiple generations if it meets the right soil characteristics, but establishment and persistence of aspen at that site may require other external inputs that would inhibit succession.

### 1.4.2 Aspen to Conifer Successional Dynamics

In the upland forests of the Intermountain West aspen and conifer species are the two major forest types. This landscape tends to be a patchwork of pure aspen stands, pure conifer, and mixed aspen conifer. For many land managers this patchwork setting of aspen and conifer is the archetype for traditional views of ecological succession. Succession is a commonly referenced natural phenomenon. In fact, it has been noticed by some of the earliest observers of nature. Henry David Thoreau published an essay in 1860 entitled “The Succession of Forest Trees” (1996), where he recognized that pine stands in upland soils gave way to hardwoods after clear-cut logging. Later the concept was systematized by Henry C. Cowles (1899) and further formalized by Frederic E. Clements (1916), both pioneers in the new discipline of Ecology. But even though succession has been observed and ensuing theory developed, discussed, and refined, a century later we have reached practical conclusions about the limitations of such theories when dealing with specific sites within defined ecosystems. We have recognized that succession is more complex than previously thought. In many systems there is not a simple succession of mutually exclusive seres from pioneer species to a climax community. Instead there are a multitude of successional pathways that a particular site can take according to many different factors, making it difficult to define species as "seral" or "climax." By the same token, it has become exceedingly difficult to generalize successional patterns across landscapes and species. Barnes et al. (1998, p. 443) also recognizes that

> forest succession progresses in nearly infinite ways and is driven by many different factors along with simultaneously occurring processes. However it can only have meaning in the context of a particular geographic framework.

This thesis project uses only GIS-derived biophysical variables within a static model to explain the patterns within this patchwork of aspen and conifer forests. However, describing and accounting for the "noise" in the model, may hinge on understanding the "many different factors" and "simultaneously occurring processes" that interact within a particular geographic area, and may therefore require a more complex and process-driven modeling approach. This modeling approach is beyond the scope of this thesis project, however, the following acknowledges the many abiotic and biotic variables that determine whether conifer will establish and eventually succeed aspen as the dominant climax forest type at a particular site. These factors and processes can be roughly categorized into: climate, disturbances, and soils.

#### *1.4.2.1 Climate*

We know that long-term climate variability in temperature and precipitation has broad-scale effects on vegetation patterns. For example during the Holocene we have been experiencing "longer warm periods…punctuated by a few prominent cooler epochs lasting several hundred years" (Shepperd et al., 2006). More recently we have experienced, what has been termed, the Little Ice Age (1400-1850 A.D.) with a transition to a warm and moist 20th century. We would assume that since aspen was one of the first pioneer species to establish on the North American continent after the last glacial retreat (Pielou, 1991), and still exists today, it has persisted through extreme climatic variability. During this time it bore witness to long durations of drought and periods of moisture, potentially expanding and contracting its abundance over a broad temporal and spatial scale according to these climatic vicissitudes. In the Sierra Nevada, cyclic shifts between red fir (*Abies magnifica*) and lodgepole pine (*Pinus* contorta) have been associated with climate patterns during the Little Ice Age (Millar and Woolfenden, 1999). Red fir established during the cool/moist early part of this period followed by an expansion of lodgepole pine in the cool/relatively drier conditions by the 19th century. Sheppard et al. (2006) believe that aspen distribution in this area "parallels those of lodgepole pine", given the similar response to climate and disturbance (Skinner and Chang, 1996). Coincident with climate, Euro-American settlement brought frequent fires to many sites, making it difficult to separate the effects of each on aspen distribution. However, both factors seem to point to a proliferation of aspen by the early part of the 20th century, leading us to assume that in some geographic areas aspen may be merely contracting from sites that are not suitable under the current climate, which may have historically (pre-19th century) supported conifer forests. This would put the current broad-scale decline of aspen (Bartos et al., 1983; Gruell, 1983; Mueggler, 1989; Bartos and Campbell, 1998; Kay, 2003; Di Orio et al., 2005) within the range of historical variation of the past several hundred years. At local scales, those scales that would affect the present study, the degree to which general historic climate patterns were translated to local weather patterns would then determine the degree to which aspen cover is contracting, by decline or conifer encroachment, due to the aforementioned effect.

### *1.4.2.2 Disturbances*

#### *1.4.2.2.1 Fire*

The vegetative reproduction strategy of aspen responds favorably to fire (Bartos and Mueggler, 1981; Brown and Debyle, 1987). Aspen is a thin-barked species that is extremely sensitive to fire; even light to moderate intensity fires have the ability to girdle the tree (Bartos, 1979). Suckering is inhibited by production of auxins in the aerial portions of the tree, when the cambium at the base of the tree is damaged the ratio of cytokinins to auxins increases in the roots and intiates suckering (Debyle et al., 1985). Warming of the soil, either directly by the fire or when intense fires remove the duff layer and expose the mineral soil to higher solar radiation, is also thought to contribute to promotion of suckering (Schier and Campbell, 1978). Maini and Horton (1966) found that even very light-intensity fires that do not kill the aspen overstory will initiate suckering due to soil warming. Exposure of bare mineral soil after a fire also provides an opportunity for aspen to propagate via seed. Such events are considered to be rare (Turner et al., 2003), however, recent molecular studies suggest sexual reproduction may be more common than previously thought (Mock et al., 2008).

Although aspen responds favorably to fire, it is not considered to be a flammable forest type, and is even commonly used as a fire break (Fechner and Barrows, 1976). Jones and Debyle (1985, p. 78) report that often times aspen stands will not burn at all, citing that "crown fires running through coniferous stands will drop to the ground…and extinguish after burning only a few yards into an aspen stand." Other studies have found that only 0.28% of aspen stands burn annually, and that most of these fires are started by humans; only 16% of fires in aspen stands were started by lightning, compared to 57% of fires started by lightning in coniferous forests (Ryan, 1976).

An abundance of dry fuel in the understory of a pure aspen canopy is required for fire to carry through the stand. When conifers and dense shrubs are present in the stand fire may be able to spread rapidly and even vertically into the crown (Debyle et al., 1985). In the case of pure aspen communities without a conifer component, a combination of dry weather and fine herbaceous fuels is needed. Accordingly, local weather patterns may largely determine fire frequency in these types of stands. In this current study, it is possible that patterns of aspen and conifer at individual study sites are the result of local weather and its affect on the interaction between fire and aspen. The Cedar Mountain, Utah study site (see chapter 3) is a plateau situated at the southern tip of the Wasatch Range and is subject to monsoonal flows in July and August. Fire conditions are very similar to those experienced further south in Arizona and New Mexico, where the windy and dry weather of May-June constitute the major fire season (Debyle et al., 1985). But with the arrival of spring, the foliage in the understory of aspen stands greens and essentially becomes nonflammable. The best time for fires at Cedar Mountain may be in September and October, after the monsoons, when the fine herbaceous understory dries out. However, the opportunity for fires during this seasonal period may be currently reduced, due to the lack of a heavy herbaceous layer. Long-term sheep grazing on the plateau with the arrival of Euro-Americans has transformed aspen understories from forb to graminoid dominated (Bowns and Bagley, 1986) and therefore reduced the fine fuels needed for aspen to burn. At other study sites sampled for this thesis project, such as the Deseret and Franklin Basin sites (see chapter 3) in the northern Wasatch and Bear River Ranges of northern Utah, the aspen stands are primarily within high elevation montane and subalpine forests. The climate here is largely not conducive for fires, since snow may fall as early as September and remain on the ground through June, after which the nonflammable herbaceous layer under aspen stands grows rapidly (Debyle et al., 1985).

There is intriguing evidence that in the subalpine zone (> ~2,750 m) the pattern of dominant forest community types may be organized primarily by the relationship of topography and the occurrence of infrequent fires. In the Medicine Bow Wilderness, Romme and Knight (1981) found that fires occurred less frequently in moist ravines and valley bottoms than on upland ridge tops, plateaus, and exposed slopes. They assume the two major factors for this occurrence are the “tendency of fire to burn uphill rather than downhill and the reduced probability of lightning strikes in low lying areas” (1981, 324). Compared to upland sites, moist ravines also have higher relative humidity. Upland sites were dominated by early succession lodgepole pine forests while north facing slopes of ravines and valley bottoms were dominated by late succession spruce-fir forests. In addition, spruce-fir reestablished much earlier in these relatively mesic sites. In the upland sites, spruce-fir are rare to non-existent on the dry exposed slopes. Since fire is infrequent in the subalpine zone, with return intervals estimated by various studies to be greater than 150 years (though probably more along the lines of 300-400 years) (Romme, 1982; Gruell, 1983; Bigler et al., 2005), secondary succession is extremely slow. This has perpetuated a mixed forest of lodgepole pine and fir in these areas. Lodgepole pine behaves very similarly to aspen ( Skinner and Chang, 1996; Shepperd et al., 2006) in its response to disturbance and role as a early successional species, thus we may consider the same explanation for the patterns we see in the aspen, spruce, and fir dominated Intermountain West subalpine forests. However, a major difference between aspen and lodgepole pine is the former’s resistance to fire when not encroached by conifer species, suggesting that fire return intervals for upland aspen in the subalpine zone parallel rates of conifer encroachment.

Mutch (1970) points out that vegetation types that respond favorably to fire normally evolve characteristics that make them especially flammable, but, as evinced by the studies listed above, aspen seems to be the exception to this rule. This leads me to believe that the landscape patterns of aspen and conifer forests cannot be completely explained by the interaction between fire and topography and that some aspen dominated sites which resist conifer encroachment could remain “stable” aspen communities reproducing without fire. By the same token, aspen stands with very slow rates of conifer encroachment may never meet the required fuel load to burn, and therefore may persist as a mixed aspen/conifer forest. However, these hypotheses hinge on ecological mechanisms that would explain a paucity or complete lack of conifer encroachment. Some possible mechanisms may be inhibition of conifer by aspen understory communities, conifer seed dispersal limitations, and reduced competitive performance of conifer species within the soil, light, and temperature environments that are conducive for aspen growth.

##### *1.4.2.2.2 Aspen Understory Communities*

The understories of aspen communities may be an important factor in whether conifer species establish. The germination and establishment of conifers, primarily subalpine fir as it is often the first colonizer under aspen canopies due to flexibility in both light and seedbed requirements, is the required vegetational change for succession to a coniferous forest. Germination may be potentially hindered or completely prevented by the conditions within the seedbed. Currently, knowledge of the inhibitory mechanisms affecting successful subalpine fir germination in aspen stands is limited, however, some studies on general germination requirements allude to potential effects. Fiedler et al (1985) found that in the Intermountain West region germination of Englemann spruce (*Picea englemannii*) and subalpine fir (*Abies lasiocarpa*) was higher on mineral soil than undisturbed forest floor, though elevation and temperature were also strongly correlated. According to Alexander et al. (1984) subalpine fir is “less exacting” than other conifers in its seedbed requirements. Studies show that it prefers exposed mineral and moist humus but it can also germinate on undisturbed forest floor, non-decomposed duff litter, and decaying wood (Day, 1964; Clark, 1969). Although subalpine fir seems to be highly versatile in its seedbed preferences, thick aspen leaf litter at the soil surface may affect the ability of seeds to come into contact with the preferable mineral soil and thus hinder germination. Studies have shown this to be the case in spruce (Coates et al., 1991), although I am not aware of any studies that have specifically looked at aspen leaf litter inhibiting germination of subalpine fir. Temperature and light germination requirements for subalpine fir are also broadly variable. It has been shown to germinate under the snow in early spring (Alexander et al., 1984) while also showing embryo dormancy, broken by stratification in moist sand or peat at 5 °C for 60 days (U.S. Dept. of Agriculture Forest Service, 1974; Alexander et al., 1984).

The mechanistic factors influencing conifer inhibition in an aspen understory may more severely affect the seedling growth stage of conifers than the germination stage. Aspen understory communities are often a highly productive and diverse mix of shrubs, forbs, and graminoids (Mueggler, 1988). The herbaceous layer in pure aspen communities is especially dense, despite commonly accepted relationships between basal area of canopy trees and understory production (Warner and Harper, 1972). In Boreal forests smothering by fallen leaves is widely considered to slow conversion to conifers (Gregory, 1966). A component of this “smothering” effect may be the susceptibility to damping-off fungi (Tappeiner and Helms, 1971). There is also evidence that draws attention to competitive interactions for light, water, and nutrients between conifer seedlings and the aspen understory. It is possible that tall forb/shrub aspen understory canopies could be dense enough to out-compete conifer seedlings. However, when considering the light requirements for the early establishment period of subalpine fir, it is not likely to be inhibited due to low light. According to Alexander et al. (1984) subalpine fir grows under nearly all light intensities found in nature but favors shade for early establishment, observing a maximum growth rate at only 20% full sun.

Langenheim (1962) reported that there was increases in conifer encroachment where the understory was thin compared to where it was thick. According to such accounts, severe long-term grazing that results in a reduction of tall forbs and shrubs to graminoids interspersed with patches of bare ground may provide the disturbance needed and release from competition for conifer to establish and recruit into the overstory.

Although there is intriguing evidence (Langenheim, 1962; Tappeiner and Helms, 1971) that productive and diverse aspen understory communities may inhibit conifer encroachment, I am not aware of any studies that have attempted to directly link severe grazing disturbances with conifer encroachment. Alternatively, there seems to be more evidence supporting aspen as a “nurse plant” for conifer seedlings (Baker, 1918, 1925; Bartos et al., 1983; Calder et al., 2011). In addition, other studies have found that the primary factor determining rate of conifer encroachment in a stand is the age of the oldest conifer (Strand et al., 2009), implying that once an individual conifer reaches maturity, the resulting “seed rain” will exponentially increase the rate of encroachment. Conifer seeds are primarily wind-borne with nearly 50% of the seeds falling within 30 meters of the parent tree, the directions determined by prevailing winds and thermals moving up slopes (Noble, 1978). This raises the question of whether pure aspen stands remain pure due to distance from nearest conifer seed source.

#### *1.4.2.3 Soils*

Soils likely play an extremely important role in determining whether conifer encroaches into aspen and the rate at which an aspen community converts to a conifer dominated community. Plant-soil feedbacks are dynamic and complex, making it difficult to assume causal relationships in the interaction between the two. Stable aspen forests have been shown to be correlated to specific soil suborders within the order of Cryoborolls (Debyle et al., 1985; Cryer and Murray, 1992). These soils are characterized by high input of soil organic matter (SOM), warm soil temperatures in upper horizons, and good soil moisture content through much of the growing season, all in turn promote microbial decomposition and therefore increased nutrient availability. These conditions support productive understory communities, which may play a role in inhibiting conifer establishment, as well as promoting reproduction of aspen (Calder et al., 2011). In these warm soil temperatures aspen have been shown to initiate suckering even in the absence of stem removal, which has been cited as the explanation for aspen invasion into grasslands (Maini and Horton, 1966; Williams, 1972; Bailey, 1974). On the other hand cool soils have been shown to suppress suckering (Zasada and Schier, 1973; Landhäusser et al., 2006). Fewer suckers were found in cool day/night temperature regimes that mimic temperatures found in the deep shade of subalpine forests (Zasada and Schier, 1973).

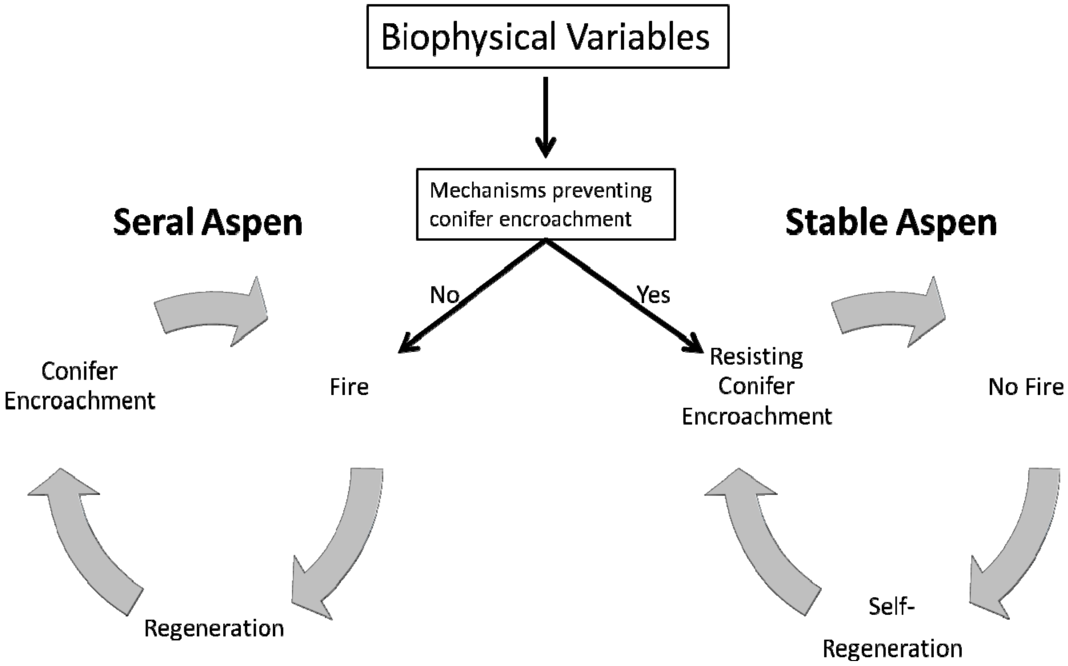

**Fig. 1.1** Conceptual model showing the theoretical distinction between seral and stable aspen communities. Seral aspen communities follow a deterministic successional cycle: conifer encroachment leads to fire, which leads to vigorous aspen regeneration, over time conifer encroaches, which then promotes stand replacing fire, and the cycle begins anew. Stable aspen communities do not experience stand replacing fire, thus undergoing self-regeneration via gap dynamics and episodic suckering. Mechanisms must be in place that explain the ability of stable aspen to resist conifer encroachment. Without such mechanisms conifer will encroach and the site will begin down a successional pathway. Biophysical variables may generally represent these mechanisms, providing justification for the conceptual model and evidence for separation between seral and stable aspen communities.

# CHAPTER 2

# ASSESSING GIS AND REMOTE SENSING METHODOLOGIES FOR ASPEN AND CONIFER HABITAT MODELING[1]

## 2.1 Introduction

Aspen plays a crucial role in the greater Intermountain West region. The high organic matter nutrient rich soils, light, and water dynamics associated with aspen communities provides an environment for a diverse assemblage of understory plants. Aspen understory communities are often found to have higher species richness and productivity then surrounding community types, and as such are an important habitat for a multitude of wildlife such as birds, wild ungulates, and domestic livestock (Debyle et al., 1985; Bartos and Campbell, 1998).

In the Intermountain West aspen often co-occurs with conifer in mixed stands as well as in adjacent pure communities. In this region, a number of studies indicate a loss of aspen cover across the landscape due to conversion to climax conifer communities (Romme et al., 1995; Baker et al., 1997; Hessl and Graumlich, 2002; Shepperd et al., 2006). This is believed to be the result of deterministic successional processes, whereas aspen requires disturbance, such as fire or logging, dominates a site for a period of 40-80 years, then succumbs to pathogens, pests, and eventually encroaching conifer species (Bartos et al., 1983; Debyle et al., 1985). However, some studies show evidence of climax aspen communities remaining free of conifer encroachment (Langenheim, 1962; Betters and Woods, 1981; Mueggler, 1988; Romme et al., 2000; Rogers et al., 2010), though biophysical factors related to aspen/conifer distribution patterns remain ill defined. Considering these issues, an approach is needed to capture aspen and conifer distributions at fine-scales across large areas of the landscape in order to determine if stand

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types are related to environmental variables. Such habitat models could answer questions concerning successional dynamics within aspen/conifer forests.

More recent developments in image processing techniques, accessibility of remotely sensed imagery, and improved processing power within geographic information systems (GIS), has provided a cost-effective means to sample forest composition with a high number of plots across large areas. In addition, it is also increasingly possible to derive predictor variables remotely within GIS that may influence plant species distributions, providing the means for modeling aspen and conifer habitat.

Sampling vegetation remotely through satellite and/or aerial imagery is commonly used in natural resource studies (Paine, 1981; Holmgren and Thuresson, 1998). There are many options and techniques available. The decision of which to use is dependent upon the specific research objectives. Our aim was to sample relative tree species canopy cover within 30x30 meter plots. Some success has been had classifying high resolution Quickbird and National Agricultural Imagery Program (NAIP) imagery into species class by canopy cover (Frescino et al., 2007). Such methodologies use automated classification algorithms that rely on multispectral, textural, structural, and contextual inputs to delineate and classify individual tree crowns (Leckie et al., 2003). Even with such methods species must be grouped into similar spectral classes and numerical accuracies only range from 48% – 63% at this level of classification (Frescino et al., 2007). High resolution hyperspectral imagery shows promise in identifying species by individual crown reflectance especially when aided with ancillary information on structure inferred from lidar (Clark et al., 2005; Dalponte et al., 2008). However, such imagery can be cost-prohibitive if it does not exist for ones intended research area.

Subpixel analysis of moderate scale imagery is another approach. Landsat thematic mapper (Landsat TM) is at 30 m spatial resolution, with seven spectral bands, and has the benefit of being free of charge. Vegetation indices, regression analysis, and neural networks from Landsat data have been shown to have reasonable accuracy in estimating forest cover for coniferous forests of the Pacific Northwest (Boyd et al., 2002), and with the use of classification algorithms can effectively identify land cover types with around 80-90% accuracies (Walsh, 1980; Lowry et al., 2007). Linear spectral unmixing is a form of subpixel analysis which assumes a mixed pixel to be a linear combination of spectral signatures of surface materials or cover types with the areal proportions as weighting factors (Gong and Zhang, 1999). Linear spectral unmixing of Landsat TM imagery has been shown to provide moderate estimates of vegetation fractions (Sohn and McCoy, 1997; Strand et al., 2009a), which is the desired output for our sampling objectives.

Another, more direct option for arriving at canopy cover estimates by species involves photointerpretation of NAIP imagery, which has the benefit of requiring less technical expertise in image processing. High resolution aerial photography is commonly visually interpreted to identify tree species (Paine, 1981). Di Orio et al. (2005) used historic aerial imagery at a maximum scale of 1:15,840 to identify aspen for change detection purposes with 85% accuracy using stereoscopy. NAIP imagery is orthorectified and therefore not available as stereo pairs. However, it is in digital format allowing for visual enhancement through composite images of spectral band combinations, as well as being easily overlayed with other layers in GIS. In addition, assuming a typical screen pixel size of 85 pixels in$^{-1}$, NAIP imagery at 1 meter resolution can be zoomed to the scale of 1:3,346. At this resolution with the aid of pseudo-color composite images using the infrared band, we would expect to have reasonable accuracy visually interpreting canopy cover by species.

Many ecological questions are answered from an analysis of the species-environment relationship, which is often considered to be a central issue in ecology. To this end species distribution models have been used to quantify an environmental niche (Austin et al., 1990; Vetaas, 2002), assessing competition and invasion (Peterson and Vieglais, 2001), and in answering questions concerning biodiversity and community assemblages (Guisan et al., 2000; Ferrier et al., 2002). Such distribution and habitat modeling analyses have been shown to be possible using GIS derived variables (McKenzie et al., 2003; Sexton et al., 2006; Lowry et al., 2007; Zimmerman et al., 2007). Models based on GIS derived variables are inherently spatially explicit and can easily be applied across multiple spatial extents, are cost-effective, and due to consistency and repeatability are transferrable between research entities. However, there are limitations to the use of such variables imposed by spatial uncertainties, due to (i) interpolation errors and lack of real ground or station data, (ii) inadequate detail to detect biologically relevant microsites, (iii) and general difficulties estimating parameters derived from complex ecological interactions such as soil water availability (Guisan and Zimmermann, 2000). Although GIS derived variables have many benefits for habitat modeling, the degree to which these limitations affect our ecological interpretations of such models should be considered. Often this comes down to a tradeoff between the benefits mentioned above and the precision or detail needed to answer specific research questions.

In this study we determined the ability of remote sensing and GIS methodologies for sampling tree species composition and modeling habitat of aspen and conifer forest communities. We address the limitations of such models imposed by both the remote sensing derived forest sampling and the GIS derived environmental variables used as input for the habitat model. Specifically our objectives are to: (1) compare the accuracy of sampling forest canopy cover by photointerpretation of NAIP color infrared imagery and forest canopy cover derived from linear spectral unmixing of Landsat TM imagery, (2) assess the strength of the relationship of GIS derived variables to forest plots, (3) assess the ability of GIS derived variables to separate aspen, conifer, and mixed aspen/conifer forest plots within environmental space, (4) evaluate issues relating to accuracy and spatial uncertainties inherent in the GIS and remote sensing methodologies used.

## 2.2 Methods

### 2.2.1 Site Description

The Deseret Land and Livestock study site (DLL) is located in the Monte Cristo range in the Northern Wasatch Mountains. It is entirely private property with the study boundaries covering the western mountainous portion of the Deseret Land and Livestock ranch (Fig. 2.1). The study area is 33,100 ha with an elevation ranging from 1,840 to 2,660 m. The topography is moderately steep with wide areas of gently sloping terrain on ridge tops. Soils are primarily alluvial and colluvial deposits derived from conglomerates, sandstone, and some limestone and shales. Soils are considered mountain loam types with plant communities dominated by Wyoming sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) , bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) and slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), quaking aspen, Doug-fir (*Psuedotsuga menziesii* var. *glauca*), subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea englemannii*), and Gamble oak (*Quercus gambelii*). Historically, as with nearly everywhere across the West, grazing was a major land use at DLL. At its peak in the early part of the 1900's reports claim there were potentially 90,000 head of sheep grazing across all Deseret Livestock companies holdings, of which the DLL study site is only a portion. During this same time, easily accessible conifer stands were heavily logged (McMurrin, 1989). Over the years ranch management has adopted a long-term sustainable use philosophy, encouraging multiple uses of the land. To this end, there are currently 2,500 elk (*Cervus canadensis*), 3,500 mule deer (*Odocoileus hemionus*), 5,000 cattle, and 3,000 sheep that migrate from the lower meadows to the higher elevations (which make up the partitioned study area) seasonally (R. Danvir, personal communication).

### 2.2.2 Plot Selection

In order to analyze distributions of aspen, conifer, and mixed forest types, it was desirable to obtain balanced random samples from each population. Initial sampling schemes showed extremely unbalanced coverages of forest types across the landscape. Conifer and mixed types were underrepresented compared to aspen and non-forested plots. To increase the number of conifer and mixed plots while still retaining a completely random sample design and ensuring statistically sound population parameter estimates, Landsat TM imagery was used to delineate a forest mask (Fig. 2.2). This forest mask allowed us to focus our sampling efforts on only the target populations.

The forest mask was created by applying the Isodata unsupervised classification algorithm to a June 2010 Landsat TM image in ENVI image processing software (Research Systems Inc., 2010). An initial 20 clusters were classified and then grouped into forest or non-forest using 1-m resolution NAIP imagery. Spectral signatures, from Landsat bands 1-5 and 7, can accurately distinguish between forested and non-forested pixels. However, Landsat pixels are 30X30 meters resolution and may represent an area that is both forested and non-forested. Therefore during the cluster grouping process, it was important to include any clusters in the forested group that represented these “ambiguous” mixed pixels. This ensured that all forested areas were included in the mask.

### 2.2.3 Forest Sampling Methods

In order to avoid misregistration errors between forest sampling and GIS derived predictor variables, plots were moved if center points fell at stand edge. In this case plots were moved in a given cardinal direction until there was a buffer of 15 m between stand edge and plot boundary. Both forest sampling methods used to arrive at percent canopy cover by species class were converted into the discrete forest type variable (Table 2.1) before being assessed for accuracy. Accuracy was assessed for each method by comparison to ground-reference data. Ground-reference data was acquired by generating random plots within forested areas. Those plots within 1 mile of accessible roads were visited for a total of 85 plots. At these plots ocular tree cover estimates were performed using the same general ocular techniques as described by Daubenmire (1959). Such ocular methods have been shown to be as accurate as estimates derived from densiometer measurements (Vora, 1988) and more closely parallel visual canopy cover estimates derived from photointerpretation. Ocular estimates were than classified into Forest Types according to table 2.1.

Forest sampling methods were compared by a general assessment of overall accuracy and Kappa analysis (Congalton, 1981), as well as a more detailed look of identification errors broken out into Forest Type groups and errors of omission and commission. Results are shown by the use of error matrices, also known as a confusion matrix or contingency table. The matrix systematically compares Forest Type plots classified from canopy cover derived from either photointerpretation of NAIP imagery or linear spectral unmixing of Landsat imagery with Forest Type plots derived from ground-reference data. Accuracy for individual groups can be assessed in two ways. "Producers" accuracy, or measure of omission error, is the total number of correctly classified plots in an individual category divided by the total number of reference plots in that category. This statistic indicates the probability of a ground reference plot for a particular category being correctly interpreted. Another way to assess accuracy of individual categories is termed "users" accuracy, which assesses errors of commission. This is the total number of correct plots in that category divided by the total number of plots interpreted to be in that category. If we consider that we are using the estimated Forest Type dataset for modeling distributions, error of commission is a measure of the degree to which it will affect our results and what categories are the most reliable. Kappa analysis gives an estimate of accuracy ($K_{hat}$) which, compared to overall accuracy, is more sensitive to accuracies of individual classes (Congalton, 1981). $K_{hat}$ values between 40-80% represent moderate accuracy, while values >80% represent good accuracy (Jensen, 2004).

### *2.2.3.1 Photointerpretation*

A total of 250 randomly generated 30x30 m plots were overlaid on 2009 NAIP Color infrared imagery for visual interpretation of percent canopy cover by species (Table 2.2). It was important to understand any sources of potential bias during the photointerpretation process in order to identify limitations and solutions. The primary limitations in identifying species using NAIP imagery are both the 1-m resolution and shadows. At 1-m resolution it was not possible to visually identify individual conifer species, e.g., identifying subalpine fir from Douglas-fir, and therefore all conifer species were lumped into one group. It may have been possible to acquire the original aerial photography used to produce the NAIP orthophotos. These original photos have a slightly higher resolution and can also be viewed using stereoscopy, allowing a 3-D view of the tree crown. It was decided that the slight increase in resolution was not enough to make stereoscopic viewing comparatively more effective, since course pixel size would still prevent species-level interpretation of crown structure. In addition, the original photography is not orthorectified and would therefore require many more additional steps for the interpretation product to be compatible with other GIS layers, decreasing the cost-effectiveness of the final product. Shadows also introduced error in the interpretation which could not be reduced. This error was manifest in steep topography resulting in deeply shadowed slopes. In these areas there was potentially a bias to interpret plots as being dominated by conifer.

To aid in identifying aspen and conifer the image was enhanced and a few basic photo interpretation principles were utilized. A pseudo-color composite image was creating by assigning, respectively, the near infrared, red, and green NAIP bands to the red-green-blue tricolor guns of the computer monitor. In this configuration aspen appears as bright red hues, and conifer as darker hues, due to differences in both leaf anatomy and crown architecture (Jensen, 2004). A linear contrast stretch was also performed to the data in each band that fell within three standard deviations. This stretches the majority of the data over the 8-bit range of 255 values, in effect, increasing the visual contrast between surface materials (Jensen, 2004). Photo interpretation principles involved synthesizing information from patterns in tone (color), texture (variation of tone across area), size and shape of objects and their shadows (Paine, 1981). This skill is improved by visiting the site and applying ecological knowledge of plant species, for example their growth forms, physiological requirements, and community associations.

#### *2.2.3.2 Linear Spectral Unmixing*

We used linear spectral unmixing as a comparative method to acquire estimates of canopy cover by species type. Linear spectral unmixing is a form of subpixel analysis which assumes a mixed pixel to be a linear combination of spectral signatures of surface materials or cover types with the areal proportions as weighting factors (Gong and Zhang, 1999). It is a well established remote sensing method to arrive at fractions of cover types within a single pixel

(Sohn and McCoy, 1997; Strand et al., 2009a). A principle components analysis (PCA) method was used to select endmembers (Theseira et al., 2003; Strand et al., 2009a). In order to reduce the number of potential endmembers, a forest mask was first created using an Isodata unsupervised classification algorithm (Jensen, 2004). The 20 unsupervised classes were than grouped into forest and non-forest using NAIP imagery as reference. Endmember spectra within the forested areas were manually circumscribed in 3-dimensional space represented by the first three principle components. Endmembers were identified and further refined using a combination of ground-reference data and NAIP imagery, resulting in five endmembers: aspen, conifer, shadow, grasses/shrubs, and bare ground (Table 2.3). Linear spectral unmixing was then performed and fraction maps were converted into Forest Types (Table 2.1). Percent cover of each endmember was determined according to the non-shadow portion of the pixel. The results were then overlaid with 85 ground-reference plots for accuracy assessment. All image processing and linear mixture analysis was done using ENVI software (Research Systems Inc., 2010) and performed on a July 2008 Landsat 5 TM image acquired from the MRLC Landsat database (http://www.mrlc.gov/). MRLC landsat products have undergone geometric and radiometric corrections and have been converted to at-sensor reflectance (Huang et al., n.d.).

### 2.2.4 Generating Climatic, Physical, and Biophysical Variables in GIS

All variables used in this study were calculated using R (R Development Core Team, 2004) and Python (Van Rossum, 2001), integrated within the ArcGIS Model Builder environment (ESRI, 2010). Variables were grouped into climate, physical, and biophysical.

#### *2.2.4.1 Climate and Physical Variables*

Raw climate data was acquired for each site from DAYMET (Thornton et al., 1997). DAYMET temperature and precipitation data are 18 year averages supplied in 1-km raster format interpolated from field weather stations. In order for the model to be sensitive to fine scale variability in forest type distributions, the raw daily average air temperature at 1-km resolution was downscaled to 30-m resolution to match other variables. DAYMET models used to interpolate temperature data from dispersed weather stations are based on a simple linear relationship with elevation, thus making the task of downscaling one of uncovering the lapse rate used in the initial DAYMET models for a given area (Zimmermann et al., 2007). A lapse rate was calculated for a site by regressing national elevation dataset values (30-m resampled to 1-km using an average elevation value) against the course grid DAYMET temperatures (Fig. 2.3). This lapse rate was then used to interpolate temperature for any given elevation. A geographic overlay of the digital elevation model (DEM) and the residuals from the regression analysis shows residuals increasing in areas of steep terrain indicating the spatial uncertainty in assigning a single temperature value to an area of 1 $km^2$ within high topographic relief, reinforcing the need to use fine scale temperature values in these areas (Appendix A).

Although precipitation is also related to elevation and could be downscaled using the same methods as used for temperature, it was decided to forego downscaling of precipitation. Precipitation events are much more widespread and irregular in their nature. For this reason it is better to keep them at a courser resolution. However, course scale 1-km resolution precipitation data was used to calculate fine scale variables such as potential evapotranspiration and soil water balance. This may have affected the ability of such variables to detect differences between forest types adjacent to one another.

Solar radiation, slope, and aspect were calculated using ArcGIS Spatial Analyst tools. The equations used to calculate solar radiation are based on a Hemispherical Viewshed Algorithm. These values were overlaid with estimates of direct plus diffuse radiation to get monthly total radiation values for each pixel in a surface raster. For the SolRad variable, these values were then converted to an annual daily average solar radiation in Wh $m^{-2}$. Radiation estimates use solar zenith angles and thus, solar radiation values will vary across sites due to differences in latitude. The equations also use azimuth angles of the intercepting DEM surface to calculate angles of incidence, so values can be interpreted as above-canopy solar radiation. Aspect (degrees) was transformed into a biologically meaningful variable based on a symmetric radiation wetness index (Roberts and Cooper, 1989).

$$Cos(aspect - 30)/180 * \pi) + 1)/2 \qquad (1)$$

*2.2.4.2 Biophysical Variables*

Potential evapotranspiration (mm $d^{-1}$) was calculated using the empirical equation of Jensen and Haise (1963) (see Appendix B), which is specifically calibrated for the arid western United States.

$$pET = R \,/\, 2450 * (0.025T + 0.08) \qquad (2)$$

where, $R$ is mean daily solar radiation in units of kJ $m^{-2}$ $d^{-1}$, and $T$ is mean daily air temperature (°C). Potential evapotranspiration values from this equation are in mm $d^{-1}$. For sake of consistency with other variables, pET is shown in cm $d^{-1}$.

Site water balance is a running sum of the difference between potential evapotranspiration and precipitation, while not allowing any excess water to exceed the site-specific soil water capacity. Soil water capacity for each cell is derived from the Soil Survey Geographic Database (http://soildatamart.nrcs.usda.gov) (see Appendix C). This “bucket” method for calculating site water balance is very similar to Zimmermann and Roberts (2007), which was based on the concept developed by Grier and Running (1977). This method differs by running the water balance from January-September (the end of the growing season) without concern for when “recharge” (e.g. precipitation exceeds evapotranspiration) occurs. It was determined that all sites reached the maximum soil water capacity during the winter months starting the growing season with as much water as the soil allows. Assessing the soil water balance in September, essentially gives an index of site dryness directly after the period during which plants need moisture the most.

### 2.2.5 Analysis of GIS-derived Variables

Due to the exploratory nature of the study, as opposed to strict hypothesis testing, canonical correlation procedure of the discriminant problem was used to look for group patterns and determine importance of variables. Canonical correlation is a general form of multivariate discriminant analysis (Hintz, 2009). Other multivariate statistical methods were eschewed in place of discriminant analysis (DA) for two reasons. First, the dependent variable was collected as a categorical group variable representing dominant tree species cover. Although very similar to logistic regression, in the regard that both require categorical groups as the response variable, DA differs primarily by aiming to uncover the correlative structure between the groups, whereas logistic regression emphasizes prediction (Tabachnick and Fidell, 1996). Furthermore, visualizing the correlative structure between groups is enhanced by ordination of the data, which is better suited for the exploratory goals of the study. Secondly, unlike most community data, our data exhibits linearity among pairs of environmental variables within Forest Type groups. It also satisfies other test assumptions, such as homogeneous within-group variances and multivariate normality, even though these assumptions are not critical unless hypothesis testing or prediction is desired (McCune and Grace, 2002). This also justified the use of DA in lieu of non-parametric multivariate ordination approaches, such as non-metric multi-dimensional scaling techniques.

Variables were first screened for outliers by calculating a Euclidean distance matrix from scaled environmental variables as recommended by McCune and Grace (2002). The average distances of a particular sample unit to all other sample units were then plotted in a frequency histogram and all sample units that fell above three standard deviations were vetted individually for errors and removed if found. Collinearity issues were addressed by calculating Pearson's correlation coefficient for all pairwise combinations of variables. Collinearity, or strong linear dependencies amongst variables, can cause substantial differences in regression results and any interpretation of the parameter estimates may be spurious (Zar, 1999). We used minimum Wilk's Lambda (multivariate equivalent to $R^2$) as the criteria to select the optimum combination of variables through a selection algorithm developed by Claude McHenry (1978) run in NCSS (Hintz, 2009). McHenry's algorithm has been shown to yield very similar results to an "all possible combinations" selection procedure (Hintz, 2009). The squared canonical correlation was used to assess how well the optimum combination of variables related to overall forest distributions. The square of the canonical correlation for each variate, or component as in a principle components analysis, in the reduced dataset explains the amount of variance accounted for in the original dataset, and can also be seen as an equivalent to $R^2$ in multiple regression (Hintz, 2009). Both Wilk's Lambda and the prediction accuracy compared to a random set of variables was used to determine the ability of the variables to distinguish between Forest Types of aspen, conifer, and mixed. Finally, a one-way Analysis of Variance was performed followed by Tukey-Kramer multiple comparison procedures, to test mean solar radiation differences amongst groups, while considering unequal group sizes. This final procedure was performed using only solar radiation, as it proved to be the most robust variable, in order to provide support for general site-scale topographic differences between Forest Types.

## 2.3 Results

### 2.3.1 Forest Sampling Methods

Photointerpretation of NAIP imagery had a higher overall accuracy of 94.11% compared to linear spectral unmixing methods with only 63.52% (Tables 2.2, 2.3). This estimate fails to account for unbalanced group sample numbers, in which case a group with a high number of samples that is accurately classified would drive up the overall accuracy. To avoid this, it is important to look at the accuracy of individual groups. The low overall estimate of accuracy for linear spectral unmixing (LSU) is primarily due to the confusion for "Other" plots as "Aspen" plots. This indicates that the spectral signature of aspen is similar to the spectra of grasses, shrubs, and other broadleafed trees. LSU was also fairly inaccurate in determining percent of aspen and conifer within a pixel. The inaccuracy involved with the photointerpretation method also primarily stemmed from classifying "Other" as "Aspen." However, the rate was much lower, as shown by a producer's accuracy of "Other" equal to 88.89%.

### 2.3.2 Assessment of GIS-derived Variables

The GIS-derived variables selected for the optimum model do not explain very well the differences in distributions between the Forest Types. Four variables were selected according to their statistically assessed influence on Wilk's Lambda, including: total annual precipitation (TP), daily average solar radiation (SolRad), daily average air temperature (DAAT), and site water balance (SWB) (Table 2.4). We can see that only SolRad and SWB are significantly related to forest type groups when considered independently, however, such relationships are poorly 'fit' by the model as indicated by high values of Wilk's Lambda. The inclusion of TP and DAAT, which are not significantly related to Forest Types on their own, indicates potential interactions with other variables. Also in the table are $R^2$ values obtained if the particular variable were regressed on all other variables (R-squared other X's). The high $R^2$ values for SolRad and SWB primarily reflect the correlation between the two, an expected result, since as solar radiation increases evapotranspiration demands also increase, causing the site water balance to drop. Collinearity issues with the model were avoided by removing those variables that had direct linear dependence on other variables. The remaining variables chosen for the model do not indicate a high degree of correlation that may affect the model results (Hintz, 2009).

Using canonical correlation as a general form of discriminant analysis we get two linear equations representing the optimal combinations of variables so that the first discriminant function (or canonical variate) provides the most overall discrimination between the groups, with successively less discriminatory power in the second canonical variate (Table 2.5). An estimate of how well the canonical variates explain the variance in the original dataset is represented by the square of the canonical correlation (Canon $Corr^2$). The Canon $Corr^2$ for the first variate with the highest discriminatory power is 27% while the second variate only partitions out 1% of the original variance in the dataset. Interpretation of variance explained is dependent on a stratified sampling of only forest areas and the use of canonical correlation to fit a multivariate response to multiple independent variables. Thus, we can say that within forested areas the linear combination of variables represented by the first canonical variate can only explain 27% of the variance in the distribution of Forest Types. It should be noted that by only including forested areas we increase our model fit. Much like the loading matrix in a principal components analysis we can look at the correlation between each variable and the canonical variates in order to assess the importance of each variable and the direction of the relationship (Table 2.6). We can see that the first variate is primarily represented by SolRad, SWB, and TP. By plotting the reduced space of the canonical correlation variates we can visually interpret these relationships (Fig. 2.4). There is a high degree of overlap in the distributions of Forest Types. However, there does seem to be separation primarily along the first variate representing a moisture, temperature, and light gradient. Though this analysis depicts general distribution patterns of aspen and conifer, the poor "fit" of the GIS-derived variables combined with a high degree of overlap between the groups makes prediction from such a model difficult. In comparing the prediction accuracy of the optimum model with that of a null model of random variables, the prediction error is only reduced by 42%, whereas a successful model would be expected to reduce prediction error upwards of 90% (Hintz, 2009).

Analysis of Variance with Tukey-Kramer multiple comparison procedures indicate that despite proportionately smaller sample sizes in the "Conifer" and "Mixed" groups, mean SolRad values for "Aspen" are significantly different from both "Conifer" and "Mixed" while "Conifer" and "Mixed" are not significantly different ($F_{2, 191= 7.96}$, p=0.0004) (Figure 2.5).

## 2.4 Discussion

### 2.4.1 Forest Sampling Methods

Photointerpretation of NAIP imagery was much more accurate in estimating forest canopy cover than linear spectral unmixing of Landsat imagery as shown by both overall accuracy and Kappa analysis (Tables 2.2, 2.3). Interestingly, in both methods most of the error was due to ground-reference plots classified as "Other" being interpreted as "Aspen." However, the rate was much higher for linear spectral unmixing (LSU). It is not surprising that the error rate for LSU in this category would be higher. LSU relies solely on spectral characteristics to distinguish canopy cover between species. Reflected radiance from the leaves of many broadleafed species can be similar (Elvidge, 1990). In addition, the extreme variability in canopy height, understory species and their biomass, and leaf area index for aspen stands causes a wide range of reflectance values that may be expected to overlap with other cover types, such as Canyon maple (*Acer grandidentatum*), chokecherry (*Prunus virginiana*), and Gambel oak (*Quercus gambelii*). Principle components analysis uncovers endmembers according to their spectral characteristics. Due to similar spectral characteristics this process did not separate out the above mentioned species as distinct endmembers, resulting in the inclusion of these species into the classification of aspen. Strand et al. (2009a) report success in using LSU methods on Landsat TM to predict aspen cover, showing a significant relationship with ground-reference cover data, ($p=0.05$, $n=83$, $r^2=0.52$). However, only pixels pre-classified as aspen and aspen/conifer mix were used in the analysis. The pre-classification stage of Strand's study yielded an overall accuracy of 72.3%, citing the error in part due to the confusion of aspen with the mountain shrub class. Frescino et al. (2007) found that when attempting to increase detail of classification from forest level to species-class level accuracies dropped from 94% to 63%. Considering these studies our overall accuracy and high error rate within the aspen class using the LSU method reflects the difficulty in classifying forests at the species level. It may be possible to further refine the aspen endmember spectra in order to breakout the unwanted species, though ancillary data or additional hyperspectral data may be needed. At our current accuracy of Forest Types sampled using LSU methods, and considering the already similar distributions of aspen and conifer, any interpretation of a distribution analysis using this data may be spurious.

As mentioned, most of the error involved in photointerpretation of NAIP imagery was also due to ground-reference plots classified as "Other" being interpreted as "Aspen." Three plots in this category were incorrectly interpreted to be "Aspen" when in fact the vegetation was Rocky Mountain maple. While LSU methods misclassified many spectrally similar cover types as “Aspen,” photointerpretation methods were able to use a combination of techniques to increase accuracy, confusing only maple for aspen in certain settings where differences could not be discerned. Photointerpretation of pseudo-color composite images easily distinguish between conifer and broadleaf species on the basis of tone, which is also due to the same spectral differences LSU and other classification algorithms use. However, the photo interpreter also simultaneously considers ancillary information to distinguish between broadleaf species, such as: canopy height and shape (by analyzing shadows), texture of canopy, and spatial patterns of stands. Such techniques require ecological knowledge of the species and specific knowledge of the frequency and growth forms of species occurring at the study site. Algorithms have been devised to incorporate such ancillary information into classification. Lidar can be used to estimate canopy heights and increase accuracies 16-20% (Bork and Su, 2007) . Texture can be calculated based on variance of tone over a given area (Haralick et al., 1973) and object oriented methods of classification can specify size and shape of particular cover classes. Knowledge and rule based methods can also be incorporated to allow the analyst to use their site-specific knowledge of cover classes (Dobson et al., 1996). However, these methods require expert image analysts and have potentially high associated costs. On the other hand, benefits are derived from automated workflows which increase efficiency when applied across large extents. This is an important consideration if the project includes a large number of sample plots from which to sample forest canopy composition, or if the goal is to produce a continuous map of actual aspen/conifer distributions.

Our results suggest using photointerpretation of NAIP imagery to sample forest canopy cover is a viable option for either moderate extent projects or projects lacking technical expertise and/or funding. This recommendation is due to the accuracy of NAIP photointerpretation methods being much higher, at 94% overall accuracy, than linear spectral unmixing methods based solely on multispectral Landsat data. In addition, Kappa analysis of photointerpretation methods also indicate very high agreement with ground-reference data (Jensen, 2004), a value that seems consistently higher than the multispectral classification methods reviewed for this study (Walsh, 1980; Frescino et al., 2007; Lowry et al., 2007; Strand et al., 2009a). However, while photointerpretation of NAIP imagery performed better than LSU methods to sample plots of aspen/conifer compositions, sampling a large number of plots or landcover mapping projects requiring aspen/conifer distribution maps continuously across landscape scales are not practical using NAIP photointerpretation methods. However, it is feasible to use NAIP sampling methods as ground-reference data to produce these large-extent continuous distribution maps with the use of LSU or other multispectral classification methods.

### 2.4.2 GIS-derived Variables

The GIS-derived variables do not show a strong relationship to forest distributions. The square of the canonical correlation (equivalent to $R^2$ in multiple regression) indicates only 27% of the variance in the original dataset can be accounted for by the variables selected for the optimum model (Table 2.5). This low percent of variance explained, however, is also characteristic of other tree species distribution models . McKenzie et al. (2003) used similar variables to individually model 14 conifer species using a generalized linear model approach. The percent deviance explained (a logistic model $R^2$) ranged from 10.7%-51.4%. Although we did not model aspen and conifer separately, due to the high degree of overlap in their habitat we would expect to see an estimate similar to 27% for each group.

The canonical correlation solution to discriminating between Forest Type groups shows a high degree of overlap in environmental space (Fig. 2.4). This indicates that aspen and conifer share very similar habitat requirements. The high degree of overlap in environmental space is also shown by the models inability to accurately predict Forest Types, hence the prediction error is only reduced 42% compared to a null model with random variables. However, with that said, there is separation in habitat between aspen and conifer-present plots primarily along the gradient (1st canonical variate) represented by topographic position (SolRad) and soil moisture (SWB). Unfortunately, ecological interpretation of these habitat patterns depicted by the discriminant analysis is difficult considering the limitations imposed by the spatial uncertainties of the site water balance variable.

Habitat patterns, indicating areas of non-overlap between aspen and conifer-present plots, may be exaggerated due to the potential bias of the site water balance variable (SWB). Soil water availability is difficult to quantify using indirect means (e.g. within GIS), and may contain a high degree of uncertainty. The greatest source of error in our method stems from the soil maps used to derive available water capacity (awc) (see Appendix C). The soil maps are course resolution and often rely on vegetation to determine soil physical properties in remote regions, whereas agricultural areas rely primarily on actual soil samples to determine soil properties (U.S. Department of Agriculture, 2011). While SWB proved to be an important variable in both predicting forest distribution and discriminating between Forest Type groups, its potential bias makes us hesitant to interpret its influence.

On the other hand, solar radiation (SolRad) is robust, is strongly related to forest distributions, and performs well on its own in distinguishing between aspen and conifer habitat. SolRad is essentially a variable integrating both slope and aspect, representing topographic position. With a resolution of 30 $m^2$, it is relatively sensitive to microclimatic conditions determined by subtle changes in topography. Topographic variables have been shown to be effective local-scale surrogates for resource gradients that directly affect physiological functions and therefore plant performance, such as water availability, temperature, and sunlight (Stage and Salas, 2007). In addition, variables directly generated from digital elevation models (DEMs), such as topographic position, can be very accurate especially in mountainous terrain, and have been successfully used in vegetation modeling (Moore et al., 1991; Guisan and Thuiller, 2005). ANOVA results indicate that even without SWB, SolRad can significantly distinguish between the group means, showing a general pattern in distributions of aspen and conifer-present plots according to topographic position. This provides a more robust model which relies on more precise variables for interpretation, while also considering unbalanced group sample numbers. It should be noted, however, that aspen distribution is often considered to be moisture limited (Mueggler, 1988). We may expect aspen to prefer sites at the higher range of solar radiation values, which ameliorate evapotranspirational demands through increased soil water capacities. Therefore variables considering soil properties, such as SWB, would be extremely important in predictive modeling applications if issues regarding spatial uncertainties and bias could be resolved.

We have only modeled aspen and conifer habitat within a specific study site. Over regional scales, relationships between topography and Forest Type distributions may break down resulting in skewed response curves that may be difficult to model. In that case, inclusion of climatic variables in our analysis, such as total precipitation (TP) and daily average air temperature (DAAT), which are considered to be important forces driving plant distribution patterns, can improve a models predictive power both spatially and temporally. Resulting models can then be applied to predict species response across large scales and to a changing climate (Guisan and Zimmermann, 2000). However, at the scale of our study site both TP and DAAT are highly correlated with elevation, and considering that they are only significantly related to forest distributions in concert with SolRad and SWB, they are most likely only accounting for elevational differences in topographic position.

### 2.4.3 Conclusions

According to our results, GIS and remote sensing methodologies can effectively be used to sample canopy cover and model habitats of aspen and conifer. Although for this study we only sampled 250 plots within a 33,000 ha area, sampling the large number of plots needed to sufficiently account for a species potential distribution could be accomplished with reasonable effort using photointerpretation of NAIP imagery. Output from such methods can accurately estimate dominant canopy cover allocated to aspen and conifer-species groups. However, interpretation of aspen and conifer habitat models would be improved with additional data on forest age structure and condition. For instance, this would aid in separating “Aspen” plots that exhibit multiple cohorts (as would be expected in a persistent aspen stand existing at the site for multiple generations) from a more singular age structure indicating a disturbance-dependent “seral” stand type.

The robust nature of SolRad, being solely derived from digital elevation models, makes it preferable to SWB. However, though they are highly correlated they may not be interchangeable due to heterogeneity of soils and the evapotranspirational demands of aspen. Although SWB adds potential bias to the analysis, our results allude to a distinct aspen environmental space occurring in habitats where particular soils have the ability to ameliorate evapotranspirational demands during the driest part of the growing season. This indicates the importance of sampling a metric for soil water availability in identifying an aspen niche. However, spatial uncertainties associated with the GIS-derived soil water availability metrics, such as SWB, need to be addressed before it can be safely interpreted.

While considering that we may be overlooking important microsites due to soil properties, a robust and accessible analysis using only solar radiation indicates that there is a general pattern in habitat between aspen and conifer at our study site, indicating the viability of using GIS-derived topographic variables in aspen/conifer habitat modeling at the site-scale. Further work needs to be done to see if such patterns hold up at regional scales.

**Table 2.1** Forest Type groups as classified from percent aspen and conifer canopy cover.

| Forest Type Groups | Description |
|---|---|
| 1 Aspen | > 90% aspen canopy cover. |
| 2 Conifer | > 90% conifer canopy cover. All conifer species are lumped within this group. |
| 3 Mixed | Mixed aspen and conifer plot. Neither is greater than 90% of the canopy. |
| 4 Other | > 90% landcover representing something other than aspen or conifer. |

**Table 2.2** Error matrix derived from photointerpreting color infrared NAIP imagery.

| | | Ground Truth Reference Data | | | | |
|---|---|---|---|---|---|---|
| | | Other | Aspen | Conifer | Mixed | Row Total |
| NAIP Interpretation | Other | 24 | 0 | 0 | 0 | 24 |
| | Aspen | 3 | 22 | 0 | 0 | 25 |
| | Conifer | 0 | 0 | 15 | 0 | 15 |
| | Mixed | 0 | 1 | 1 | 19 | 21 |
| | Column Total | 27 | 23 | 16 | 19 | 85 |

Overall Accuracy = 80/85 = 94.11%

| Producers Accuracy | Users Accuracy |
|---|---|
| Other = 24/27 = 88.89% | Other = 24/24 = 100% |
| Aspen = 22/23 = 95.65% | Aspen = 22/25 = 88% |
| Conifer = 15/16 = 93.75% | Conifer = 15/15 = 100% |
| Mixed = 19/19 = 100% | Mixed = 19/21 = 90.47% |

$K_{hat}$ Coefficient of Agreement = 92.07%

**Table 2.3** Error matrix derived from linear spectral unmixing of Landsat TM imagery.

| | | Ground Truth Reference Data | | | | |
|---|---|---|---|---|---|---|
| | | Other | Aspen | Conifer | Mixed | Row Total |
| Linear Unmixing | Other | 13 | 1 | 0 | 2 | 16 |
| | Aspen | 11 | 18 | 1 | 5 | 35 |
| | Conifer | 1 | 0 | 12 | 1 | 14 |
| | Mixed | 2 | 4 | 3 | 11 | 20 |
| | Column Total | 27 | 23 | 16 | 19 | 85 |

Overall Accuracy = 54/85 = 63.52%

| Producers Accuracy | Users Accuracy |
|---|---|
| Other = 13/27 = 48.14% | Other = 13/16 = 81.25% |
| Aspen = 18/23 = 78.26% | Aspen = 18/35 = 51.42% |
| Conifer = 12/16 = 75% | Conifer = 12/14 = 85.71% |
| Mixed = 11/19 = 57.89% | Mixed = 11/20 = 55% |

$K_{hat}$ Coefficient of Agreement = 51.05%

**Table 2.4** Variable selection results for discriminant analysis. Variables were selected using McHenry's algorithm (1978) run in NCSS (Hintz, 2009). The variables selected were: total annual precipitation (TP), annual average solar radiation (SolRad), daily average air temperature (DAAT), and site water balance (SWB). Selection of variables was based on an F-test using the amount of decrease in Wilk's Lambda if the variable was removed from the model (α=0.05) (shown in the columns labeled "Removed"). Also shown is the significance of the variables on their own according to Wilk's Lambda (α=0.05) (shown in the columns labeled "Alone"). The column "R-Squared Other X's" indicates the correlation with the currently selected model (all variables up to that point) and the next proceeding variable.

| Variable | Removed Lambda | Removed F-Value | Removed F-Prob | Alone Lambda | Alone F-Value | Alone F-Prob | R-Squared Other X’s |
|---|---|---|---|---|---|---|---|
| TP | 0.8027 | 23.10 | 0.000000 | 0.9943 | 0.55 | 0.5799 | 0.6935 |
| SolRad | 0.7890 | 25.12 | 0.000000 | 0.9230 | 7.96 | 0.0004 | 0.8295 |
| DAAT | 0.9002 | 10.41 | 0.000051 | 0.9930 | 0.67 | 0.5138 | 0.6148 |
| SWB | 0.9418 | 5.81 | 0.003567 | 0.9629 | 3.67 | 0.0272 | 0.7956 |

**Table 2.5** Discriminant analysis using canonical correlation to find optimum combination of variables represented by two canonical variates. "Ind'l Pcnt" and "Total Pcnt" represent the amount of variance explained in the reduced dataset for each variate compared to the total explained, respectively. The significance of the variate in explaining the variance in the original dataset is estimated by an F-test (α=0.05) of the canonical correlation (Canon Corr). The square of the canonical correlation (Canon Corr$^2$) is equivalent to an $r^2$ in multiple regression. Wilk's Lambda represents the ability of the variate to seperate the Forest Type groups, whereas lower value equals better discrimination.

| Variate | Eigenvalue | Ind'l Pcnt | Total Pcnt | Canon Corr | Canon Corr$^2$ | F-Value | Numer DF | Denom DF | Prob Level | Wilks' Lambda |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | 0.3791 | 95.2 | 95.2 | 0.5243 | 0.2749 | 8.7 | 8.0 | 376.0 | 0.0000 | 0.7114 |
| 2 | 0.0191 | 4.8 | 100.0 | 0.1371 | 0.0188 | 1.2 | 3.0 | 189.0 | 0.3085 | 0.9812 |

**Table 2.6** Correlation between variables selected for the final model and canonical variates. The variables represented are: total annual precipitation (TP), annual average solar radiation (SolRad), daily average air temperature (DAAT), and site water balance (SWB).

| | Canonical Variate | |
|---|---|---|
| Variable | Variate 1 | Variate 2 |
| TP | -0.1228 | -0.0024 |
| SolRad | 0.4451 | 0.6533 |
| DAAT | -0.0120 | 0.6019 |
| SWB | -0.2445 | -0.9070 |

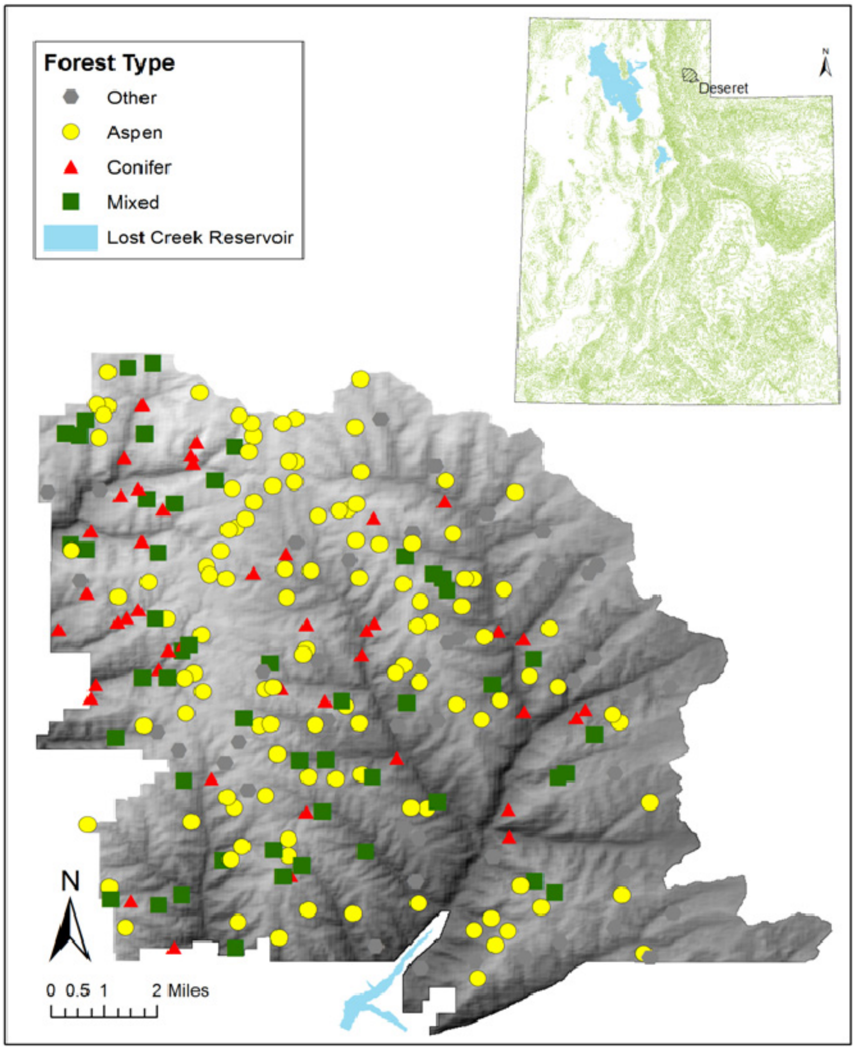

**Fig. 2.1** Map of the Deseret Land and Livestock (DLL) ranch study site showing distribution of sample plots classified into Forest Types. DLL study site is 33,100 ha and located in the Monte Cristo range in the Northern Wasatch Mountains within the western mountainous portion of DLL. A total of 250 sample plots were randomly distributed within the forest mask and classified into Forest Types using photointerpretation methods on NAIP CIR imagery.

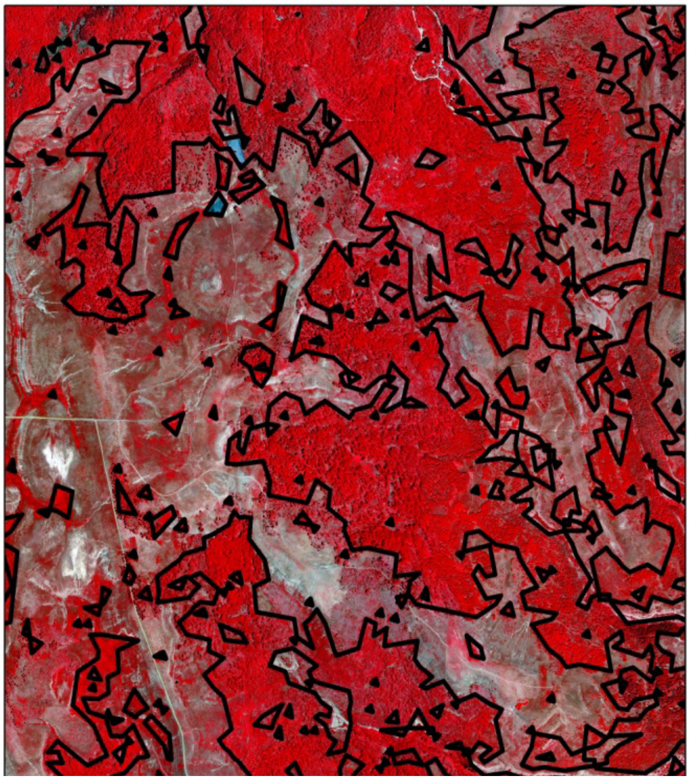

**Fig. 2.2** Forest mask overlaid on a pseudo-color NAIP CIR image of aspen forests on the Cedar Mountain plateau. Forested areas (within black polygons) were separated from non-forested areas using an ISODATA unsupervised classification algorithm on a June 2010 Landsat TM image in ENVI image processing software (Research Systems Inc., 2010). An initial 20 clusters were classified and then grouped into forest or non-forest using 1-m resolution NAIP imagery. Clusters that represented mixed forest and non-forest pixels were included within the forest polygons.

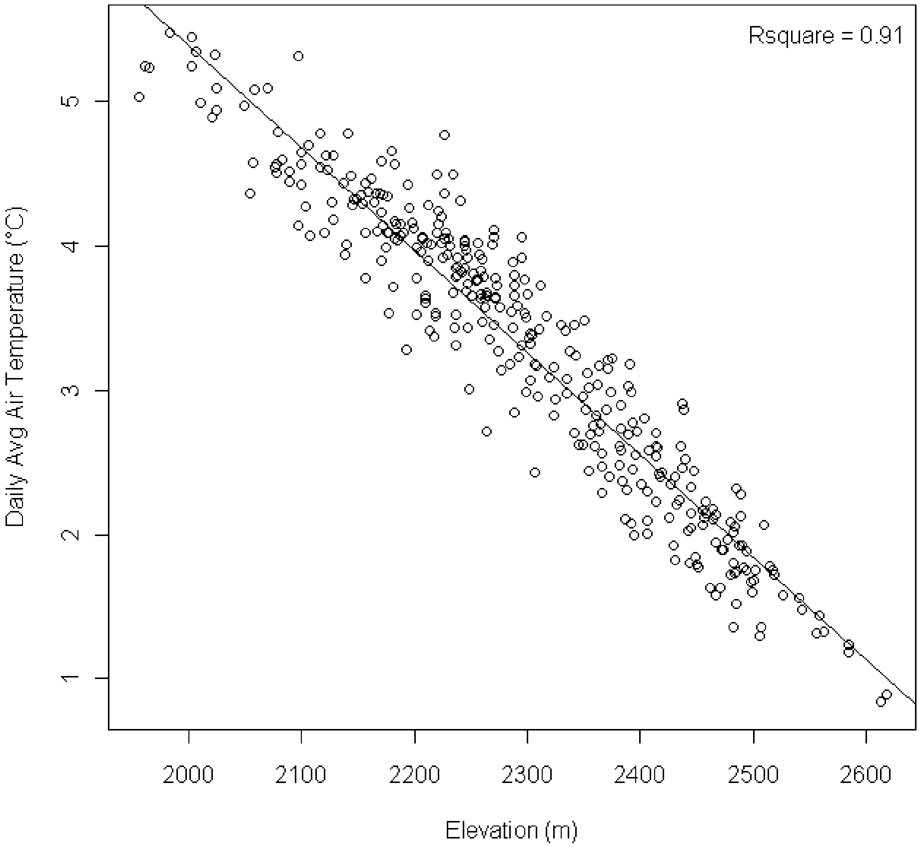

**Fig. 2.3** Regression of DAYMET temperature data with elevation. Elevation was resampled to 1-km grid using average elevation value, in order to match resolution of temperature grid. Best fit line ($\hat{Y}=19.58-0.007092X_i$) represents lapse rate across entire DLL study site and was used to interpolate temperature values down to 30-m resolution.

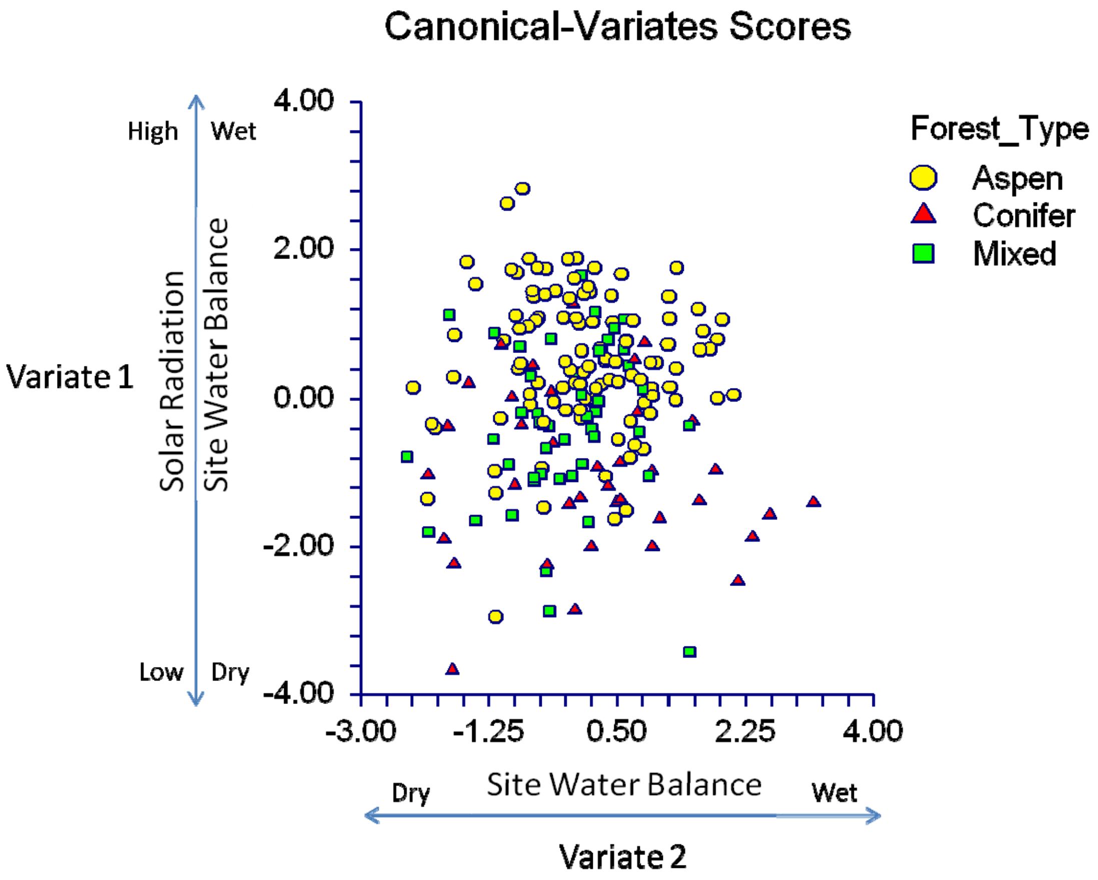

**Fig. 2.4** Plot of the first two canonical variate scores. Variables with the highest loadings are depicted next to their associated variate axes. The direction of the relationship of the variables to their associated canonical variate is shown by the arrows.

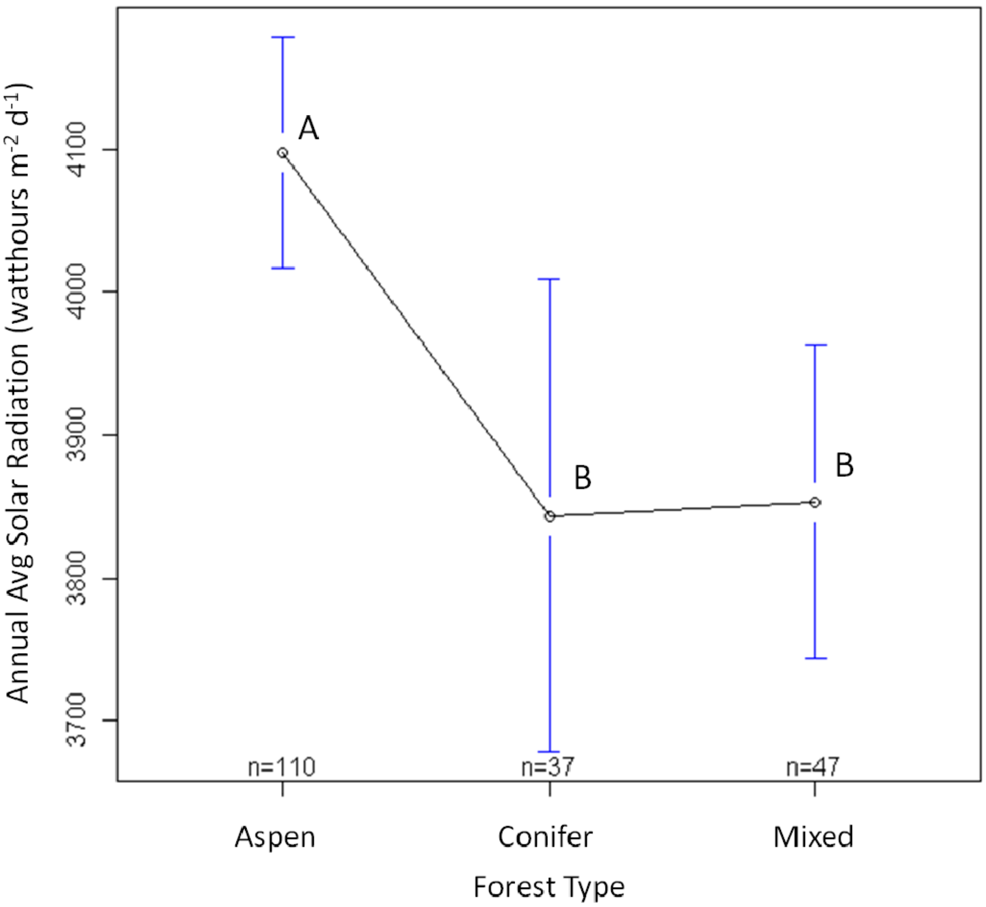

**Fig. 2.5** One-way Analysis of Variance for the DLL dataset. Letters indicate significant differences according to Tukey-Kramer multiple comparison procedures. Bars show individual 95% confidence intervals about the means. The number of samples in each Forest Type group are indicated above the X axis.

## CHAPTER 3

## MODELING A STABLE ASPEN NICHE WITHIN ASPEN-CONIFER FORESTS OF UTAH[1]

### 3.1 Introduction

In the Intermountain West aspen (*Populus tremuloides* Michx.) occurs with conifer in mixed stands as well as in adjacent pure communities and is often assumed to be seral to conifer species within this landscape (Baker, 1918, 1925; Bartos et al., 1983). The successional trajectory of aspen to conifer is described as deterministic, where aspen requires disturbance or will eventually be replaced by encroaching conifer species (Debyle et al., 1985). However, many studies show evidence for both "seral" and "stable" aspen community types (Langenheim, 1962; Betters and Woods, 1981; Mueggler, 1988; Romme et al., 2000), describing a "stable" aspen community as one that persists free of conifers and is self-regenerating. Though individual studies have documented stable aspen communities, environmental factors describing this stable aspen niche space have not been thoroughly explored on a landscape scale. With aspen cover potentially decreasing (Bartos and Campbell, 1998; Rogers, 2002; Di Orio et al., 2005), there is an immediate need for such a study to model and classify stable and seral aspen sites in order to manage and prioritize aspen restoration projects.

Aspen plays a crucial role in Utah and the greater Intermountain West. Aspen understory communities are often found to have higher species richness and productivity then surrounding community types (Debyle et al., 1985), and as such is an important habitat for a multitude of wildlife such as birds, wild ungulates, and an essential summer range for domestic livestock (Debyle et al., 1985; Bartos and Campbell, 1998). It is considered an important icon of the West (Ritter, 2005) and has been used in tourism and advertising.

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A number of studies show that aspen cover, throughout portions of its range, is declining (Bartos and Campbell, 1998; Rogers, 2002; Di Orio et al., 2005). This decline has been associated with a change in fire regimes, herbivore populations, and climate (Romme et al., 1995; Baker et al., 1997; Hessl and Graumlich, 2002; Shepperd et al., 2006). Bartos et al. (1983), using a deterministic stand simulation model based on the interspecific dynamics of aspen-conifer forests, suggests that without disturbance over the past century, a shift from aspen to conifer dominance will occur. This trend seems to be supported by field evidence of aspen stand structure. Mueggler (1989, p. 42) looked at 713 aspen dominated forest plots over nine National Forests in Utah, southeastern Idaho, and western Wyoming. He found that 95% of these stands are dominated by "mature or over-mature trees," and one-sixth of these are in the 120 year category and "expected to deteriorate rapidly." Sheppard (1990) sampled 140 aspen stands in Colorado and southern Wyoming and grouped them into age classes, recording 14% young stands (<40 years), 23% middle aged stands (50–60 years), 60% mature stands (80–100 years), and 4% old stands (>140 years). In addition to over-mature stands, repeat photography methods have shown a general trend towards increased conifer cover. Gruell (1983, p. 24) looked at photographs from 1871-1982 in the northern Rockies and found that due to fire suppression in moist upland forest systems there was a "striking… widespread increase in the density and distribution of conifers." In the Fishlake National Forest of central Utah, Kay (2003, p. 10) found that aspen was "usually replaced by invading conifers" in 64% of the aspen photosets.

While aspen is undoubtedly being encroached by conifer in some areas, there is intriguing evidence that it may be persisting and even expanding its distribution in others (Langenheim, 1962; Betters and Woods, 1981; Mueggler, 1988; Romme et al., 2000). Manier and Levan (2002) found a general increase in forest cover in the upper montane and sub-alpine forests of Colorado and, in particular, found that aspen cover increased on 79% of all sites. Sheppard et al. (2006, p. 47) notes that in the Sierra Nevada the photographic record "seems to bear out historic and climatic evidence of intense disturbance in the $19^{th}$ century followed by advancing succession of shade-tolerant trees in the $20^{th}$ century," but also points out certain instances where aspen has remained vibrant and stable and even expanding over a hundred year period. These temporal studies suggest that at some sites aspen has remained in a persistent or stable state. Furthermore, despite light-limiting requirements of young aspen shoots, juvenile aspen have been shown to grow under the canopy of pure aspen stands and in gaps, enabling self-regeneration and suggesting a persistent stand type (Kurzel et al., 2007). With an aim to develop a more detailed typology of "persistent" and "seral" stand structures, Kurzel et al. (2007) report that over 70% of the aspen dominant stands they surveyed did not require stand-replacing disturbance events; alternatively, they regenerated through a variety of modes, surprisingly with the majority (60%) regenerating "episodically" with a large pulse of suckering unrelated to course scale disturbance. Although persistent aspen stands have been well documented, the biophysical factors that determine whether a particular aspen stand is "seral" or "stable" have not been sufficiently explored.

It is likely that successional processes in aspen-conifer forests are site specific, being influenced by both broad and fine-scale mechanisms. In spite of this, some studies have uncovered patterns of seral and stable aspen types according to easily measured biophysical variables. On the Owyhee Plateau in southwestern Idaho, Strand et al. (2009b)found that 14% of their pure aspen plots seemed to occupy a realized niche on south-facing slopes above 1,900 m. These aspen stands also showed characteristics of persistent stands being uneven-aged and self-regenerating. Over a 30-year period, Crawford et al. (1998, p. 201) did not notice any appreciable conifer encroachment into pure aspen stands in a study performed in the montane and subalpine forests of Gunnison County, Colorado. Where conifer establishment did occur in aspen stands it was on the “cooler, moister north-facing slopes,” noting that this was “consistent with the observation that in the Crested Butte area, aspen on northern slopes are more commonly seral to coniferous forests.”

These studies suggest that biophysical variables, such as topographic position, act as a surrogate for distinct environmental conditions that may influence conifer encroachment. We believe that using a habitat approach based on biophysical variables to model distributions of aspen and conifer will provide insight into the potential ecological mechanisms that would allow a stable aspen community to persist on the landscape and provide an ecologically meaningful classification of seral and stable aspen communities. Borrowing from the concept of a realized niche introduced by Hutchinson and Evelyn (1965) we would expect that if biophysical variables act as surrogates for the above mentioned ecological mechanisms, stable aspen communities will inhabit an environmental space, i.e. niche space, which is distinctly separate from conifer species (whereas seral aspen communities will inhabit environmental space similar to conifer species). Hutchinson recognized this as a realized niche. Within this study we propose that the realized niche is equivalent to a stable aspen niche.

We used a traditional static modeling approach to explore a stable aspen niche under the assumption that the majority of observed plots were at equilibrium. Static distribution models based on empirical datasets across large scales have been shown to effectively predict the realized ecological niche of many plant species (Guisan and Zimmermann, 2000). However, such models rely on an assumption of equilibrium in community composition, a situation that is unlikely in highly disturbed habitats and communities undergoing ecological succession. Both situations may characterize aspen stands and therefore it is difficult to assume that observed forest compositions are in equilibrium. However, with that said, a century of fire suppression policies and a moist climate (Bartos et al., 1983; Gruell, 1983; Kay, 2003; Kulakowski et al., 2004; Kusbach, 2010; Rogers et al., 2011) suggest aspen-conifer distributions are generally in the late stages of succession. This implies that if conifer has not encroached by now, it will likely not encroach within a reasonable forest management timeframe. In addition, if the majority of observed forest plots have reached an equilibrium, it was thought that sampling across multiple large study sites at a high intensity would uncover general patterns despite the possibility of pure forest compositions representing or being the result of disclimax states, recent fire, and delayed succession to conifer.

Understanding the relationship between seral and stable aspen stands and habitat variables may prove to be an important factor in deciding when and how to restore aspen at a particular site. Recently the Utah Forest Restoration Working Group (UFRWG) was formed with the purpose of reaching a consensus on critical forest issues facing Utah’s National Forests. The current issues of aspen decline are at the forefront of their agenda. Before aspen restoration projects can be implemented UFRWG recommends following a decision making framework to facilitate desired outcomes. As part of this framework, aspen habitat models classifying potential climax states for a particular treatment site in question would be efficacious in prioritizing aspen restoration efforts (O’Brien et al., 2010).

In this paper we model a stable aspen niche according to climatic and topographic variables using a generalized linear model approach. The primary objective for this research is to produce a spatially explicit model depicting seral and stable aspen habitat in order to provide additional criteria for prioritizing aspen restoration efforts. It was determined that the best way to accomplish this objective was through the use of remote sensing and GIS applications. To this end, we used photointerpretation of National Agricultural Imagery Program (NAIP) color infrared imagery to sample dominant forest cover types and GIS to derive potential predictor variables for use in the model. First, in order to characterize the study sites and determine whether we had captured the entire range of "upland" aspen stands, we compare the presence of aspen and conifer species across study sites and determine distributional limits to aspen and conifer imposed by site boundaries, potential distributional limits imposed by ecological tolerance, as well as a general comparison of the range of climatic variables between sites. We then use a generalized linear model (GLM) of the "binomial" family to predict the probability of aspen dominated sites. Finally, we interpret the results of the GLM in terms of a stable aspen niche and discuss the limitations of such interpretations imposed by both the ecological processes involved and the analytical methods used. Considering these limitations and various management scenerios, we produce potentially useful spatial products depicting relative rate of conifer encroachment and categorical maps classified from decisions made based on receiver operating characteristic curves and prediction-conditioned fall-out rates.

## 3.2 Methods

### 3.2.1 Study Areas

Four sites within the state of Utah were systematically chosen for this study (Fig. 3.1). At these sites prior aspen research had been conducted by researchers at Utah State University (Kusbach, 2010; Rogers et al., 2010). Much of the data from this prior research was adapted and used as "ground-reference" data for this current study. Although the selection of study sites was not random, we hoped to capture the majority of the regional range of "upland" aspen by sampling within these climatically distinct study sites.

The Deseret study site (DLL) is located in the Monte Cristo range in the Northern Wasatch Mountains. It is entirely private property with the study boundaries covering the western mountainous portion of the Deseret Land and Livestock ranch. The study area is 33,100 ha with elevation ranging from 1,840 to 2,660 m. The topography is moderately steep with wide areas of gently sloping terrain on ridge tops. Soils are primarily alluvial and colluvial deposits derived from conglomerates, sandstone, and some limestone and shales. Soils are considered mountain loam types with plant communities dominated by Wyoming sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) and mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle) , bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) and slender wheatgrass (*Elymus trachycaulus* (Link) Gould ex Shinners), quaking aspen, Doug-fir (*Psuedotsuga menziesii* var. *glauca*), subalpine fir (*Abies lasiocarpa*), Englemann spruce (*Picea englemannii*), and Gamble oak (*Quercus gambelii*). Historically, as with nearly everywhere across the west, grazing was a major land use at DLL. At its peak in the early part of the 1900's reports claim there were potentially 90,000 head of sheep grazing across all Deseret Livestock companies holdings, of which the DLL study site is only a portion (McMurrin, 1989). During this same time, easily accessible conifer stands were heavily logged (McMurrin, 1989). Over the years ranch management has adopted a long-term sustainable use philosophy, encouraging multiple uses of the land. To this end, there are currently 2,500 elk (*Cervus canadensis*), 3,500 mule deer (*Odocoileus hemionus*), 5,000 cattle, and 3,000 sheep that migrate from the lower meadows to the higher elevations (which make up the partitioned study area) seasonally (R. Danvir, personal communication).

Franklin Basin (FB) study site is located in the Bear River range in the Northern Wasatch Mountains. FB study site is composed of both private and Forest Service lands. The study area is 23,388 ha with elevation ranging from 1,770 to 3,030 m. Topography is moderately steep with large valleys and toe slopes. Soils in higher elevations are primarily residuum weathered from limestone, whereas the valley bottoms are composed of colluvium derived from sandstone. Soil types are considered to be shallow and stony high mountain loams in the higher elevations with more silty and clay loams elsewhere. Plant communities are dominated by curl-leaf mountain mahogany (*Cercocarpus ledifolius* Nutt. ex Torr. & Gray), mountain big sagebrush, quaking aspen, and mixed conifer stands of Douglas-fir, subalpine fir, and limber pine (*Pinus flexilis*). Grazing across the area, especially within the last half of the 20th century, is thought to be more intense than the Deseret study site, due to the latter implementing both big game and livestock population management practices to reduce grazing impacts. Logging was equally important throughout the study area, where clear-cutting practices stripped nearly all the available timber from Cache County by 1880 (Bird, 1964). Both cutting and grazing regimes are thought to have resulted in the current forest structure which is characterized by mid to late-seral stages (Kusbach, 2010).

Cedar Mountain (CM) study site is located southeast of Cedar City on the northern edge of the Colorado Plateau, abutting the southern reach of the Wasatch Mountains. CM study site is nearly all private property with a small portion of Forest Service at the northeast corner. The study area is 27,210 ha with elevation ranging from 2,480 to 3,160 m. The study site covers a high-elevation plateau characterized by gently rolling topography, dropping precipitously near the study boundary edge into arid sandstone canyons. Soils are primarily colluvium, alluvium, and residuum derived/weathered from sedimentary rock and igneous rock. Soil types are generally high mountain loams with some stony loams. Land use on the plateau since Euro-American settlement has been largely defined by intensive sheep grazing, which is thought to have “transformed understory communities…from forb to graminoid dominated” (Rogers et al., 2010, p. 488). Intensive land use on this landscape is thought to have influenced the forest structure that is seen on the plateau today. Mature and decadent stands of pure aspen are the dominant forest cover type with some mixed conifer/aspen and a noticeable paucity of pure conifer.

Book Cliffs (BC) study site is located north of Green River on the eastern edge of the Tavaputs plateau at the state boundary with Colorado. BC study site is on Bureau of Land Management lands. The study area is 18,000 ha with elevation ranging from 2,075 to 2,611 m. Topography is very steep with sharp ridges and narrow valleys and generally lacks plateau-like areas. Soils are a mix of colluvium and alluvium derived from sandstone and shale with some eolian deposits over residuum derived from sandstone and shale. Soil types are generally very steep stony loams characterized by sandy textures. Lower elevations are dominated by pinyon (*Pinus edulis*) and juniper (*Juniperus scopulorum*), and Doug-fir, while aspen and subalpine fir are seen at higher elevations.

### 3.2.2 Sample Design

For the purposes of this study only the "upland" aspen stand type is considered, as defined by the Utah Forest Restoration Working Group (O'Brien et al., 2010). This stand type includes primarily large contiguous stands that are not restricted to hydrologic features, as opposed to "stringers" and "snow-pocket" aspen types. We refined our target population for two reasons: (1) according to the UFRWG, the upland aspen type is one of the major ones "for which management or restoration decisions are repeatedly being made on the National Forests of Utah" (O'Brien et al., 2010, p. 8); (2) and not including aspen types defined by unique hydrologic features allowed us to circumvent using resource gradients, instead using direct and indirect gradients within the model, as defined by Austin (1980).

A stratified random sample design was used to generate approximately 250 30x30 meter plots within forested areas at each study site. Forest and non-forest areas were stratified by creating a forest mask using an ISODATA unsupervised classification algorithm in ENVI image processing software (Research Systems Inc., 2010) on a July 2008 Landsat 5 TM image acquired from the MRLC Landsat database (http://www.mrlc.gov/). MRLC landsat products have undergone geometric and radiometric corrections and have been converted to at-sensor reflectance (Huang et al., n.d.). At each plot canopy cover was interpreted using NAIP color infrared 2009 imagery. At 1-m resolution it was not possible to visually identify individual conifer species; therefore, conifers were lumped into one group during the photointerpretation phase. Canopy cover was then classified into Forest Type groups (Table 3.1). An accuracy assessment of Forest Type groups was performed using approximately 80 ground-reference plots for each site. Ground-reference data was gathered by using on-the-ground ocular estimates of canopy cover by species and then classified into Forest Type groups. The general accuracy of the photointerpretation sampling method was considered to be high enough for use in the analysis (Table 3.2). Errors in the photointerpretation process were primarily the result of confusing aspen with other structurally and spectrally similar broadleaf species such as canyon maple (*Acer grandidentatum*), in addition to varying canopy heights casting shadows, which were in a few cases misinterpreted to be conifer.

### 3.2.3 Generating Climatic, Physical, and Biophysical Variables in GIS

All variables used in this study were calculated using R (R Development Core Team, 2004) and Python (Van Rossum, 2001), integrated within the ArcGIS Model Builder environment (ESRI, 2010). Variables were grouped into climate, physical, and biophysical (Table 3.3).

#### *3.2.3.1 Climate and Physical Variables*

Raw climate data was acquired for each site from DAYMET (Thornton et al., 1997). DAYMET temperature and precipitation data are 18-year averages supplied in 1-km raster format interpolated from field weather stations. In order for the model to be sensitive to fine scale variability in forest type distributions, the raw daily average air temperature at 1-km resolution was downscaled to 30-m resolution to match other variables. DAYMET models used to interpolate temperature data from dispersed weather stations are based on a simple linear relationship with elevation, thus making the task of downscaling one of uncovering the lapse rate used in the initial DAYMET models for a given area (Zimmermann et al., 2007). A lapse rate was calculated for a site by regressing national elevation dataset values (30-m resampled to 1-km using an average elevation value) against the course grid DAYMET temperatures (Fig. 2.3). This lapse rate was then used to interpolate temperature for any given elevation. A geographic overlay of the digital elevation model (DEM) and the residuals from the regression analysis shows residuals increasing in areas of steep terrain indicating the spatial uncertainty in assigning a single temperature value to an area of 1-km$^2$ within high topographic relief, reinforcing the need to use fine scale temperature values in these areas.

Although precipitation is also related to elevation and could be downscaled using the same methods as used for temperature, it was decided to forego downscaling of precipitation. Precipitation events are much more widespread and irregular in their nature. For this reason it is better to keep them at a coarser resolution. However, coarse scale 1-km resolution precipitation data was used to calculate fine scale variables such as potential evapotranspiration and soil water balance. This may have affected the ability of such variables to detect differences between forest types adjacent to one another.

Solar radiation, slope, and aspect were calculated using ArcGIS Spatial Analyst tools. The equations used to calculate solar radiation are based on a Hemispherical Viewshed Algorithm. These values were overlaid with estimates of direct plus diffuse radiation to get monthly total radiation values for each pixel in a surface raster. For the SolRad variable, these values were then converted to an annual daily average solar radiation in Wh m$^{-2}$. Radiation estimates use solar zenith angles and thus, solar radiation values will vary across sites due to differences in latitude. The equations also use azimuth angles of the intercepting DEM surface to calculate angles of incidence, so values can be interpreted as above-canopy solar radiation. Aspect (degrees) was transformed into a ecologically meaningful variable based on a symmetric radiation wetness index (Roberts and Cooper, 1989).

$$Cos(aspect - 30)/180 * \pi) + 1)/2 \qquad (1)$$

*3.2.3.2 Biophysical Variables*

Potential evapotranspiration (mm $d^{-1}$) was calculated using the empirical equation of Jensen and Haise (1963), which is specifically calibrated for the arid western United States.

$$pET = R \ / \ 2450 * (0.025T + 0.08) \qquad (2)$$

where, $R$ is mean daily solar radiation in units of kJ $m^{-2}$ $d^{-1}$, and $T$ is mean daily air temperature (°C). Potential evapotranspiration values from this equation are in mm $d^{-1}$. For sake of consistency with other variables, pET is shown in cm $d^{-1}$.

Site water balance is a running sum of the difference between potential evapotranspiration and precipitation, while not allowing any excess water to exceed the site-specific soil water capacity. Soil water capacity for each cell is derived from the Soil Survey Geographic Database (http://soildatamart.nrcs.usda.gov) (see Appendix C). This “bucket” method for calculating site water balance is very similar to Zimmermann and Roberts (2007), which was based on the concept developed by Grier and Running (1977). This method differs by running the water balance from January-September (the end of the growing season) without concern for when “recharge” (e.g. precipitation exceeds evapotranspiration) occurs. It was determined that all sites reached the maximum soil water capacity during the winter months starting the growing season with as much water as the soil allows. Assessing the soil water balance in September, essentially gives an index of site dryness directly after the period when plants need moisture the most.

### 3.2.4 Data Analysis

The categorical Forest Type groups were transformed into a binary dependent variable by assigning a 1 for “Aspen” Forest Type and a 0 for “Mixed” and “Conifer” Forest Types (referred to as conifer-present Forest Types). In this way, the model predictions of higher probabilities are the result of both higher frequencies of the “Aspen” Forest Type occupying that habitat as well as a low occurrence of conifer-present Forest Types (e.g. “Mixed” and “Conifer” Forest Types). The habitat with the highest probability can then potentially be interpreted as a stable aspen niche space. However, as later discussed, this interpretation is dependent on other factors. A generalized linear model (GLM) of the binomial family was then fit using 100% of the data from all four sites. All analyses were conducted in R (R Development Core Team, 2004).

Other modeling approaches were considered for this study, such as discriminant function analysis (DA) and classification and regression trees (CART). While the former is very similar to logistic regression in a GLM, in the regard that both require categorical groups as the response variable, DA differs primarily by aiming to uncover the correlative structure between the groups, whereas logistic regression emphasizes prediction (Tabachnick and Fidell, 1996). GLM’s are also very flexible in their statistical assumptions as the linear predictor is related to the dependent variable through a link function, which allows for non-normal distributions and unequal variances to be transformed to linearity (Guisan et al., 2002). DA on the other hand has strict assumptions not often meet by plant species data (McCune and Grace, 2002). CART models are also nonparametric in nature and have become fairly common in ecological applications that involve geographic information systems due to the binary, “if…then…,” statements as represented within the model tree (Moore et al., 1991). These trees act much the same as a dichotomous key used for plant identification, and therefore exhibit a familiar format and explanatory model for researchers to follow. For our dataset it was determined that due to the high degree of environmental overlap in the categorical response variable, classification trees were both “unstable” and left the task of “pruning” the tree as arbitrary and difficult decisions to make.

Multivariate outliers were located by calculating a Euclidean distance matrix from scaled environmental variables as recommended by McCune and Grace (2002). The average distances of a particular sample unit to all other sample units were then plotted in a frequency histogram and all sample units that fell above three standard deviations were vetted individually for errors and removed if found.

#### *3.2.4.1 Model Calibration*

Model calibration as defined by Guisan and Zimmerman (2000) involves both optimizing the model by assessing “fit,” as well as predictor variable selection and transformation. The first and often most difficult step is selecting which variables to use in the model. Since the goals of the analysis were to both explain and predict patterns in the data, the selection of independent variables hinged on both the explanatory power of the final variables and the model “fit.” Although variable selection algorithms exist to automate the process, such as stepwise and backward selection routines, we applied instead a “knowledge-based” concept which takes into account the precision of each variable as well as the modeling project goals.

Austin (1980) makes the distinction between resource, direct, and indirect ecological gradients, which is pertinent to selection of predictor variables. Resource gradients are variables such as water, nutrients, and light. Direct gradients have direct physiological importance but are not necessarily consumed, such as temperature. Indirect gradients are those that have no direct influence on physiological performance such as topography, slope, and aspect. Direct climatic variables and the biophysical variables that are derived from them are less precise than indirect topographic variables (Guisan and Zimmermann, 2000). Surface climate maps of temperature and precipitation have multiple sources of error, such as interpolation errors and the inability to track spatially unique microclimates. These errors for the DAYMET temperature data have been magnified during the downscaling process, thus making it less precise. On the other hand, indirect topographic variables, derived from an accurate digital elevation model, are comparatively very precise, especially in mountainous terrain (Guisan and Zimmermann, 2000). These variables such as elevation, slope, aspect and in our case solar radiation (which is essentially an integration of both slope and aspect) have been shown to be effective surrogates for resource gradients (Moore et al., 1991; Stage and Salas, 2007). However, over large scales these relationships break down and the skewed response curves to these variables may be difficult to model. Resource gradients such as site water balance (SWB) also come with a degree of spatial uncertainty when calculated remotely using GIS methodologies. The greatest source of error stems from soil maps used to derive soil water availability or "bucket size" (see Appendix C). The maps are coarse resolution and often rely on vegetation to delineate soil types in remote regions, whereas comparatively more soil samples are taken in agricultural areas to determine soil type (U.S. Department of Agriculture, n.d.). In addition soil surveys are not complete for each study site.

A trade-off between precision and spatial uncertainties was made. In order to retain some degree of large-scale prediction capability within the model, total annual precipitation (TP) (Fig. 3.2) and growing-degree-days (GDD) was selected (Fig. 3.3), along with all physical variables of solar radiation, elevation, aspect, and slope in order to capture fine scale distribution patterns. SWB was not selected due to the high degree of potential error involved in its calculation. In order to avoid any collinearity issues within the model, those variables that showed a strong linear dependency were eliminated. A linear dependency occurs when one variable is a weighted average of another variable(s). Potential evapotranspiration was removed as it was essentially a linear adjustment to solar radiation, indicated by a Pearson's product moment correlation value between the two variables of 0.99. A quadratic term for total precipitation was included, as it would be expected for tree species to show a unimodal response across a large scale moisture gradient.

To optimize the model an exhaustive procedure was performed where all possible combinations of selected variables were fit within the regression model. The best fit model was determined by the amount of deviance reduction estimated through adjusted deviance squared (adjusted $D^2$). This takes the number of observations and predictors into account by weighting $D^2$ by the residual degrees of freedom (Weisberg, 2005).

$$Adjusted\ D^2 = 1 - \left[\frac{n-1}{n-p}\right] * \left[1 - D^2\right] \tag{3}$$

Significant differences in deviance reduction were assessed using a $\chi^2$ approximation with $\alpha=0.05$.

### *3.2.4.2 Model Evaluation*

There are many different methods for evaluating a binary linear model, which can essentially be thought of as quantifying in some way the predictive accuracy of the model (Harrell Jr. et al., 1996). Predictive accuracy is often divided into: quantifying the "fit" of the model through some criterion of goodness-of-fit and assessing how well the model discriminates between sites that are occupied and sites that are unoccupied (McKenzie et al., 2003). Though the two measures are often related, Manel et al. (2001) point out the need to use a range of criteria to assess model performance. In order to assess the stability of the model "fit," we used an optimism estimate of residual deviance ($D^2$) with 200 bootstrapped samples (Harrell et al., 1996; Guisan and Zimmermann, 2000). Bootstrapping allows the bias of a parameter estimate, such as $D^2$, to be assessed by multiple resampling with replacement to get an unbiased estimate. The bias is the difference between the parameter estimate and the true population value (e.g., unbiased bootstrap estimate). Overfitting results when the difference between the parameter estimate and bias-corrected value is too high leading to an unstable model (Harrell et al., 1996). In conjunction with estimating stability, the ability of a model to discriminate is also related to $D^2$. When $D^2 = 1$ the model is able to perfectly separate between occupied and unoccupied sites.

Although $D^2$ gives us a measure of predictive accuracy, binary linear models with predictions stated as probabilities can be further explored by using contingency tables and/or receiver operating characteristic (ROC) curves. For our particular model the predicted response represents probability of a stable aspen habitat, and low probability represents potential conifer habitat. Since we were aware of the potential for a high degree of overlap between aspen and conifer distributions, we used ROC curves to assess the fractions of model predictions for any given probability cutoff point (e.g., threshold) with the aim of finding an optimum threshold, and exploring thresholds with high ratios of aspen to conifer. Curves shown in this study represent the true positive rate as a function of the false positive rate. True positive rate being the proportion of correctly predicted presences and the false positive rate being the proportion of incorrectly predicted presences. A model's ability to identify sites that are occupied is always a trade-off with the rate in which it incorrectly identifies presences. If the model has no ability to discriminate the ROC curve would be a 45° line and the area under the line would be equal to 0.5. To quantify the discrimination ability of the model the area under the ROC curve can be approximated by the Wilcoxon-Mann-Whitney statistic, which gives the probability of the model correctly identifying a randomly drawn sample (Sing et al., 2005). An “optimum” probability threshold was identified by averaging 10 bootstrapped ROC curves and choosing the threshold with the highest accuracy. Accuracy is defined here, for the sake of identifying an “optimum” probability, as:

$$Accuracy = TP + TN/P + N \tag{4}$$

where, $TP$= number of true positives, $TN$= number of true negatives, $P$= number of observations labeled “1”, $N$= number of observations labeled “0”.

Further visual analysis of the model results was done to assess residuals and to help explain interactions. Model output, in terms of probability, was overlaid onto the environmental space of important predictor variables and compared to scatterplots of Forest Types for better interpretation. Data was further organized into strip plots of aspen and conifer presence for elevation, growing degree days, and total precipitation over the entire range of the site in order to determine the distributional limits to aspen and conifer imposed by site boundaries, potential distributional limits imposed by ecological tolerance, and to compare the range of the variables amongst sites. Presence data of aspen and conifer plots was derived from Forest Type groups. Plots classified as “Aspen” and “Mixed” Forest Types were grouped as aspen-presence. Plots classified as “Conifer” and “Mixed” Forest Types were grouped as conifer-presence. In addition, sample size by Forest Type groups was compared across sites to determine if certain sites may be disproportionately influencing the GLM results; a preponderance of observations of the response variable as either 0 or 1 has been shown to lead to biased estimated probabilities of presence in GLMs (McKenzie et al., 2003). To further assess site differences, frequencies of “Aspen” and conifer-present plots within interpreted stable aspen habitat were compared by site, as well as comparing boxplots showing solar radiation by Forest Types and site.

### 3.3 Results

A broad climatic range is covered across the four sites represented by total annual precipitation (TP) and growing-degree-days (GDD) (Figs. 3.2, 3.3). Elevation is highly correlated with climatic variables at the local or “site-scale” and is at a much finer resolution to aid in interpretation (Fig. 3.4), but is only biologically meaningful when considered in concert with the latter. Cedar Mountain is the only site where distributions seem to be truncated by the site boundary. At this site, the boundary was delineated according to the contour line at 2,500 m in order to be consistent with previous studies from which ground reference data was used in the accuracy assessment (Rogers et al., 2010). Otherwise, according to elevation, the entire site-specific distributions of aspen and conifer were captured within the site boundaries. At the Deseret and Cedar Mountain sites, aspen and conifer are present within the same general range of elevation. At the Book Cliffs site we can see that, with the exception of a couple of “Aspen” plots, conifer is present at lower elevations (2,100-2,300 m), while aspen is not. In this case elevation may be acting as a local proxy indicating what could be the limit of ecological tolerance for aspen in the region. This is supported by looking at GDD and TP where we can see that the Book Cliffs site is at the edge of the range of these two variables recorded across all four sites. At the Franklin Basin site we seem to have captured the other end of the spectrum. At this site TP of aspen-present plots does not exceed 115 cm, implying an upper limit. Considering that the upper elevations of Franklin Basin have the highest values of TP (primarily in the form of snowpack) and the lowest values of GDD, we also expected to see Franklin Basin exhibiting the lower GDD distributional limits of aspen-present plots. However, both Cedar

Mountain and Deseret show aspen existing at lower values of GDD than at Franklin Basin, which leads us to consider other potential reasons for the upper TP limit to the distribution of aspen.

### 3.3.1 Model Results

The final model parameters meeting the selection criteria are shown in Table 3.4. It achieved the highest adjusted $D^2$ at 0.214. Competing models containing slope and aspect were also very similar in predictive accuracy, but were "penalized" for using extra terms. Whereas, solar radiation is highly correlated with slope and aspect, essentially integrating the two variables so that high solar radiation sites are those on steep southwest facing slopes and those sites with low solar radiation are found on steep north aspects. It performs much the same way a "heat-load" index does when based on aspect, slope, and latitude (McCune et al., 2002).

Visual results of the model are shown in Figure 3.5. The model indicates that potentially stable aspen habitat exists at sites between 70-95 cm of total annual precipitation and at topographic positions receiving greater than 4,500 Wh $m^{-2}$ $d^{-1}$ of solar radiation. This range of solar radiation is equivalent to landscape positions roughly categorized as gently sloping areas, plateau tops, and south-facing slopes. The GLM predicted response of "Aspen" to solar radiation is linear. Within logistic regression when the linear relationship is back-transformed from the logit to probability we get the sigmoidal curve shown in Figure 3.6. The response of the "Aspen" forest type to TP is fit within the model using a negative quadratic term indicating a hump shaped unimodal curve (Fig. 3.7). A unimodal response of vegetation to climatic variables such as precipitation is expected and documented in other tree distribution studies (McKenzie et al., 2003). TP also interacts with solar radiation (SolRad) to significantly increase the fit of the model (Table 3.4). We can see this interaction by looking at the visual results of the model in

Figure 3.5. At low precipitation values model probabilities are higher when we also have low solar radiation values, but as we move up into areas of higher precipitation model probabilities are higher at high solar radiation values. However, at the highest precipitation values the model response is constrained by the quadratic relationship.

As we can see by comparing the scatterplot of Forest Types in Figure 3.8 to the model output shown in Figure 3.5, higher probabilities are predicted in the environmental space with high densities of "Aspen" Forest Types while also having a low degree of overlap with "Conifer" and "Mixed" Forest Types.

The dependent variable input into the model as a total of all four sites did not exhibit a preponderance of 0 or 1 (Table 3.5) and therefore should not be expected to yield analytically biased results. However, since sample plots were randomly distributed within the study sites, the total number of plots each site contributed, as well as the ratio of aspen to conifer-present plots, are unbalanced. Though this data is representative of the actual populations, it affects our interpretation of a stable aspen habitat and how we couch the overall model results. By including all four sites within the model, instead of modeling them individually, the probability of stable aspen habitat is disproportionately influenced by Cedar Mountain. This is indicated in Figure 3.9, where Cedar Mountain has a much higher frequency of both "Aspen" and conifer-present plots, within model predicted probabilities over 0.70, than the other sites. Modeling each site separately would produce different results, potentially leading to larger or smaller areas delineated as stable aspen habitat.

Site-specific solar radiation values shown in Figure 3.10, indicate similar Forest Type distribution patterns according to topography between the Deseret, Franklin Basin, and Cedar Mountain study sites. A linear response of aspen to solar radiation is shown at these sites, where "Aspen" plots are in topographic positions with high solar radiation, with "Mixed" plots at lower solar radiation and “Conifer” plots with the lowest solar radiation. The Book Cliffs are the exception to this pattern, where “Aspen” is occurring at much lower solar radiation values, which is the primary reason for the significant interaction between SolRad and TP used in the four-site model. The distinct differences of the mean SolRad values between Forest Types at the Deseret, Franklin Basin, and Cedar Mountain sites alludes to the possibility of modeling each of these sites separately, only using topographic variables, in order to arrive at site-specific interpretations of a stable aspen habitat.

### 3.3.2 Model Evaluation

The “optimism” estimate, or bias of $D^2$, from 200 nonparametric bootstrapped samples is extremely small at 0.0024, indicating a stable model. In other words, the predictive accuracy after applying the model to the population will be similar to the original estimate of $D^2$=0.2177. The bootstrapped standard error for the original $D^2$ estimate is 0.0258.

The ROC curve generated from model predictions on the original dataset shows moderate to low discrimination ability (Fig. 3.11). The area under the curve approximated by the Wilcoxon-Mann-Whitney test statistic is = 0.8026, indicating that 8 out of 10 times the model will predict a higher probability for a randomly drawn “Aspen” sample compared to a randomly drawn conifer-present sample. The accuracy, as defined by equation (4), varies depending upon probability threshold selected (Fig. 3.12). The highest accuracy is achieved when the threshold or “cutoff” is set at approx. 0.6. Setting the cutoff for classifying “Aspen” at a prediction probability of 0.6 gives us the contingency table shown in Table 3.6. This is the best balance between correctly identified “Aspen” plots and incorrectly identified “Aspen” plots. Overall accuracy, as calculated from equation (4), is the peak accuracy this model can achieve at 73%. The proportion of conifer-present plots within predicted “Aspen” habitat at this threshold cutoff is 33%. If we consider the proportion of conifer presence as a metric for interpreting stable aspen habitat we can make the decision on where to choose the probability threshold cutoff point according to this metric. Conditioning this proportion by total positive predictions gives us what is known as the "Prediction-conditioned fallout" rate (PF rate) (Sing et al., 2005), which in terms of this study can be considered the rate of conifer-present plots to all plots predicted by the model to be "Aspen" habitat.

$$PFrate = FP/TP + FP \tag{5}$$

where $FP$= number of plots falsely predicted to be "Aspen," and $TP$= number of plots correctly predicted to be "Aspen." In Figure 3.13 we can see the PF rate, or ratio of conifer-present plots, generally trending downwards to a probability cutoff point somewhere between 0.7 to 0.8. The environmental space delineated by this cutoff point has the lowest ratio of "conifer-present" plots to "Aspen" plots, and may be interpreted as stable aspen habitat. A contingency table for this threshold is shown in Table 3.7.

## 3.4 Discussion

In this study we explored the possibility of a stable aspen niche by using a generalized linear model to assess the overlap in environmental characteristics between aspen and conifer at four distinct sites across Utah. The concept of a stable aspen niche is non-traditional, as aspen is considered to be a species whose life history traits are defined by ecological succession. Aspen forests are assumed to be early seres that eventually lead to climax end-point communities composed of shade-tolerant and slow growing conifer species. Intriguing evidence in the literature suggests that at some sites aspen may remain free from conifer encroachment indefinitely, therefore existing as a stable aspen community (Langenheim, 1962; Betters and Woods, 1981; Mueggler, 1988; Romme et al., 2000; Shepperd et al., 2006; Rogers et al., 2010).

Borrowing from the concept of a Hutchinsonian, or realized niche (1965), we assumed that a stable aspen community should inhabit environmental space which does not overlap with environmental space inhabited by conifer. According to the environmental space defined by the climatic and physical variables used in our analysis, we did not find evidence of an exclusive realized aspen niche. However, we did find habitat in which aspen plots were proportionately much higher than conifer plots. While not specifically meeting the definition for a realized aspen niche, we suggest our results indicate a meaningful relationship between biophysical variables and conifer encroachment, as well as indicating habitat that has a high potential for stable aspen communities. In the following we explain our interpretation of a stable aspen habitat predicted by the model while considering the limitations to such an interpretation by both the model variables and the analytical methods used. We then address the specific objective of this research project: to produce a spatially explicit model to classify seral and stable aspen habitat in order to provide additional criteria for prioritizing aspen restoration efforts.

### 3.4.1 Interpreting a Stable Aspen Niche

The modeling approach used in this study is static. It relies on input of observational data as opposed to dynamic simulation modeling which relies more on physiological behavior of the species involved as well as detailed knowledge of successional mechanisms (Guisan and Zimmermann, 2000). However, mechanisms that affect succession in aspen-conifer systems are poorly understood, requiring dynamic modeling approaches to make potentially inappropriate assumptions. On the other hand, static model predictions of plant species distributions are commonly interpreted as a realized niche, as it is based on empirical observations of a species presence which is subject to biotic interactions and competitive exclusion. However, in order to interpret a stable aspen niche or realized niche of aspen using a static model approach, as in any niche-based analysis, we are making the major assumption that aspen-conifer distributions have reached an equilibrium, in other words sample plots represent climax or stable communities. For this reason systems influenced by successional dynamics are difficult to model using a static approach (Lees and Ritman, 1991; Guisan et al., 1999). In order to compensate for this analytical drawback, a high number of plots were sampled across four large-extent study sites under the assumption that the majority of plots have reached equilibrium and general patterns would therefore be evident in the results. There is evidence that aspen and conifer forests across the Intermountain West, in general, have shifted to late successional stages due to limited fire events caused by moist climates and wide-scale fire suppression over the past century (Bartos et al., 1983; Gruell, 1983; Kay, 2003; Kulakowski et al., 2004; Kusbach, 2010; Rogers et al., 2011). If the landscape has in general reached an equilibrium, a large-extent intensive sampling effort should therefore uncover general relationships of stable aspen-conifer distributions to environmental factors, despite the analytical “noise” induced by non-stable, or disclimax states. Considering this modeling limitation, we would assume the GLM results, showing environmental space distributions of aspen and conifer, to be "noisy", with some observed forest compositions being the result of disclimax states, recent fire, and delayed conifer encroachment (Fig. 3.14). Despite these possible states, our results indicate a strong pattern due to a relationship between biophysical variables and conifer encroachment.

If the biophysical variables used in this model were entirely representative of ecological mechanisms that explain the persistence of a stable aspen community or the prevention of conifer encroachment, we would expect to see "Aspen" Forest Type plots inhabiting an environmental space which is distinctly separate from conifer species. This was not the case.

Instead, the results indicate that an interaction between topographic position and moisture progressively influence the rate of conifer encroachment but do not prevent it entirely. We can see this progressive relationship by looking at the bivariate plot shown in Figure 3.8. Within the precipitation range of 60-100 cm, we can see the proportion of conifer to aspen generally decreasing along the vertical gradient represented by solar radiation. This same relationship is shown in the spatial representation of the model predictions (Fig. 3.5), where fewer plots with conifer-present occur with increasing solar radiation, equivalent to moving onto plateau tops and south-facing slopes. In addition, if we consider that we have taken a “snap-shot” at a particular point in the successional process, conifer to aspen proportions along this topographic gradient likely indicate probability of encroachment. In these terms, habitat delineated at the furthest end of this gradient has the highest proportion of aspen to conifer and can be interpreted as aspen communities that are the least vulnerable to conifer encroachment. It is possible the rate of conifer encroachment into these stands is extremely slow, along the lines of hundreds to thousands of years. For management purposes, such stands are often classified as stable aspen communities (Mueggler, 1988). However, this is only a possibility, since our study does not specifically consider temporal changes. Interestingly though, studies on succession and fire in lodgepole pine systems have found similar habitat where succession to climax spruce-fir forests is extremely slow (Romme and Knight, 1981). This study found that fire frequency is related to topography. Fire occurred less frequently in moist ravines and valley bottoms than on upland ridge tops, plateaus, and exposed slopes, resulting in upland sites being dominated by early succession lodgepole pine forests while north-facing slopes of ravines and valley bottoms were dominated by late succession spruce-fir forests. Lodgepole pine behaves similarly to aspen (Skinner and Chang, 1996; Shepperd et al., 2006) in its response to disturbance and role as an early successional species. Thus, we may consider fire regimes to play a role in the pattern we see in our results.

This progressive decrease in encroachment along a topographic gradient is also supported by what we know about dispersal of conifer seedlings. Conifer seeds are primarily wind-borne with nearly 50% of the seeds falling within 30 m of the parent tree, the directions determined by prevailing winds and thermals moving up slopes (Noble, 1978). Our results show conifers readily encroaching on steep north facing slopes and gradually decreasing towards the top of the slope and onto the gentle sloping plateau tops, suggesting upslope movement of conifer "seed rain" resulting in progressive conifer establishment.

While our results indicate that topographic position strongly influences the ability of conifer to encroach into aspen stands, the degree of its influence is dependent upon the amount of total annual precipitation (TP). Our results show the "Aspen" Forest Type shifting from relatively steep north facing slopes, found at the Book Cliffs site, to higher solar radiation sites on plateau tops and gentle south facing slopes as we move to higher precipitation values (Fig. 3.5). The highest probability for "Aspen," and therefore the most likely habitat for stable aspen communities, is found at the upper range of solar radiation within 60 to 90 cm of TP (Fig. 3.8). Many plant distribution studies have found similar interactions, where plant species environmental requirements can be met by shifting topographic positions along an elevational, or climatic gradient (Daubenmire, 1943; Whittaker, 1967). Although aspen has the ability to grow in many disparate environmental conditions, its distribution has been noted to be water-limited. In Mueggler’s (1988) extensive survey of both aspen and mixed aspen-conifer communities in the Intermountain Region, he found that these communities required at least 38 cm, but more commonly over 51 cm of total annual precipitation. Our results indicating the overall distributions of aspen-present plots align well with this. Interestingly, however, in a niche-based analysis, we found that at sites with less than 60 cm of TP it was more likely for aspen to share the same topographic position as conifer species, and therefore more likely to be encroached and, barring significant disturbance, converted to a conifer climax community. This is evident at the Book Cliffs site, where large contiguous stands of pure upland aspen are rare. Topographic positions, such as gently sloping areas, plateau tops, and south-facing slopes, that support aspen at the other sites, are instead inhabited primarily by Gambel oak and the occasional sparse and shrub-like aspen—which appears to be a phenotypic response to low water availability.

On the other end of the TP spectrum, at sites with TP values greater than 90 cm, conifer dominates, with no aspen or even mixed aspen-conifer plots found above 115 cm (precipitation values that are only found at the Franklin Basin site). This likely does not indicate a limit of ecological tolerance to moisture; aspen is often found in riparian areas with very high soil water availability (Mueggler, 1988). It is possible that this pattern is due to the length of the growing season. Distributions of aspen are thought to be constrained by short growing seasons at high elevations (Mueggler, 1988). Growing-degree-days is a surrogate for length of the growing season. Total annual precipitation is strongly correlated with both growing degree days (GDD) and elevation at the spatial extent of the Franklin Basin site. This correlation indicates that plots at the highest elevation, receive the highest TP, in the form of snow, and have the lowest GDD, due to long periods of low temperatures. Deciduous trees such as aspen would not be expected to do as well as coniferous species in this reduced growing season. Interestingly, however, while aspen-present plots are truncated at approximately 1,800 GDD at Franklin Basin, they are present at even shorter growing seasons at some plots at both the Deseret and Cedar Mountain sites. This suggests that aspen distribution in the upper elevations at Franklin Basin may not be entirely limited by length of growing season. It is possible that at these specific plots TP represents an environmental factor that has a strong positive influence on conifer encroachment. Such a factor may be low fire return intervals at high elevations resulting in long successional time-scales allowing conifer dominance. Fire return intervals into the subalpine zone (considered to be approximately 2,750 m for latitudes similar to the Franklin Basin site) have been estimated by various studies to be greater than 150 years, though probably more along the lines of 300-400 years (Romme, 1982; Gruell, 1983; Bigler et al., 2005), allowing plenty of time for conifer to dominate even at a slow rate of encroachment.

While the results of the niche-based analysis can be soundly interpreted as solar radiation and precipitation progressively affect conifer encroachment into aspen stands, the very low ratio of conifer-present plots to aspen plots within habitat delineated by using prediction-conditioned fallout rates, is intriguing and warrants further research. It is possible that aspen and conifer could be differentiated even further within this environmental space if plot-scale variables were included in the analysis that specifically considered soil water availability or similar soil characteristics. Our current model shows a very specific environmental space where aspen dominates, characterized by an interaction between solar radiation and precipitation, which indicates that stable aspen communities may be the result of a very specific moisture regime. Unfortunately, it is difficult to interpret exactly what the details of that moisture regime may be using only TP. Generally, throughout the Intermountain West, these are sites that experience high precipitation during the winter and periods of low soil moisture during summer, due to high insolation values. Upland aspen has been shown to effectively deal with drought stress, and is considered to “react conservatively to low soil moisture and high vapor pressure deficits” (Lieffers et al., 2001, p. 315), by regulating its stomatal conductance on days with high evaporational demand, resulting in daytime transpiration rates that are constant over a wide range of vapor pressure deficits (Hogg and Hurdle, 1997). It is possible that aspen has a higher tolerance to summer drought periods than fir and spruce, which would be appurtenant to understanding the low presence of conifer in this habitat.

In addition, specific soil characteristics and resulting soil water availability is shown to be related to pure aspen communities. These communities have been shown to be correlated to specific soil suborders within the order of Cryoborolls (Debyle et al., 1985; Cryer and Murray, 1992). These soils are characterized by high input of soil organic matter (SOM), warm soil temperatures in upper horizons, and good soil moisture content through much of the growing season, all in turn promote microbial decomposition and therefore increased nutrient availability. These warm soil conditions have been shown to promote suckering and expansion of aspen clones (Maini and Horton, 1966; Williams, 1972; Bailey, 1974), providing a mechanism for self-regenerating stands.

These same soil conditions also support productive understory communities, which may play a role in inhibiting conifer establishment. Thick aspen and understory leaf litter at the soil surface may affect the ability of seeds to come into contact with the preferable mineral soil and thus hinder germination of conifer seedlings. Studies have shown this to be the case in spruce (Coates et al., 1991). In Boreal forests smothering by fallen leaves is widely considered to slow conversion to conifers (Gregory, 1966). A component of this “smothering” effect may be the susceptibility to damping-off fungi (Tappeiner and Helms, 1971). Additionally, Langenheim (1962) reported that there were increases in conifer encroachment where the understory was thin compared to where it was thick. According to such accounts, severe long-term grazing that results in a reduction of tall forbs and shrubs with a conversion to graminoids interspersed with patches of bare ground may provide the disturbance needed and release from competition for conifer to establish and recruit into the overstory at sites that would normally support stable aspen communities.

While our modeling approach does not pinpoint specific ecological mechanisms that explain the ability of some aspen stands to remain free of conifer encroachment, it does however offer a useful tool to classify potential stable and seral aspen habitat using landscape-scale biophysical variables. This is a good starting point to begin to look for important successional mechanisms which could further refine this landscape-scale model and make it more useful for management decisions.

### 3.4.2 Management Applications

Due to recent issues raised over decline of aspen cover, in part due to conifer encroachment, aspen restoration projects are planned across many forested lands in Utah (O'Brien et al., 2010). The results from this study provide an accessible model, based on landscape-scale biophysical variables, that can be used to classify potential stable and seral aspen habitat. Such a classification is needed to provide additional criteria in deciding where and how to initiate aspen treatment projects.

The model was designed with its spatial application in mind. It has a high degree of "generality" (Levins, 1966) as it uses total precipitation as a resource gradient which is directly consumed by plants. Such resource gradients are considered robust across large spatial extents since values affect tree species distributions independent of locality. The model also considers topography, which affects site-scale distributions, lending the model a degree of "precision" (Levins, 1966). In addition, predictor variables are available and seamless for any management area of interest and can easily be made spatially explicit within GIS. Model predictions can therefore be applied, within its inferential power, to areas considering aspen treatment projects by overlaying maps of model output with maps of existing aspen cover. Products derived from this study that would be useful in this process would be the relative probability of conifer encroachment, as well as categorical maps, delineating potential seral and stable aspen habitat, classified from decisions made based on ROC curves and prediction-conditioned fall-out rates.

The relative probability of conifer encroachment is a way to represent the continuous output of the generalized linear model results. We interpret the probability of conifer to be equivalent to the probability of conifer encroachment. According to our model, a logistic transformation of the log odds gives probability of aspen compared to conifer ($\prod_{aspen}$). We get the probability of conifer by $1-\prod_{aspen}$, which can then be mapped as a continuous surface. Since this metric is on a continuous scale we can make decisions about particular aspen stands relative to other aspen stands, either within the same management area or across management areas. This may be useful in areas such as the Book Cliffs study site where the probability of conifer is very high and decisions to remove conifer through selective logging or prescribed burning must be made relative to other aspen stands in the immediate area. Using this logic, stands with a lower probability of conifer may be expected to have slower rates of encroachment and therefore longer treatment intervals.

Categorical maps, on the other hand, require an interpretation of the results into seral and stable aspen habitat. Prediction-conditioned fall-out rates provide an analytically based criteria to classify the continuous output from the model. Within the context of this study, considering the limitations of the model variables and the analytical methods used, we interpret potential stable aspen habitat to be environmental space with the lowest proportion of conifer presence. By graphing the prediction-conditioned fall-out rate, i.e. proportion of conifer to aspen conditioned on number of positive predictions, as a function of the probability cutoff point, we can see that the lowest ratio, while still retaining the highest number of positive predictions, is achieved at approximately 0.70 cutoff (Fig. 3.13) (Table 3.7). Using this method, the best possibility for stable aspen communities exists at the Cedar Mountain study site, followed by the Deseret and Franklin Basin sites, respectively (Fig. 3.9). The Book Cliff site is not predicted to have any stable aspen communities. Considered independently, both the Deseret and Cedar Mountain sites indicate a very low ratio of conifer to aspen. However, across the regional scale represented by the four-site model, there is an equivalent number of Cedar Mountain conifer-present plots as there are Deseret “Aspen” plots. At this regional scale then only Cedar Mountain retains a much higher ratio of aspen to conifer plots within this environmental space, and therefore can be interpreted more clearly as potential stable aspen habitat. Aspen habitat falling outside of that classified as stable, can be considered seral to conifer.

Such an approach may help to identify stable and seral aspen communities and prioritize restoration efforts. It must be kept in mind that this model is based on landscape-scale variables and may classify some actual stable aspen communities as seral and vice versa. However, in addition to providing a research tool for improving our knowledge of plot-scale mechanisms, it also provides a useful habitat classification of stable and seral aspen for management purposes. At a landscape scale, it may be used to prioritize restoration efforts. Maps indicating actual cover of potential stable and seral aspen cover can be produced by overlaying the discretely classified model output using the prediction-conditioned fall-out rates with actual forest cover (Figs. 3.15-3.18). Forest cover was generated by an ISODATA unsupervised classification algorithm on a Landsat TM image. Considering these maps, sites with a high frequency of seral aspen stands may be chosen for conifer-thinning or prescribed fire, while sites such as Cedar Mountain, that have a high frequency of stable aspen stands, may focus on treatments that aim to mimic stable aspen communities. These treatments might include promoting an uneven age structure through selective thinning and removing or reducing grazing pressures.

**Table 3.1** Forest Type groups binned according to percent canopy cover. Canopy cover was derived using photointerpretation of NAIP imagery.

| Forest Type Groups | Description |
|---|---|
| 1 Aspen | > 90% aspen canopy cover. |
| 2 Conifer | > 90% conifer canopy cover. All conifer species are lumped within this group. |
| 3 Mixed | Mixed aspen and conifer plot. Neither are greater than 90% of the canopy. |
| 4 Other | > 90% canopy cover of forest type other than aspen or conifer. |

**Table 3.2** Accuracy assessment of NAIP photointerpretation sampling methods. Overall accuracy is calculated by dividing the total correctly classified plots by the total plots in an error matrix.

| Study Site | Overall Accuracy |
|---|---|
| Deseret | 94.11% |
| Franklin Basin | 94.18% |
| Cedar Mountain | 94.68% |
| Book Cliffs | 88.70% |

**Table 3.3** Variables considered for use in GLM. Variables were calculated using R and Python scripting languages and integrated within ArcGIS Model Builder.

| Climate | Physical | Biophysical |
|---|---|---|
| DAAT (daily average air temperature)<br>Annual daily average air temperature averaged over an 18 year period. Downscaled to 30 meter resolution. | SolRad (solar radiation)<br>Annual daily average radiation (WH/m$^2$/day). | SWB (site water balance)<br>Running sum of the difference between TP and pET, never exceeding soil available water capacity (cm/cm; negative values indicate deficit). |
| GDD (growing degree-days)<br>Annual summation of daily average air temperatures > 0.0 $^{o}$C. | Elevation<br>30 meter National Elevation Dataset | pET (potential evapotranspiration)<br>Annual daily average potential evapo-transpiration (cm/day) |
| TP (total precipitation)<br>Total accumulated precipitation over a year (cm/yr). | Aspect<br>Cosine transformation ranging from 0-1 (wet –dry) | |
| | Slope<br>(percent) | |

**Table 3.4** Generalized linear model results. Four terms were included in the final model: solar radiation (SolRad), total annual precipitation (TP), unimodal response to TP (TP$^2$), and an interaction term between SolRad and TP (SolRad X TP). GLM was parameterized using "Aspen" (1) and conifer-present plots (0) from all four sites.

| | Estimate | Std. Error | z-value | p-value |
|---|---|---|---|---|
| Intercept | 0.7467 | 3.242 | 0.230 | 0.8171 |
| SolRad | -0.004037 | 0.0009802 | -4.118 | <0.0001 |
| TP | 0.1237 | 0.05265 | 2.349 | 0.0188 |
| TP$^2$ | -0.002967 | 0.0003715 | -7.985 | <0.0001 |
| SolRad X TP | 0.00007584 | 0.00001387 | 5.467 | <0.0001 |
| Adjusted Deviance Squared = 0.214 | | | | |

**Table 3.5** Percentage of plots by site. Forest Types are grouped according to binary response variable used in GLM. Total numbers are in parentheses.

| Forest Types | DLL<br>(199) | Franklin Basin<br>(238) | Book Cliffs<br>(128) | Cedar Mountain<br>(228) | Total<br>(793) |
|---|---|---|---|---|---|
| Aspen<br>(GLM input = 1) | 56%<br>(111) | 27%<br>(68) | 14%<br>(18) | 56%<br>(128) | 41%<br>(325) |
| Conifer & Mixed Combined<br>(GLM input = 0) | 44%<br>(88) | 73%<br>(170) | 86%<br>(110) | 44%<br>(100) | 59%<br>(468) |

**Table 3.6** Error matrix generated from model predictions on original data. Probability threshold classifying "Aspen" set at 0.60.

| | **Observations** | |
|---|---|---|
| **Predictions** | Conifer presence | Aspen |
| Conifer presence | 412 | 158 |
| Aspen | 56 | 167 |

Overall Accuracy = total correct/total sample = 579/793 = 73.01%

**Table 3.7** Error matrix generated from model predictions on original data. Probability threshold classifying "Aspen" set at 0.70.

| | **Observations** | |
|---|---|---|
| **Predictions** | Conifer presence | Aspen |
| Conifer presence | 440 | 215 |
| Aspen | 28 | 110 |

Overall Accuracy = total correct/total sample = 550/793 = 69.35%

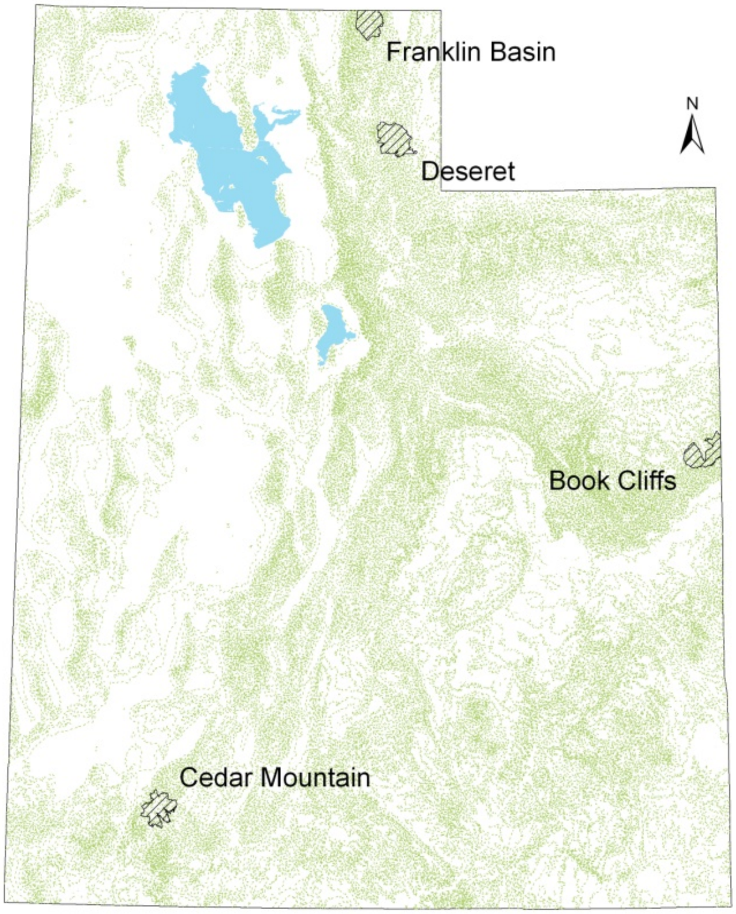

**Fig. 3.1** The geographic context of the four study sites sampled for input into the stable aspen niche model. Site locations were systematically selected according to previous aspen research. Site boundaries were delineated in order to capture entire site-scale distributions of aspen.

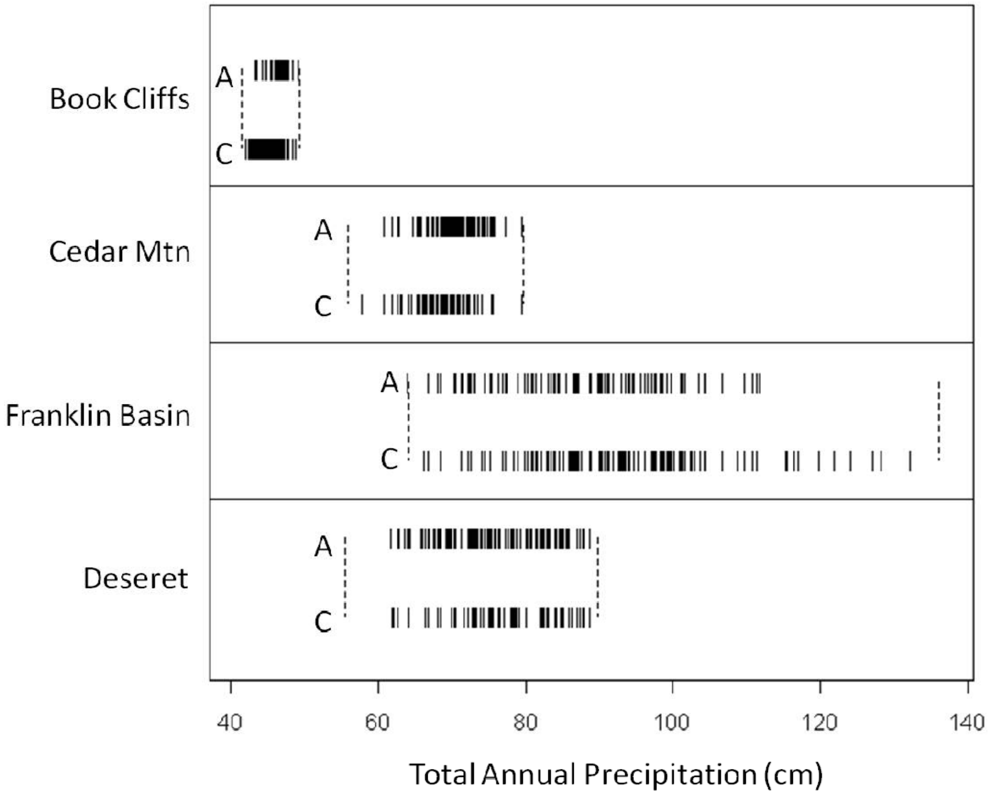

**Fig. 3.2** Range of total annual precipitation (TP) for aspen and conifer presence across all four sites. Aspen presence is indicated by "A", conifer presence by "C". Each line in stripchart represents individual sample plots. Dashed lines indicate TP limits of site.

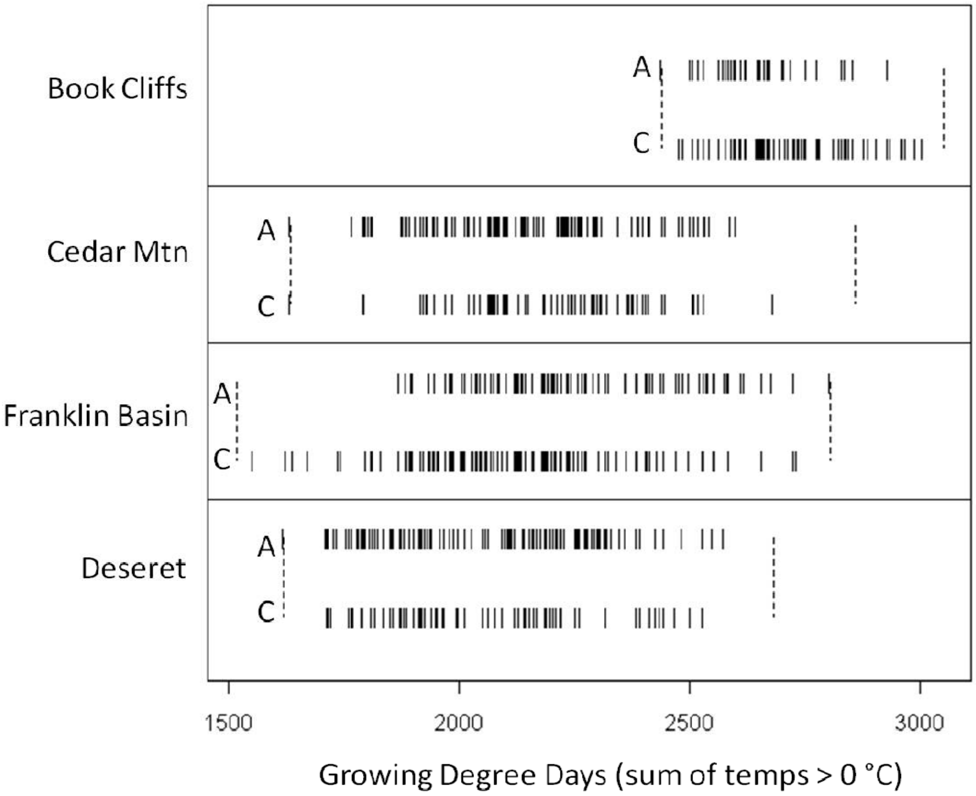

**Fig. 3.3** Range of growing degree days (GDD) of aspen and conifer presence across all four sites. Aspen presence is indicated by "A", conifer presence by "C". Each line in stripchart represents individual sample plots. Dashed lines indicate GDD limits of site.

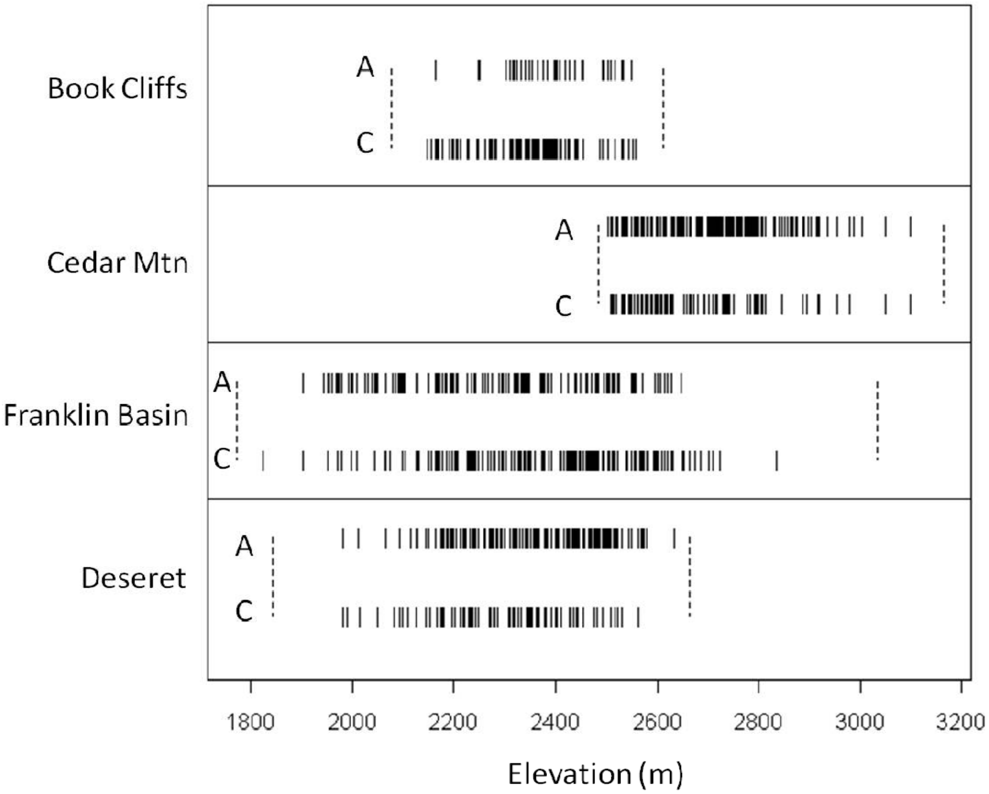

**Fig. 3.4** Range of elevation for aspen and conifer presence across all four sites. Aspen presence is indicated by “A”, conifer presence by “C”. Each line in stripchart represents individual plots. Dashed lines indicate elevation limits of site.

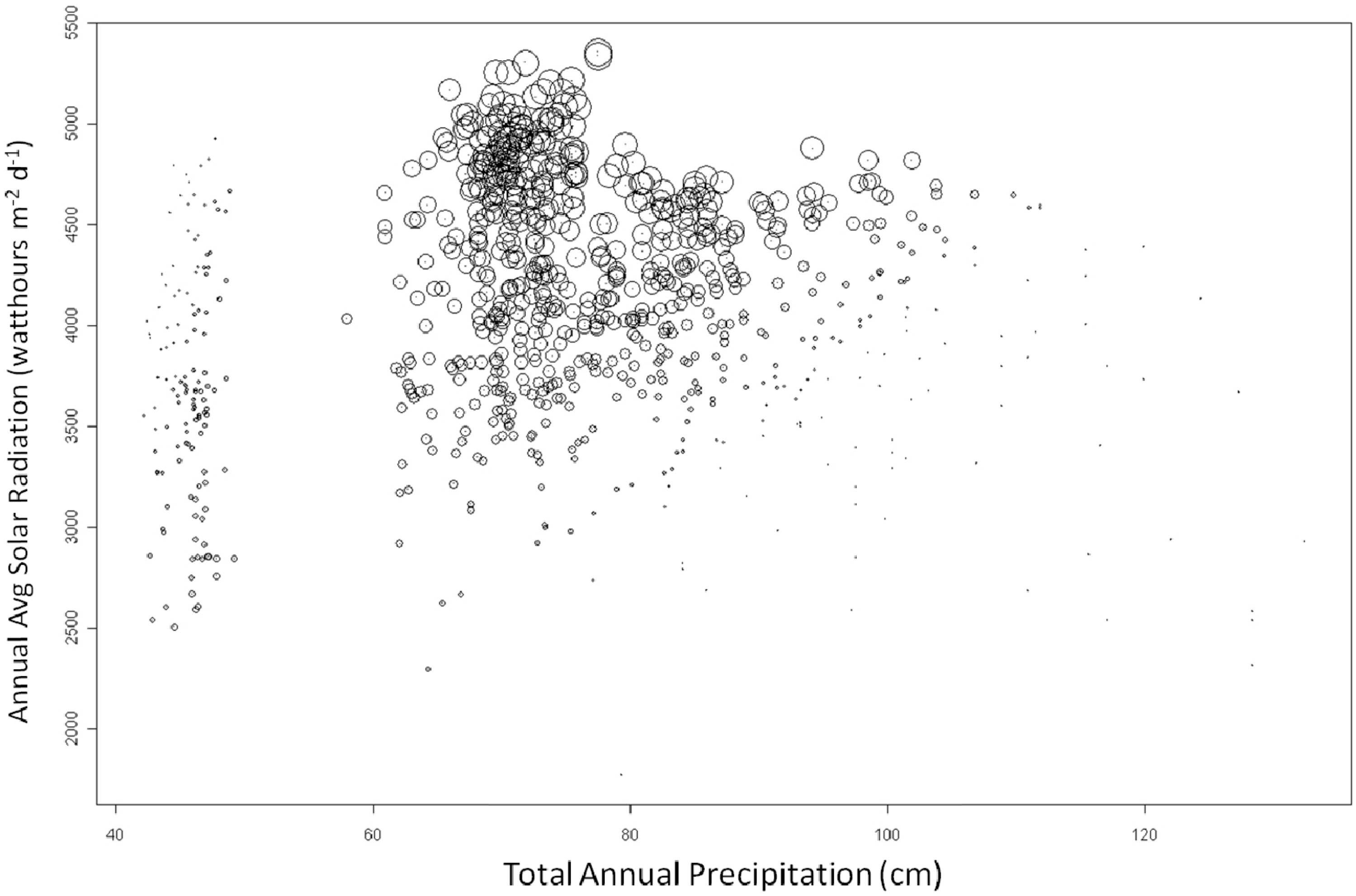

**Fig. 3.5** GLM results in environmental space of the independent variables. Points are actual observations. Size of circle around point represents model output as probability of stable aspen habitat. Larger circles represent greater probabilities.

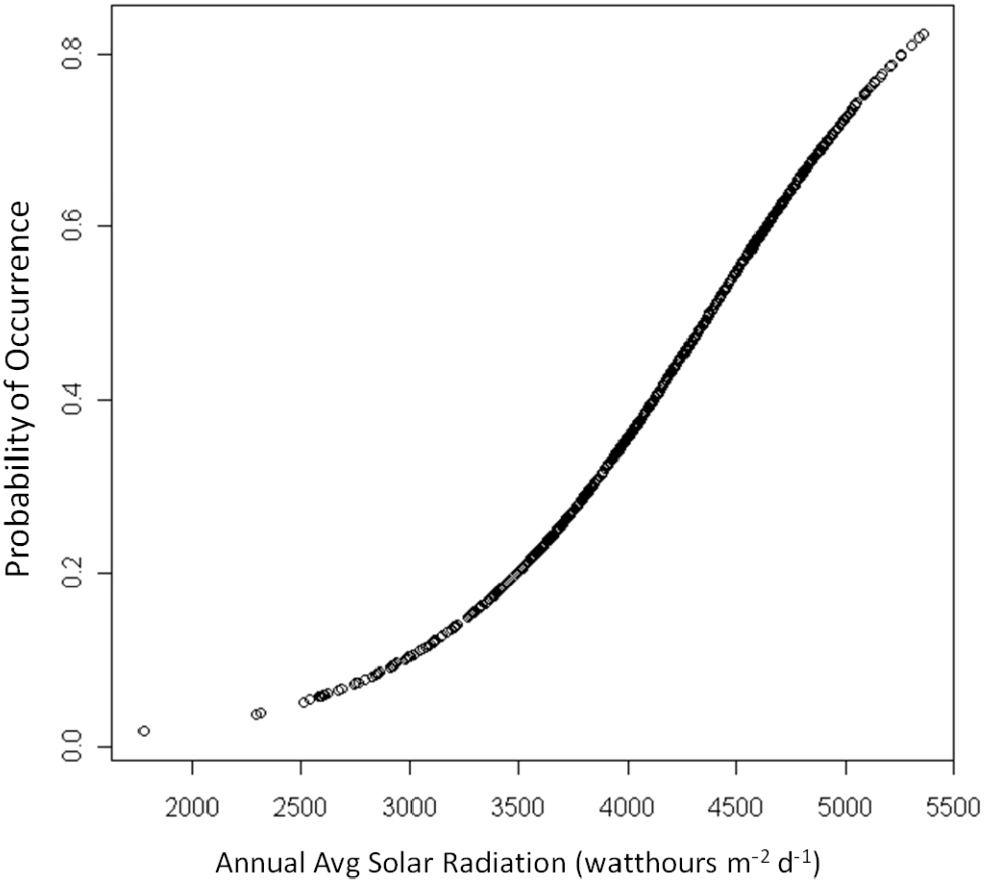

**Fig. 3.6** Response of the “Aspen” Forest Type to solar radiation (SolRad) predicted by the GLM. Circles represent individual values of the predictor variable.

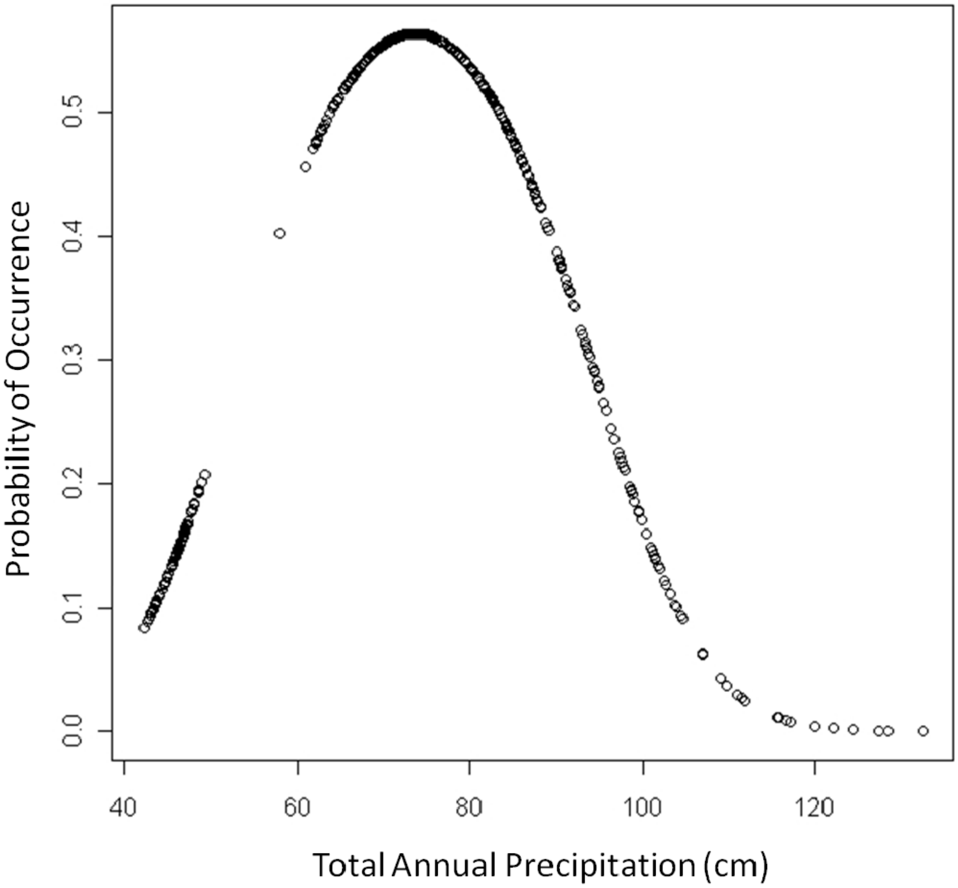

**Fig. 3.7** Unimodal Response of the “Aspen” Forest Type to total annual precipitation (TP) predicted by the GLM. Circles represent individual values of the predictor variable. The Book Cliffs site is discontinuous with the other sites and is represented with the lowest TP values.

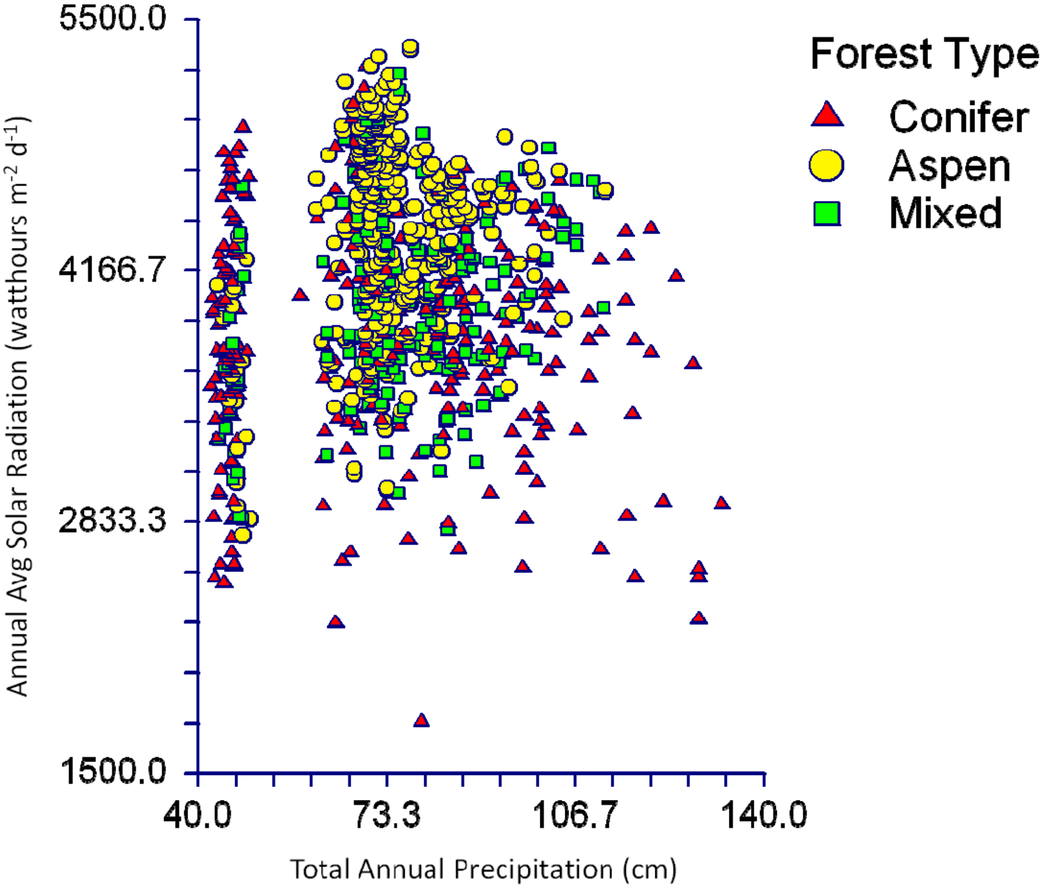

**Fig. 3.8** Scatterplot of Forest Type sample plots used as input for GLM. Book Cliff sample plots have the lowest total annual precipitation and are distinctly separate from the other sites. In comparison with the GLM results (Figure 3.5), which is in the same environmental space, we can see that the highest probability of “Aspen” is determined by both high density of “Aspen” plots and a low degree of overlap with conifer-present plots.

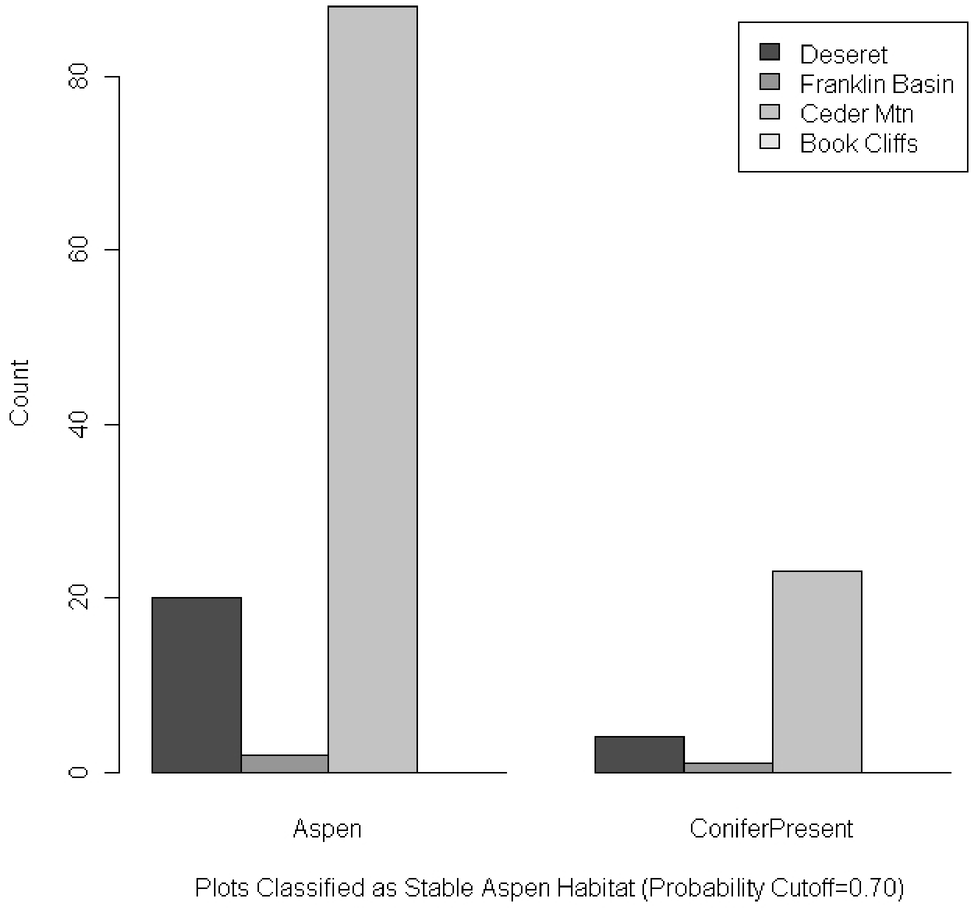

**Fig. 3.9** The number of plots for each site within stable aspen habitat classified according to predicted probabilities > 0.70. Plots within this habitat are separated by “Aspen” plots and “Conifer-present” plots.

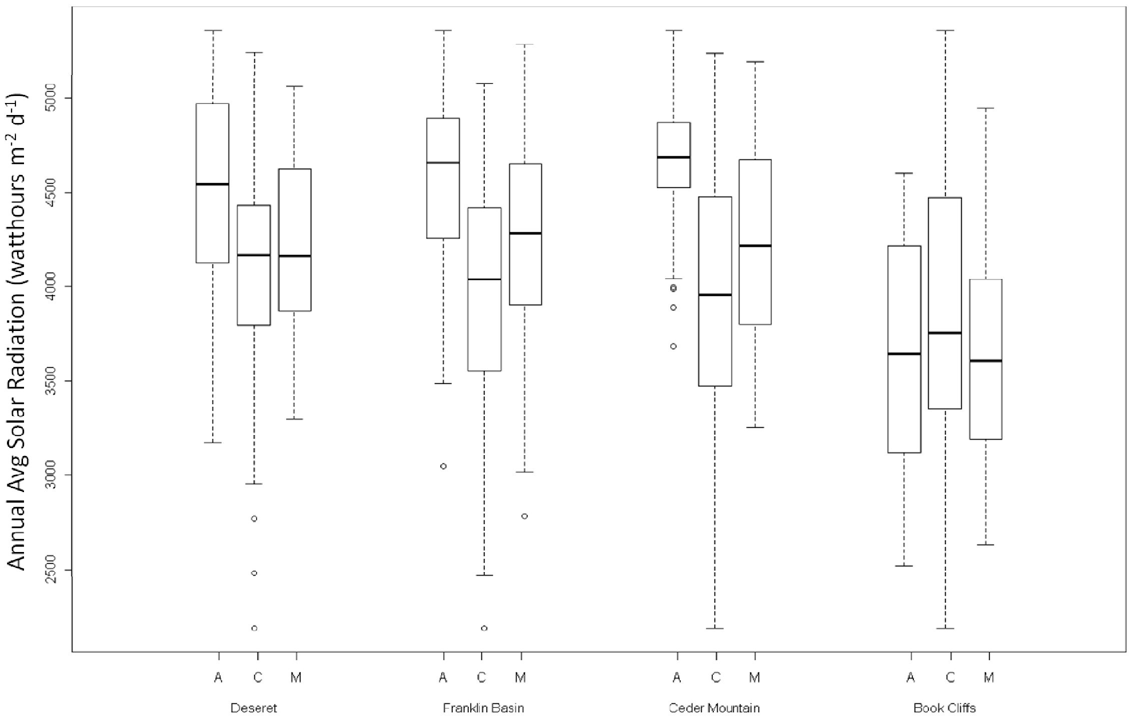

**Fig. 3.10** Boxplots indicting solar radiation distribution patterns of Forest Types by site. High solar radiation sites are equivalent to gently sloping areas, plateau tops, and south facing slopes. Forest types for each site are shown by A= "Aspen", C= "Conifer", M= "Mixed". Dark lines represent medians. Edges of the box represent the first and third quartiles. Whiskers extend out to 1.5 * *interquartile range*.

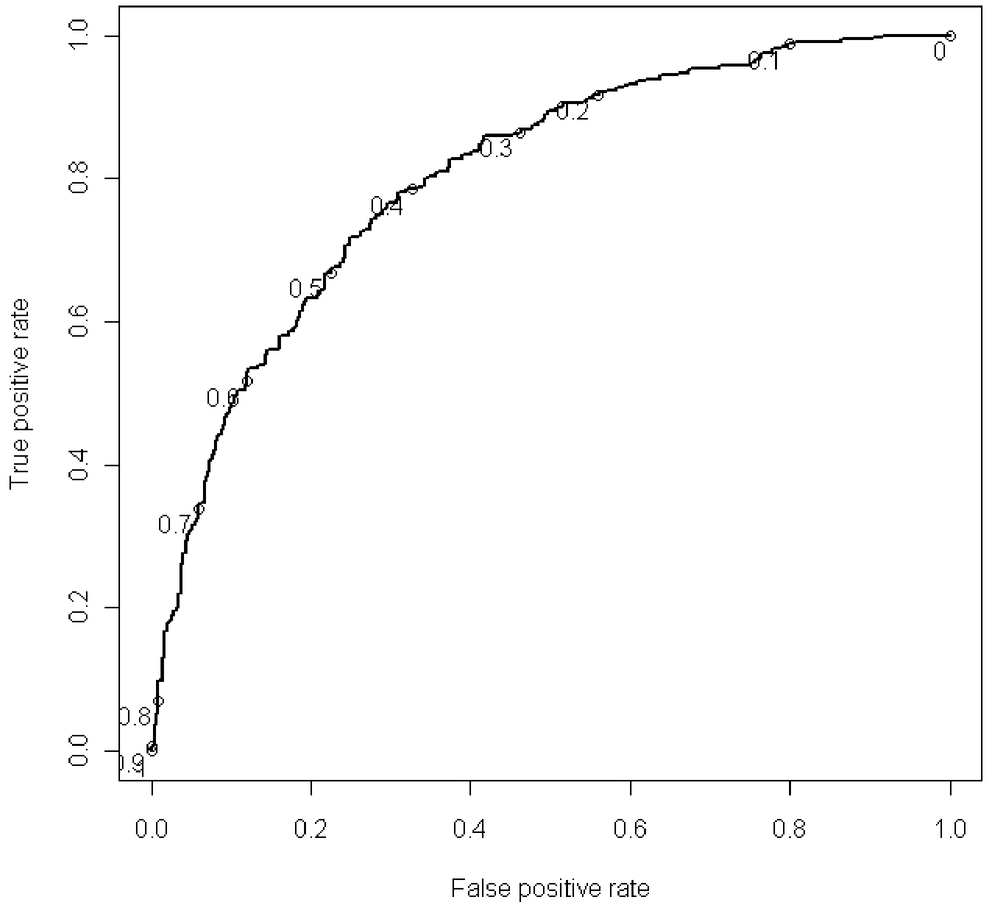

**Fig. 3.11** Receiver operating characteristic (ROC) curve generated from original model predictions. Numbers along curve represent probability cutoff thresholds. Curve is calculated as the true positive rate (correctly predicted presences) as a function of the false positive rate (incorrectly predicted presences). The curve indicates that the model has moderate to low discriminatory ability between aspen and conifer-present plots.

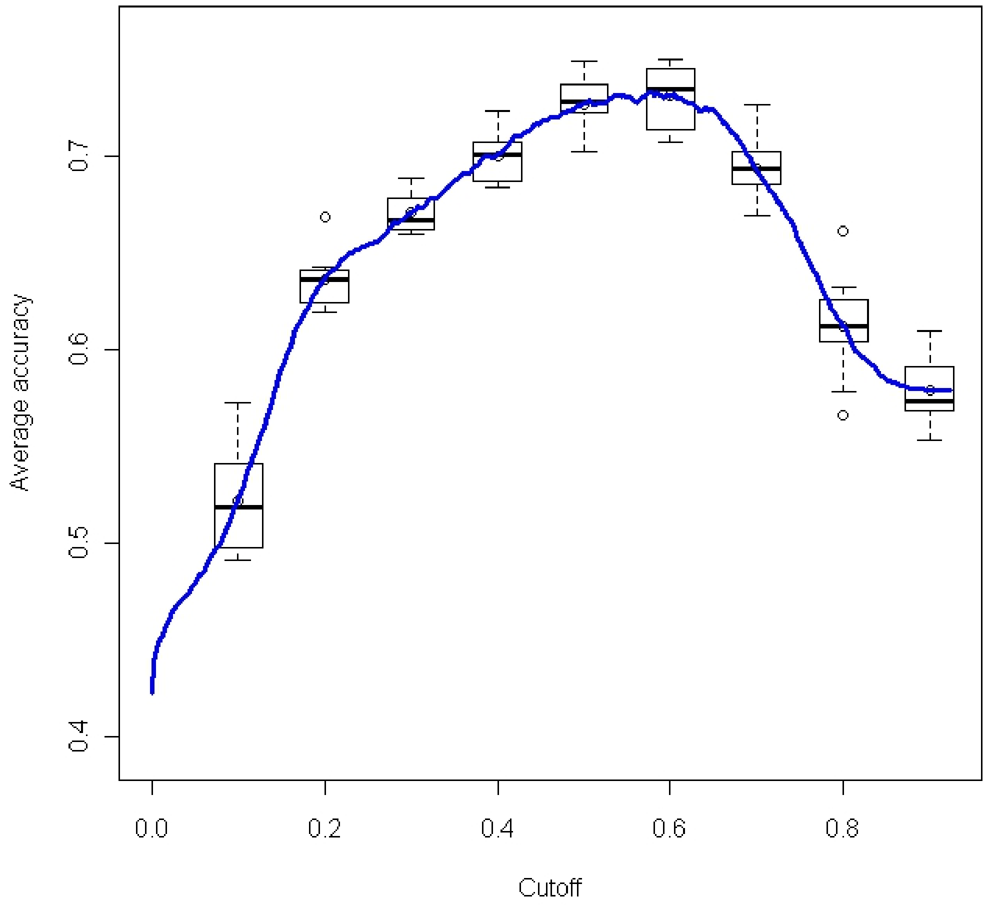

**Fig. 3.12** Average accuracy of 10 bootstrapped ROC curves as a function of probability threshold, i.e., “cutoff” point. Prediction accuracy of the GLM is optimized at a 0.6 probability threshold with a peak accuracy of 73%.

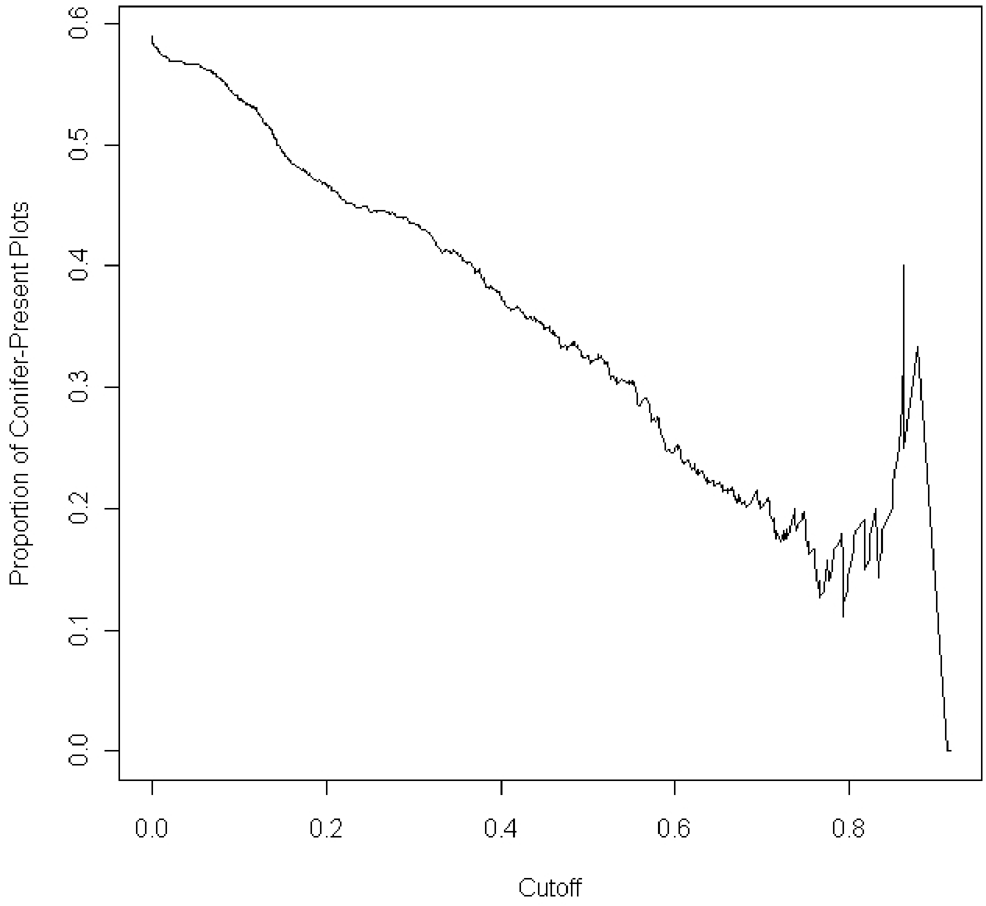

**Fig. 3.13** Proportion of "conifer-present" plots (i.e., prediction-conditioned fall-out rate) as a function of the probability threshold cutoff point. Proportions are conditioned on the total number of plots predicted to be in aspen habitat. The lowest ratio of conifer-present plots within aspen habitat exists when a cutoff point between 0.7-0.8 is chosen for the model.

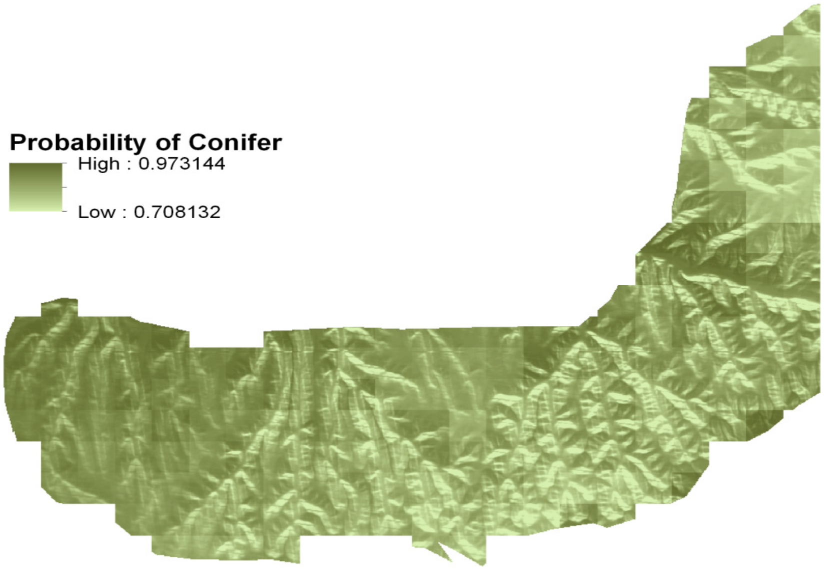

**Fig. 3.14** GLM results as a continuous surface raster applied to a portion of the Book Cliffs study site. A logistic transformation was performed on the log odds to get probability of occurrence (i.e., probability of the “Aspen” Forest Type), which was then inverted to get probability of conifer. Probability of conifer can be interpreted as probability of conifer encroachment. Since the model was parameterized using data from all four study sites, the probability of conifer shown here is relative.

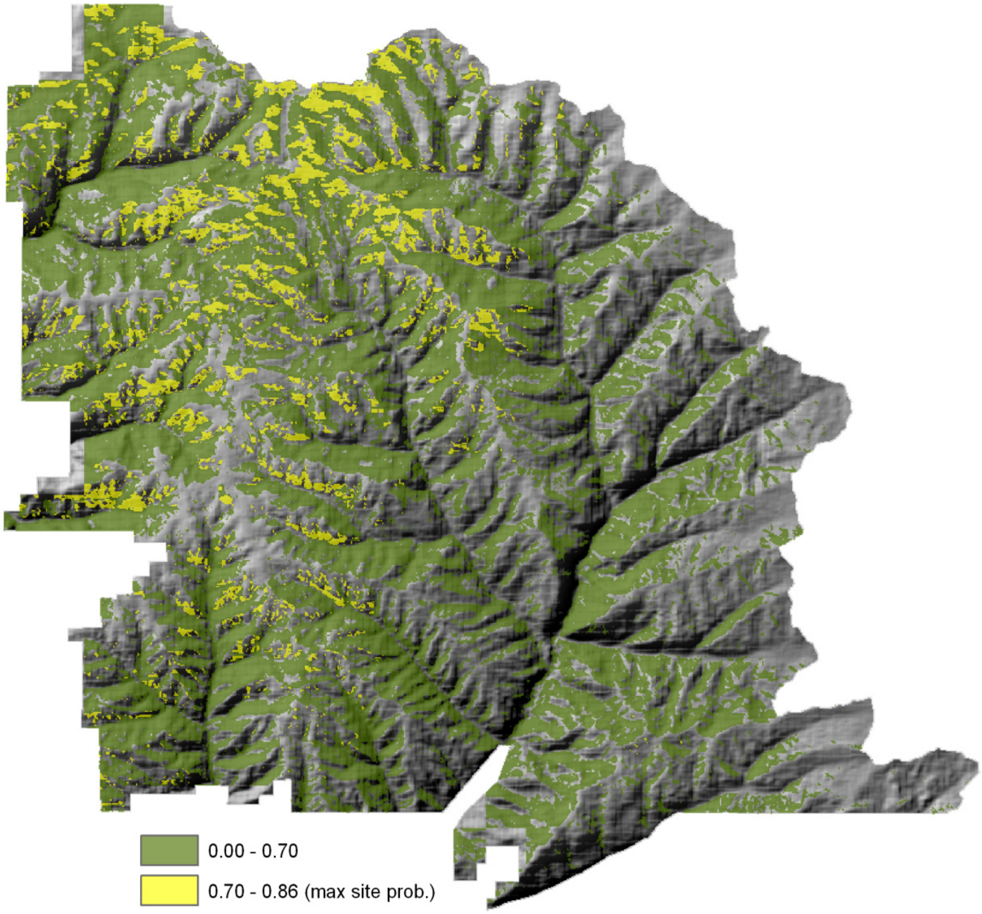

**Fig. 3.15** The Deseret study site depicting the GLM probability of occurrence discretely classified according to prediction-conditioned fall-out rates. Potentially stable aspen communities are determined to be above the 0.70 probability threshold cutoff point. GLM results are only shown for forested areas. Forested areas were classified using an ISODATA unsupervised classification algorithm on a Landsat TM image.

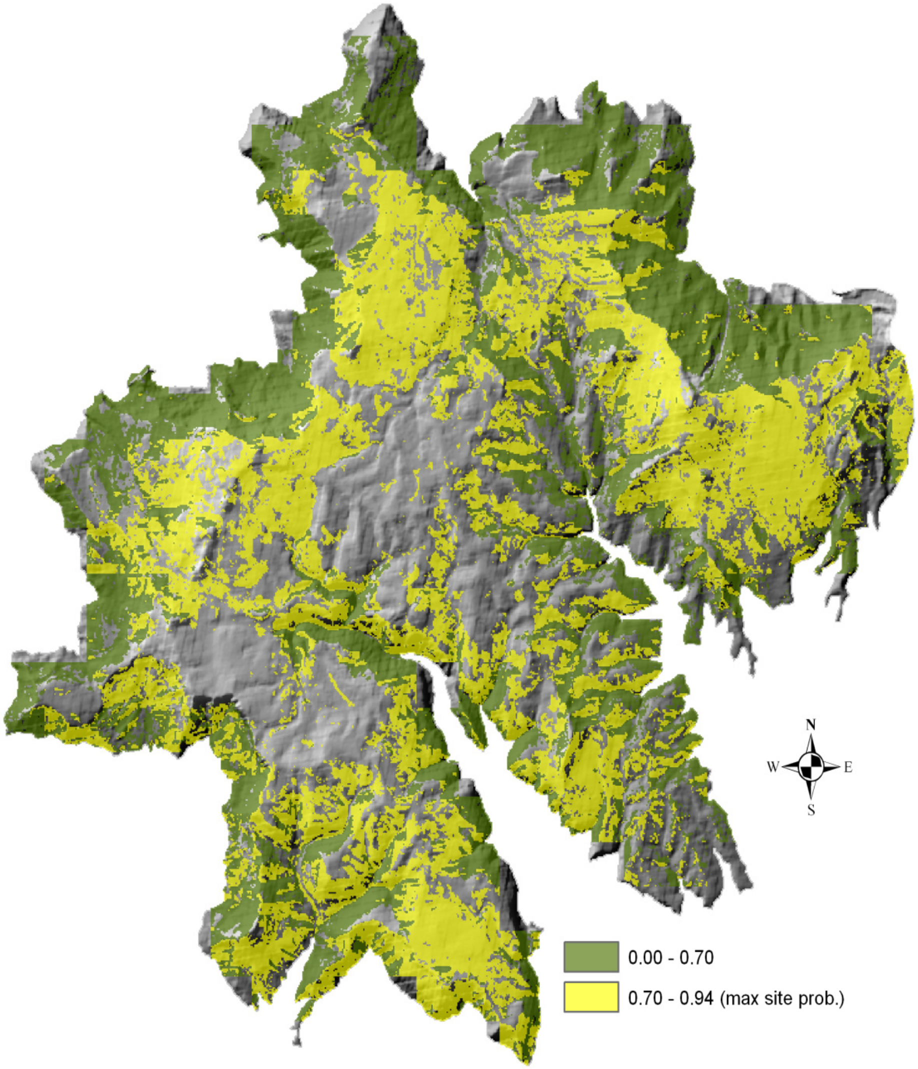

**Fig. 3.16** The Cedar Mountain study site depicting the GLM probability of occurrence discretely classified according to prediction-conditioned fall-out rates. Potentially stable aspen communities are determined to be above the 0.70 probability threshold cutoff point. GLM results are only shown for forested areas. Forested areas were classified using an ISODATA unsupervised classification algorithm on a Landsat TM image.

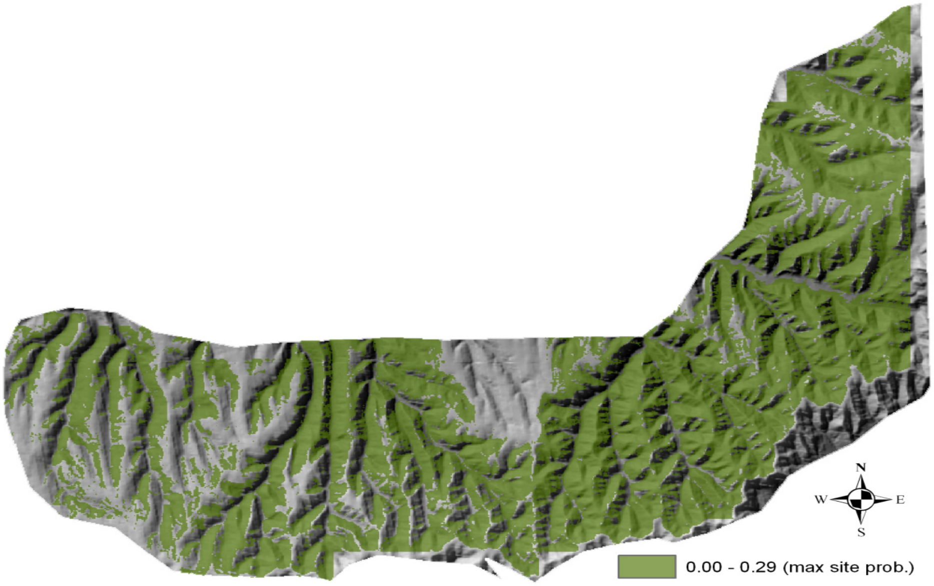

**Fig. 3.17** The Book Cliffs study site depicting the GLM probability of occurrence discretely classified according to prediction-conditioned fall-out rates. Potentially stable aspen communities are determined to be above the 0.70 probability threshold cutoff point. GLM results are only shown for forested areas. Forested areas were classified using an ISODATA unsupervised classification algorithm on a Landsat TM image.

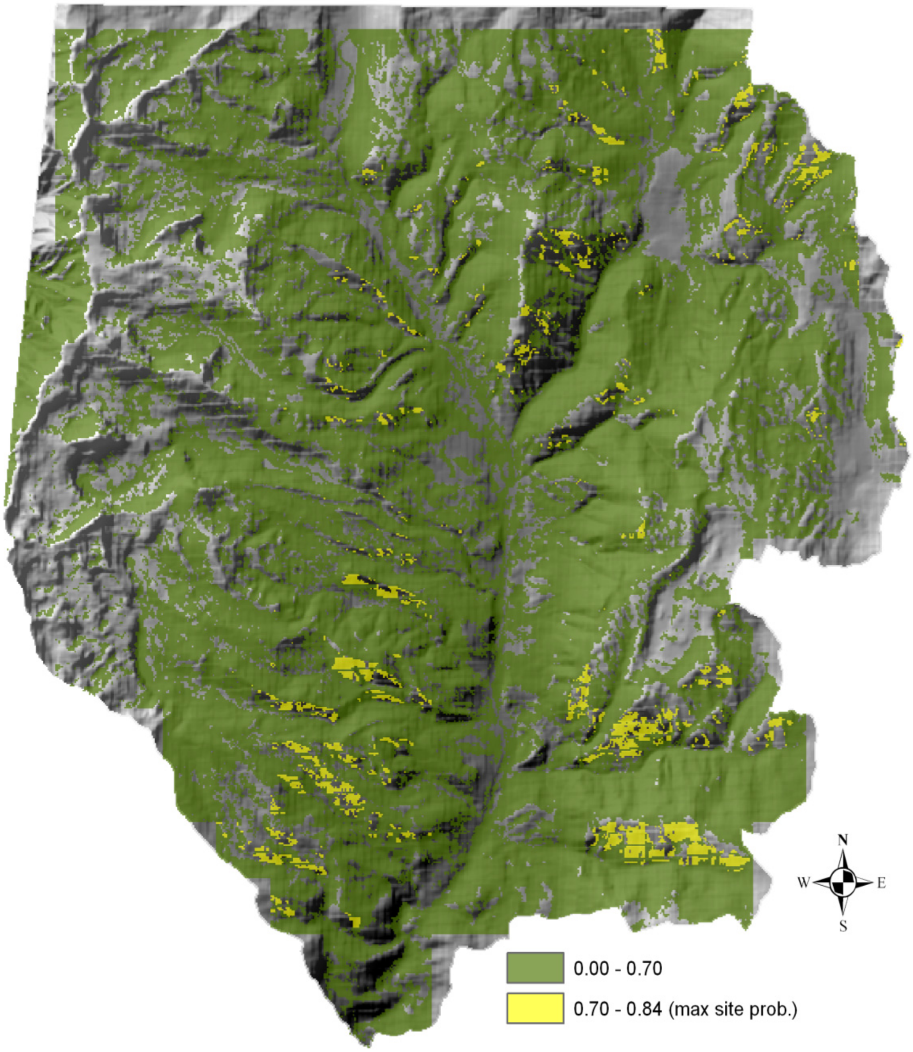

**Fig. 3.18** The Franklin Basin study site depicting the GLM probability of occurrence discretely classified according to prediction-conditioned fall-out rates. Potentially stable aspen communities are determined to be above the 0.70 probability threshold cutoff point. GLM results are only shown for forested areas. Forested areas were classified using an ISODATA unsupervised classification algorithm on a Landsat TM image.

# CHAPTER 4

# CONCLUSIONS

## 4.1 Objective 1

The first objective of our study was to determine the effectiveness of remote sensing and GIS methodologies for sampling tree species composition and modeling habitat of aspen and conifer forest communities. The study from chapter 2 aims to accomplish this overall objective by: (1) comparing the accuracy of sampling forest canopy cover by photointerpretation of NAIP CIR imagery with forest canopy cover derived from linear spectral unmixing of Landsat TM imagery, (2) assessing the strength of the relationship of GIS derived variables to forest plots, (3) as well as their ability to separate aspen, conifer, and mixed aspen/conifer forest plots within environmental space, (4) and addressing the issues relating to accuracy and spatial uncertainties inherent in the GIS and remote sensing methodologies used.

We found that photointerpretation of NAIP imagery was much more accurate in estimating forest canopy cover than linear spectral unmixing of Landsat imagery. Accuracy of NAIP photointerpretation is much higher, at 94% overall accuracy, than linear spectral unmixing methods (LSU) based solely on multispectral Landsat data. Kappa analysis of photointerpretation methods also indicate very high agreement with ground-reference data (Jensen, 2004), a value that seems consistently higher than most multispectral classification methods reviewed within this study. The comparatively higher error rate using LSU methods was due to the inability to separate spectral similarities between aspen and other broadleaf species at the study site. Photointerpretation methods on the other hand, were able to use a combination of techniques to increase accuracy, such as tone (by use of pseudocolor composite images), canopy height and shape (by analyzing shadows), texture of canopy, and spatial patterns of stands. While such ancillary information can be employed using linear spectral unmixing and other more automated methods with the use of complicated classification algorithms, it requires high image processing expertise and costly image data sources. Our results suggest photointerpretation of NAIP imagery is a more viable option for sampling dominant forest cover where manual interpretation is not impractical due to the need for sampling a high number of plots or when continuous-scale/large extent forest cover is needed.

In addition, the results of our study suggest, GIS and remote sensing methodologies can effectively be used to model habitats of aspen and conifer. The GIS-derived variables are able to explain 27% of the variance in the original forest dataset (canonical correlation$^2$=0.27), a figure which is on par with other tree species modeling studies (McKenzie et al., 2003). However, the canonical correlation solution to discriminating between Forest Type groups of aspen, conifer, and mixed aspen/conifer shows a high degree of overlap in environmental space. This indicates that aspen and conifer share very similar habitat requirements making it difficult to accurately predict Forest Types, hence the prediction error is only reduced 42% compared to a null model with random variables.

We also showed that remote sensing and GIS methodologies have limitations and potential sources of error that could influence our interpretation of the analysis. Data from photointerpretation methods only allows for the assessment of potential patterns. For instance, additional data on forest age structure and condition would aid in separating “Aspen” plots that exhibit multiple cohorts, as would be expected in a persistent aspen stand existing at the site for multiple generations, from a more singular age structure, indicating a disturbance-dependent “seral” stand type. Further field work would be needed to collect stand structure data and validate model results. In addition, spatial uncertainties within the site water balance (SWB) variable may bias results. We found that the robust nature of solar radiation (SolRad), being derived from digital elevation models, makes it preferable to SWB. However, though they are highly correlated, they may not be interchangeable due to heterogeneity of soils and the evapotranspirational demands of aspen. Although SWB adds potential bias to the analysis, results allude to a realized aspen niche in habitats where soils have the ability to buffer evapotranspirational demands, which leads to higher soil water availability at the end of the growing season. This indicates the importance of sampling soil water availability in identifying stable aspen habitat. However, spatial uncertainties associated with the calculation of SWB need to be addressed. However, while considering that we may be overlooking important microsites due to soil properties, a robust and accessible analysis using only solar radiation indicates that there is a general pattern in habitat between aspen and conifer at our study site. This suggests the viability of using GIS-derived topographic variables in aspen/conifer habitat modeling at a landscape-scale. Field data on stand structure and plot-scale variables such as soil characteristics need to be collected to further assess habitat differences between aspen and conifer.

### 4.2 Objective 2

The second objective of our study was to use data obtained from remote sensing and GIS methodologies to model and explore the possibility of a stable aspen niche. In chapter 3 we aimed to accomplish this objective by modeling habitat of aspen and conifer according to climatic and topographic variables using a generalized linear model approach. In this study we tested our research hypothesis shown in chapter 1. Interpretation of the results were applied to produce maps indicating potential stable and seral aspen habitat. Such maps can be used to provide additional criteria for determining treatment options for aspen restoration projects.

Borrowing from the concept of a Hutchinsonian, or realized niche (1965), we hypothesized that if biophysical variables used within the model are representative of mechanisms that allow stable aspen communities to resist encroachment, then a stable aspen niche will be shown by no overlap with conifer in environmental space. If overlap exists, then either biophysical variables used in the model are incomplete, i.e. not entirely representative of important mechanisms, or a stable aspen niche does not exist within the study area. According to the environmental space defined by the climatic and physical variables used in our analysis, we found there was nearly complete overlap in environmental space between aspen and conifer, and therefore no evidence of an exclusive realized aspen niche. However, we did find habitat, characterized by an interaction between topographic position and precipitation, in which aspen plots were proportionately much higher than conifer plots. We interpret these results to indicate that these specific variables do influence the ability of an aspen stand to remain free of conifer encroachment, however, they are not entirely representative of mechanisms that determine succession within aspen-conifer systems. Considering these results, we feel that the habitat model derived from the niche-based analysis is useful in delineating potential stable and seral aspen habitat at a course landscape-scale for management purposes. We feel that it is also provides a means to more effectively explore plot-scale mechanisms that explain why some aspen stands are encroached and others are not.

The key predictors used to model a stable aspen niche were total annual precipitation (TP) and daily average solar radiation (SolRad). Aspen plots showed a unimodal response to TP, as well as being influenced by an interaction between SolRad and TP. Our results show aspen shifting from relatively steep north facing slopes, in areas with low annual precipitation, to plateau tops and gentle south-facing slopes as we move to higher precipitation values. This aligns with other aspen studies which have found the distribution of aspen to be generally water-limited (Mueggler, 1988). Using niche-based analysis methods, we found that the highest probability for stable aspen communities occurrs between 60 to 90 cm of total annual precipitation on topographic sites receiving greater than 4,500 Wh $m^{-2}$ $d^{-1}$ of solar radiation per day (this range of solar radiation is equivalent to landscape positions roughly categorized as gently sloping areas, plateau tops, and south-facing slopes). At sites with less than 60 cm of TP, it was more likely for aspen to share the same topographic position as conifer species, and therefore more likely to be encroached, and barring any significant disturbance, converted to a conifer climax community. At sites receiving more than 90 cm of TP it is thought that TP likely correlates with variables that affect conifer encroachment, but is not directly responsible itself. It is likely that within our model, high TP represents high elevation and resultantly short growing seasons. Broad-leafed species such as aspen are out-competed within this environment (Mueggler, 1988) and low fire return intervals (Romme, 1982; Gruell, 1983; Bigler et al., 2005) mean long successional time scales allowing conifer dominance.

Within the TP range of 60-90 cm, we find that solar radiation strongly influences the probability of having a stable aspen community. Considering the progressive pattern of overlap between aspen and conifer-present plots, we suggest this result likely indicates topographic positions influence conifer seed dispersal patterns and fire regimes. Fires have been shown to be more likely to initiate on plateau tops and tend to burn upslopes (Romme and Knight, 1981), resulting in shorter duration fire regimes in topographic positions equivalent to our stable aspen niche space. In addition, conifer seed-rain tends to be dispersed by thermals moving upslope (Noble, 1978). After disturbance we would expect to see a gradual establishment of conifer into landscape positions characterized by higher solar radiation. This aligns well with our results.

However, while this may explain the overall progressive pattern that we see in our results, there is an overwhelmingly high proportion of aspen to conifer found within the ideal precipitation range of 60-90 cm and at sites receiving greater than 4,500 Wh $m^{-2}$ $d^{-1}$ of solar radiation. This suggests that in addition to topographic positions presenting a barrier to conifer seed dispersal, this specific environmental space may not be conducive for conifer establishment or be representative of mechanisms that inhibit conifer. The specific moisture regime of this niche space is likely key to understanding such interactions. Unfortunately, it is difficult to interpret exactly what the details of that moisture regime may be only using TP. Generally, throughout the Intermountain West, these are sites that experience high precipitation during the winter and periods of low soil moisture during summer (due to high insolation values). It is possible that aspen has a higher tolerance to summer drought periods than fir and spruce, which would be appurtenant to understanding the low presence of conifer in this habitat. Other complex inhibitory mechanisms may be generally explained by the specific combination of moisture and solar radiation that characterizes our stable aspen niche space. For instance, aspen understory communities that would be expected to flourish in these environments may prevent conifer encroachment at both the germination and establishment phase (Langenheim, 1962).

While our modeling approach does not pinpoint specific ecological mechanisms that explain the ability of some aspen stands to remain free of conifer encroachment, it does however offer a useful tool to classify potential stable and seral aspen habitat using landscape-scale biophysical variables. It is also a good starting point to begin to look for important successional mechanisms which could further refine this landscape-scale model and make it more useful for management decisions.

### 4.3 Management Applications

In addition to exploring and contributing to the ecological knowledge of aspen ecosystems, this thesis project was designed to specifically address needs proposed by the UFRWG (O'Brien et al., 2010), such as:

- The need to find cost effective methods of assessing extent of pure upland aspen and upland aspen/conifer forest across a large landscape.
- And to provide additional criteria for determining potential climax vegetation for treatment site in question, in order to prioritize restoration efforts.

The first need was addressed by comparing remote sensing sampling methodologies using publicly available imagery to produce an accurate and cost effective way to assess the extent of upland aspen forest types. We determined that photointerpretation of NAIP imagery was much more accurate in estimating forest canopy cover than linear spectral unmixing of Landsat imagery. It is likely the best option for sampling dominant forest cover where manual interpretation is not impractical due to the need for sampling a high number of plots or when continuous-scale/large extent forest cover is needed. However we did uncover certain issues that should be considered in using this method, namely: 1-m resolution and shadows. At 1-m resolution it was not possible to visually identify individual conifer species (i.e., identifying subalpine fir from Doug-fir) and therefore all conifer species were lumped into one group. This certainly decreased the precision of our analysis, as conifer species have different ecological tolerances and distributions. We would expect this to add another facet to our interpretation of successional dynamics within aspen ecosystems. This may also be an issue in terms of applying this methodology to assess the extent of forest types for aspen treatment projects. Species-level detail within the conifer group would certainly provide more information on the extent of forest types in a proposed treatment area. However, aside from field data collection, this may only be possible with < 1-m resolution imagery and/or the use of stereoscopy to determine crown differences. Shadows also introduced error in the interpretation which could not be reduced. This error was manifest in steep topography resulting in deeply shadowed slopes. In these areas there was potentially a bias to interpret plots as being dominated by conifer.

For the second need we hoped to produce a parsimonious predictive model delineating geographic locations of stable and seral aspen community types. Such a model would provide managers with an initial filter, or additional criteria, in order to inform and prioritize aspen treatment projects. Unfortunately, due to limitations imposed by the modeling approach and input variables, the results from our niche-based analysis do not indicate an exclusive stable aspen niche. However, they do soundly indicate that conifer encroachment is influenced by biophysical variables. Considering this outcome there are two products that may suit the needs of forest managers: continuous-scale maps indicating relative probability of conifer, and categorical maps delineating aspen that has the highest probability of being a stable aspen community.

The relative probability of conifer encroachment is a way to represent the continuous output of the generalized linear model results. We interpret the probability of conifer to be equivalent to the probability of conifer encroachment. According to our model, a logistic transformation of the log odds gives probability of aspen compared to conifer ($\prod_{\text{aspen}}$). We get the probability of conifer by $1-\prod_{\text{aspen}}$, which can then be mapped as a continuous surface. Since this metric is on a continuous scale we can make decisions about particular aspen stands relative to other aspen stands, either within the same management area or across management areas. This may be useful in areas such as the Book Cliffs study site where the probability of conifer is very high and decisions to remove conifer through selective logging or prescribed burning must be made relative to other aspen stands in the immediate area. Using this logic, stands with the lower probability of conifer may be expected to have slower rates of encroachment and therefore longer treatment intervals.

Categorical maps, on the other hand, require an interpretation of the results into seral and stable aspen habitat. Considering the limitations imposed by the model variables and the analytical methods used in this study, we interpret the environmental space with the lowest proportion of conifer presence to have the highest potential for stable aspen communities. Prediction-conditioned fall-out rates provide a statistically based criteria to do this. It must be kept in mind that we can only classify areas as having the highest potential for stable aspen communities and not actual stable aspen communities. Consequently, the categorical map delineating stable and seral aspen habitat is best used in concert with other actual stand structure data or if used on its own, used only to assess and compare large landscapes where actual "on-the-ground" identification of stable and seral aspen communities is not possible.

Categorical maps delineating cover of stable and seral aspen habitat can be produced by overlaying the discretely classified model output, using the prediction-conditioned fall-out rates, with landcover data showing actual aspen and conifer distributions. Considering these maps, areas with a high frequency of seral aspen habitat may be chosen for conifer-thinning or prescribed fire. A priority may be placed on these areas over others that display a high frequency of stable aspen habitat, as they may be converted to conifer more quickly. Areas that show a high frequency of stable aspen habitat may be selected for ground surveys to identify stands that, in addition to existing within highly probable stable aspen habitat, also exhibit characteristics associated with stable aspen communites, such as uneven age structures, and soil characteristics indicating multiple generations of aspen at the site. These stands should be considered for management as stable aspen communities and would require different management strategies than seral aspen communities.

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# APPENDICES

# APPENDIX A

## DOWNSCALE SCRIPT

```
#This script was intended to be used for downscaling DAYMET temperature
#grids.

#Process works by calculating mean elevation values within temperature
#pixels then regressing temperature with elevation.  Best fit line is
#equivalent to lapse rate.  Using lapse rate temperatures are
#interpolated according to elevation of pixel.

#Note: Uses entire input raster to fit lapse rate.  Estimated
#temperatures may not be accurate for very large raster datasets since
#lapse rates may vary over large areas.  Check residuals for accuracy.

#Author: Cody Mittanck, contact: codymitt@hotmail.com

#Program: Python
#Script was written to be used within ArcGIS.


import arcpy
from arcpy.sa import *

arcpy.env.workspace = arcpy.GetParameterAsText(0)

arcpy.env.overwriteOutput = True

in_raster_daymet = arcpy.GetParameterAsText(1) #raster; input
point_daymet = "point_daymet.shp" #feature class
pointpolys =  "pointpolys.shp" #feature class
in_raster_elev = arcpy.GetParameterAsText(2) #raster; input
elevstatstable = "elevstatstable.dbf" #table
olsresiduals = "olsresiduals.shp" #feature class
coefficients = "coefficients.dbf" #table
diagnostics = "diagnostics.dbf" #table
out_raster = arcpy.GetParameterAsText(3) #raster; output


#Convert temperature to points
arcpy.RasterToPoint_conversion(in_raster_daymet,point_daymet,"VALUE")

#Make Thiessen polygons
arcpy.CreateThiessenPolygons_analysis(point_daymet,pointpolys,"ALL")

#Zonal stats as Table
arcpy.sa.ZonalStatisticsAsTable(pointpolys,"POINTID",in_raster_elev,ele
vstatstable,"DATA","ALL")

#Join Fields to pointpolys
arcpy.JoinField_management(pointpolys,"POINTID",elevstatstable,"POINTID
","")
```

```
#Run OLS
arcpy.OrdinaryLeastSquares_stats(pointpolys,"POINTID",olsresiduals,"GRI
D_CODE","MEAN",coefficients,diagnostics)


#Create raster from coefficients
elev = arcpy.Raster(in_raster_elev)


mylist = []
rows = arcpy.SearchCursor(coefficients)

for row in rows:
      mylist.append(row.Coef)  #first one is the y intercept and second
#is the x coefficient

a = mylist[0]
b = mylist[1]


#Checkout license
arcpy.CheckOutExtension("Spatial")

scaledraster = elev * b + a

#Save raster to output
scaledraster.save(out_raster)
```

# APPENDIX B

## POTENTIAL EVAPOTRANSPIRATION SCRIPT

```
#This script calculates potential evapotranspiration for a given month
#using the Jensen and Haise equation (Jensen and Haise, 1963).

#Note:  Solar radiation input raster is derived using the ArcGIS “Solar
#Radiation Area” tool with parameters set to output Watt Hours/m2/day
#(global radiation,i.e. direct + diffuse) at monthly intervals.  This
#script requires those daily averages to be summed for the month. Air
#temperature must be an average daily air temperature for a given
#month.

#Author: Cody Mittanck, contact: codymitt@hotmail.com

#Program: Python
#Script was written to be used within ArcGIS.

import arcpy
import math
from arcpy.sa import *

arcpy.env.workspace = arcpy.GetParameterAsText(0)

arcpy.env.overwriteOutput = True

in_raster_solarrad = arcpy.GetParameterAsText(0) #watthours/m2/month
in_raster_temp = arcpy.GetParameterAsText(1) #mean daily air temp/month
out_raster = arcpy.GetParameterAsText(2)

arcpy.CheckOutExtension("Spatial")

#Modify parameters
WH = arcpy.Raster(in_raster_solarrad)
T = arcpy.Raster(in_raster_temp)

Ta = T * 0.1 #convert to 1/10 degree celsius
R = WH * 3.6 #convert watt hours to kilojoules

#Apply equation
PET_mm = (R/245) * (((Ta/10) * 0.025) + 0.08)

#Convert to cm
PET_cm = PET_mm * 0.1

#Converting negative values to “0”.
out_pet = Con(PET_cm,0.0,PET_cm,'VALUE < 0')

#Save raster to output
out_pet.save(out_raster)
```

# APPENDIX C

## SITE WATER BALANCE SCRIPT

```
#This script calculates site water balance.  It is a running sum of the
#difference between potential evapotranspiration and precipitation,
#while not allowing any excess water to exceed the site-specific soil
#water capacity.

#Note: This “bucket” method for calculating site water balance is very
#similar to Zimmermann and Roberts (Zimmermann and Roberts, 2007),
#which was based on the concept developed by Grier and Running (1977).
#This method differs by running the water balance from January-
#September (the end of the growing season) without concern for when
#“recharge”, e.g. precipitation exceeds evapotranspiration, occurs.  It
#was determined that all sites reached the maximum soil water capacity
#during the winter months starting the growing season with as much
#water as the soil allows.  Assessing the soil water balance in
#September, essentially gives an index of site dryness directly after
#the period during which plants need moisture the most.

#Note on inputs:
#in_raster_diff = monthly raster datasets of precipitation subtract
#potential evapotranspiration in centimeters on a monthly basis.
#Parameter is set to a multivalue parameter.
#in_raster_sws = soil water supply derived from the Soil Survey
#Geographic Database (SSURGO) (http://soildatamart.nrcs.usda.gov). This
#database gives available water capacities (awc) in a volume fraction
#for a soil series. In order to get soil water capacity for a given
#soil series:
```

\# $swc_{series} = \sum awc_h * depth_h$

```
#where, awc is the “available water capacity” as a volume fraction for
#a given horizon and depth is the depth of a given horizon in cm units.
#The SSURGO database consists of multiple soil series per mapunit.
#Constrained by the spatial resolution of the mapping units, soil water
#supply was calculated as a weighted average according to percent of
#each soil series within the mapping unit. We end up with soil water
#supply for each mapunit polygon.  Polygons were than rasterized for
#input into script.

#Output is a raster ranging from maximum bucket size to increasingly
#negative values indicating a negative water balance for dry sites.

#Author: Cody Mittanck, contact: codymitt@hotmail.com

#Program: Python
#Script was written to be used within ArcGIS.


import arcpy
```

```
from arcpy.sa import *

arcpy.env.overwriteOutput = True

in_raster_diff = arcpy.GetParameterAsText(0) #raster, multivalue
in_raster_sws = arcpy.GetParameterAsText(1) #raster
out_raster = arcpy.GetParameterAsText(2) #raster

#Make list from difference rasters
difflist = in_raster_diff.split(";")

arcpy.CheckOutExtension("Spatial")

#Name parameter
sws = in_raster_sws

#Calculate SWB
sum_1 = Raster(sws) + Raster(difflist[0]) + Raster(difflist[1]) +
      Raster(difflist[2]) + Raster(difflist[3]) + Raster(difflist[4]) +
      Raster(difflist[5]) + Raster(difflist[6]) + Raster(difflist[7]) +
      Raster(difflist[8])
con_1 = Con(Raster(difflist[0]),0,1,'VALUE >= 0')

sum_2 = Raster(sws) + Raster(difflist[1]) + Raster(difflist[2]) +
      Raster(difflist[3]) + Raster(difflist[4]) + Raster(difflist[5]) +
      Raster(difflist[6]) + Raster(difflist[7]) + Raster(difflist[8])
con_2 = Con(Raster(difflist[1]),0,1,'VALUE >= 0')

sum_3 = Raster(sws) + Raster(difflist[2]) + Raster(difflist[3]) +
      Raster(difflist[4]) + Raster(difflist[5]) + Raster(difflist[6]) +
      Raster(difflist[7]) + Raster(difflist[8])
con_3 = Con(Raster(difflist[2]),0,1,'VALUE >= 0')

sum_4 = Raster(sws) + Raster(difflist[3]) + Raster(difflist[4]) +
      Raster(difflist[5]) + Raster(difflist[6]) + Raster(difflist[7]) +
      Raster(difflist[8])
con_4 = Con(Raster(difflist[3]),0,1,'VALUE >= 0')

sum_5 = Raster(sws) + Raster(difflist[4]) + Raster(difflist[5]) +
      Raster(difflist[6]) + Raster(difflist[7]) + Raster(difflist[8])
con_5 = Con(Raster(difflist[4]),0,1,'VALUE >= 0')

pick=con_1 + con_2 + con_3 + con_4 + con_5

done=Pick(pick,[sum_5,sum_4,sum_3,sum_2,sum_1])

done.save(out_raster)
```