

MONTANE MEADOWS AS INDICATORS OF ENVIRONMENTAL CHANGE

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Abstract. We used a time series of satellite multispectral imagery for mapping and monitoring six classes of montane meadows arrayed along a moisture gradient (from hydric to mesic to xeric). We hypothesized that mesic meadows would support the highest species diversity of plants, birds, and butterflies because they are more moderate environments. We also hypothesized that mesic meadows would exhibit the greatest seasonal and interannual variability in spectral response across years. Field sampling in each of the meadow types was conducted for plants, birds, and butterflies in 1997 and 1998. Mesic meadows supported the highest plant species diversity, but there was no significant difference in bird or butterfly species diversity among meadow types. These data show that it may be easier to detect significant differences in more species rich taxa (e.g., plants) than taxa that are represented by fewer species (e.g., butterflies and birds). Mesic meadows also showed the greatest seasonal and interannual variability in spectral response. Given the rich biodiversity of mesic montane meadows and their sensitivity to variations in temperature and moisture, they may be important to monitor in the context of environmental change

Keywords: biodiversity, butterflies, birds, climate change, montane vegetation, remote sensing, Greater Yellowstone Ecosystem

1. Introduction

Montane, or subalpine meadows, are defined as nonforested habitat types occurring below timberline, but ecologically and geographically distinct from nonforested intermontane parklands. Montane meadows may exist as a result of patch disturbances (fire, mass movement, or snow), natural geomorphic processes (underlying geology or soils), or animal disturbances (e.g., beaver dam meadows). The species composition and vegetation condition of montane meadow communities are closely linked to environmental conditions, and based on narrowly defined adaptations to gradients of temperature and moisture (Knight 1994).

In these meadows, short-term changes in environmental conditions are manifested as changes in vegetation condition, while long-term, directional shifts in temperature and moisture regimes drive changes in species composition and diversity (Harte and Shaw 1995). Under conditions of warmer and dryer climate, the habitat of individual meadow plant and animal species may be reduced or eliminated (Romme and Turner 1991). If montane meadows are to function as indicators of environmental change, baseline conditions and variability must be



documented such that departures from baselines can be used as an indicator of change.

We used satellite remote sensing data and field data of birds, butterflies, and plants to characterize montane meadows in the Yellowstone ecosystem. Multispectral satellite remote sensing provides a powerful means for detecting and characterizing environmental changes at multiple spatial and temporal scales. By calibrating remotely sensed multispectral data with field measurements, vegetation properties measured at sample points can be extrapolated across a large geographic region (Graetz 1990). Biotic properties derived by this empirical method may include the successional state of the vegetation, or an intrinsic property of the vegetation, such as biomass, leaf area index, cover, or moisture content (Jensen 1983, Waring et al. 1986, Graetz 1990). Analysis of changing spectral patterns can provide precursor measurements of terrestrial ecosystem dynamics (Waring et al. 1986, Lancaster et al. 1996, Peters et al. 1997, Reed and Yang 1997).

Seasonal changes in spectral reflectance at local scales are a function of the species composition and the environmental conditions of a site (Stow et al. 1993, Kremer and Running 1993, Senseman et al. 1996, Everitt and Escobar 1996). Changes in spectral reflectance patterns, therefore, may signal changes in vegetation structure or composition, or changes in environmental conditions that later may trigger changes in the vegetation. If seasonal and interannual patterns of spectral response can be linked to distinct plant species assemblages, this may provide a means to predict potential plant and animal species diversity (Walker et al. 1992, Stoms and Estes 1993, Jorgenson and Nohr 1996, Nagendra and Gadgil 1999).

The butterfly community provides an excellent set of potential indicators that complement the plant community assessment. Butterflies are speciose and they respond to microhabitat, plant structure and plant chemical composition. Over one hundred species of butterflies occur in the Yellowstone ecosystem (Brussard 1989) and many are tightly correlated with specific meadow habitats (Debinski et al. in press). A strong connection between climate and butterflies has been recognized by many authors (Turner et al. 1987, Pollard and Yates 1995). The implications of climate change for butterflies are potentially serious (Dennis 1993), and particular concern has been expressed about the montane butterfly communities where habitats are predicted to contract (Pullin 1995).

The bird community was chosen as an indicator for the vertebrate groups. Birds are ecologically diverse and use a wide variety of food and other resources, thereby reflecting the condition of many aspects of the ecosystem. They also represent several trophic groups or guilds, and by having a relatively short generation time, they exhibit relatively quick responses to environmental change (Steele et al. 1984).

The objectives of this study were to: 1) characterize the seasonal and interannual spectral variability of six classes of montane meadow vegetation communities along a moisture gradient (from hydric to mesic to xeric), and 2) document the plant, bird, and butterfly species diversity associated with each of the six meadow

types. We hypothesized that mesic meadows would support the highest species diversity of plants, birds, and butterflies because they are more moderate environments. We also hypothesized that mesic meadows would exhibit the greatest seasonal and interannual variability in spectral response across years. This combination of high biodiversity and high variability would thus make mesic meadows important sites to monitor in the context of environmental change.

2. Methods

Our research was conducted in the Gallatin National Forest and the northwest corner of Yellowstone National Park, Montana. Yellowstone and Grand Teton National Parks, and the surrounding national forests form what has come to be known as the Greater Yellowstone Ecosystem, roughly defined as the Yellowstone Plateau and elevations above 2130 m in the surrounding region (Marston and Anderson 1991). Nonforest cover types within the ecosystem range from hydric willow and sedge meadows to high-altitude tundra and rock meadows. The study area extends north-south from Porcupine Creek to Bacon Rind Creek and east-west from the crest of the Madison Range to the Gallatin Range, an area defined approximately by 111°00' W – 111°30' W, 44°50' N – 45°30' N. In this part of the Yellowstone ecosystem, the annual minimum and maximum temperature ranges between -15°C (December) and 25°C (August), and the average monthly precipitation ranges between 2.0 cm to 7.0 cm, peaking in late spring/early summer (May-June). Average total annual snowfall exceeds 3 m, with January receiving the greatest average monthly accumulation at slightly less than 1 m. Onset of vegetation greenness in meadows occurs by mid to late May, depending on seasonal variations in snowfall depth and spring temperatures. Grasses and forbs progress at a more rapid phenological rate than shrubs in this region, initiating greenup and senescence earlier in the season (Blaisdell 1958). Vegetation greenness is at a maximum in early to mid July, and by late August to early September, most non-forested vegetation communities have ceased photosynthetic activity for the growing season.

2.1 HABITAT CLASSIFICATION

SPOT satellite multispectral imagery was used to map the meadows within the study area as a means to guide selection of sites for field sampling of plant and animal data. The SPOT multispectral scanner acquires data in three bands (green, 0.50–0.59 μm ; red, 0.61–0.68 μm) and near-infrared, 0.79–0.89 μm), with a spatial resolution of 20 meters. SPOT images were acquired for late May, mid-July, and early September 1994, and mid-July and late August for both 1997 and 1998. Late spring (May) images were not available for 1997 and 1998 due to excessive cloud cover over the study area. The July 1997 and July 1998 imagery were ac-

quired coincident with field sampling of the meadow communities. Each satellite image was georeferenced to a Universal Transverse Mercator (UTM) geographic coordinate system, and digital values were converted to reflectance to facilitate comparison between dates.

An unsupervised approach using multitemporal data was adopted for producing a map of the meadow communities. The two dates of satellite imagery for May 25, 1994 and September 6, 1994 were combined into a single six-band data file. An unsupervised classification procedure using a minimum-distance-to-means clustering algorithm was used to produce a preliminary map of fifty spectral classes. Each spectral class is composed of pixels that share statistically similar spectral reflectance characteristics. Each spectral class was then identified and assigned to an information class representing a vegetation type. Based on spectral similarity, and visual interpretation of the classes with the assistance of aerial photography and knowledge of the study area, the 50 preliminary classes were combined to create a final map of six spectrally-distinct meadow types (M1 to M6). M1 and M2 meadows were classified as hydric, M3 and M4 as mesic, and M5 and M6 meadows as xeric. To facilitate location of study sites during fieldwork, the map was converted to vector format and plotted on translucent Mylar for overlay onto 1:24,000 scale USGS topographic maps of the study region. Field sampling was conducted in 1997 and 1998 at sites within polygons selected from the meadow classes. Sites were considered suitable for sampling if they were at least 100 x 100 m in size, a distance of 500 m or farther from other sites, and within 8 km of a road or trail. Five sites for each of the six meadow classes were sampled (total study sites = 30). Particular care was taken to ensure that sites were located in the center of a given class polygon on the satellite classification map.

2.2 FIELD SAMPLING

Twenty 1 m x 1 m vegetation plots were established at each sampling site and the aerial percent cover of all plant species was estimated during midsummer (July) sampling period to derive a measure of plant species composition. Aerial percent cover estimations were conducted using a modified Daubenmire (1959) methodology. Means were calculated across each of the five replicates for each meadow class.

Abundance data were collected for butterflies employing previously developed methods (Debinski and Brussard 1992). Taxonomy followed Scott (1986). Butterflies were censused between 1000–1630 hrs on sunny days by netting and releasing for 20 minutes in one randomly selected 50 x 50 meter plot located with one corner on the center point of the sampling site. Surveys were repeated at each sampling site four times during each of the 1997 and 1998 field seasons. Abundance data were collected for birds using 50 m-radius point-count surveys. Surveys were performed three times at each site during the hours of 0530–1030 and

between June 1–July 17 in 1997 and 1998. Each survey involved two observers for 15 min. For details of bird surveys, see Saveraid (1999).

2.3 ANALYSIS METHODS

2.3.1 *Computation of seasonal and interannual changes in greenness*

Red and near-infrared reflectance has been used to measure vegetation condition, based on the negative relationship between red reflectance and chlorophyll content, and the positive relationship between leaf structure and near-infrared (NIR) reflectance (Jensen 1983, Curran 1985). The Normalized Difference Vegetation Index (NDVI) is calculated using the red and near-infrared bands, using the equation $[\text{NDVI} = (\text{NIR} - \text{RED}) / (\text{NIR} + \text{RED})]$. NDVI values are often referred to as “greenness” values because they have been shown to be well-correlated with vegetation cover, fraction of photosynthetically active radiation (*f*PAR) absorbed by green foliage, leaf area index (LAI), and biomass (Bartlett et al. 1990, Duncan et al. 1993, Hope et al. 1993, Goward et al. 1994, Everitt et al. 1996, Jorgensen and Nohr 1996, Jakubauskas et al. in press). Furthermore, seasonal and interannual changes in NDVI are increasingly used to monitor natural and anthropogenic changes in vegetation communities (Lloyd 1990, Reed et al. 1994, Lancaster et al. 1996, Peters et al. 1997).

An NDVI was computed for each pixel of each date of imagery. Seasonal changes in greenness for 1994, 1997, and 1998 were computed by subtracting the earlier seasonal date in each year from the later seasonal date (e.g., $[\text{NDVI}^{\text{July } 1994} - \text{NDVI}^{\text{May } 1994}]$). Increases in NDVI value (greenness) between two dates were therefore expressed as positive values, and decreases in NDVI as negative values. A similar procedure was used to compute interannual NDVI change for the three mid-summer (July) NDVI images (1994–1997, 1997–1998). NDVI change values for each field sampled site were extracted from each image using the UTM coordinates for each site. Tests for changes in NDVI (both seasonally and interannually) were conducted using a Scheffe’s ANOVA (PROC ANOVA, SAS Institute 1990).

2.3.2 *Species diversity measures*

Species diversity is a measure that incorporates both the species richness (the number of species) and abundance at a particular site. Species diversity for each taxonomic group was calculated using the Shannon diversity index (Magurran 1989). Because diversity indices combine two variables into one index, we also present a separate analysis of abundance (for butterflies and birds) and species richness by taxa. In all comparisons, data were summed across the multiple temporal replicates (for birds and butterflies) or averaged across the multiple spatial replicates (for plants) at each site within a year. Tests for significant differences in diversity between mesic meadows (M3 & M4) and all other meadow types were conducted using an ANOVA (PROC GLM, SAS Institute 1990). Tests for differences in species richness and abundance were conducted using a Scheffe’s

ANOVA (PROC ANOVA, SAS Institute 1990). Because the results showed similar trends during both years, we report on results from only 1998.

3. Results and Discussion

3.1 GENERAL MEADOW CHARACTERISTICS

M1 meadows were dominated by willow species and were located near streams. M2 meadows were dominated by sedge species and usually had some standing water. M3 and M4 meadows were of medium moisture and dominated by cinquefoil (*Potentilla gracilis*) and mixed herbaceous vegetation, while M5 and M6 meadows were characteristically xeric, rocky, and dominated by sagebrush (*Artemisia tridentata*). Plant species distinctive to specific meadow types include: *Salix wolfii*, *Aster integrifolius* (M1), *Carex rostrata*, *Juncus balticus* (M2), *Achillea millefolium*, *Artemisia cana* (M3), *Potentilla gracilis*, *Geranium viscosissimum* (M4), *Festuca idahoensis*, *Aster campestris* (M5), and *Artemisia tridentata*, *Stipa nelsonii* (M6) (Debinski et al. 1999).

3.2 SPECIES RICHNESS AND ABUNDANCE PATTERNS

Plant data showed the expected trend of peaking in diversity in the mesic meadows (M3 and M4). Species diversity for plants was significantly explained by meadow type ($P = 0.018$, $F = 3.4$, $df = 5, 24$), and the contrast of M3 and M4 versus the other meadow types was significant at the $\alpha < 0.10$ level ($P = 0.083$, $F = 3.26$, $df = 1$, Table I). Plant species richness in mesic meadows was significantly higher than that in M2 meadows due to the hydric meadows being dominated by a few species of sedges and rushes (Figure 1), but no other contrast was significantly different.

Butterflies and birds showed no significant difference in species richness, diversity, or abundance across meadow types, but butterfly richness was highest in M4 meadows. Trends of species richness and diversity were expected to be stronger for butterflies, given their close association with the plant community for nectar and hostplants.

Because birds respond to habitat structure as well as moisture gradients, it is not surprising that they showed highest richness and abundance in the hydric meadows where the structure of the willow (*Salix* sp.) communities creates greater habitat diversity. Birds may be more complex to predict in these meadows because they probably respond to both plant structure (which peaks in both hydric willow meadows and xeric sagebrush meadows) and plant diversity (Saveraid 1999).

As in most ecological systems, these results were affected greatly by variations in diversity within meadow types. If we had had a larger number of spatial replicates per meadow type, we may have been able to detect differences in bird and butterfly diversity between meadow types. These data also show that it may be

Table I

Plant species diversity and richness and butterfly and bird species diversity, richness, and abundance by meadow type in 1998. Data are shown as means (standard error) across three temporal replicates per site for bird, four temporal replicates per site for butterfly, and twenty 1 x 1 m² spatial replicates per site for vegetation data.

	Hydric		Mesic		Xeric	
	M1	M2	M3	M4	M5	M6
Plant						
diversity*	0.71 (0.09)	0.59 (0.14)	0.65 (0.13)	0.72 (0.09)	0.67 (0.15)	0.62 (0.08)
richness**	15.9 (0.81)	9.0 (1.03)	17.0 (1.04)	21.0 (0.67)	13.9 (1.01)	14.7 (0.70)
Butterfly						
diversity	1.91 (0.36)	1.92 (0.31)	1.97 (0.23)	2.10 (0.25)	2.12 (0.20)	1.94 (0.19)
richness	13.0 (1.04)	12.6 (0.96)	13.6 (0.81)	15.4 (0.65)	14.2 (0.57)	12.4 (0.79)
abundance	75.4 (2.72)	74.2 (2.56)	90.0 (2.44)	103.6 (1.77)	92.0 (2.22)	80.8 (2.09)
Bird						
diversity	1.14 (0.42)	1.13 (0.24)	1.34 (0.23)	0.93 (0.16)	0.97 (0.30)	0.76 (0.17)
richness	3.8 (0.76)	3.6 (0.47)	3.0 (0.77)	2.2 (0.52)	3.0 (0.71)	2.2 (0.57)
abundance	11.6 (1.01)	7.6 (0.92)	11.2 (1.51)	5.0 (0.92)	10.0 (1.31)	7.8 (1.14)

* M3 and M4 were significantly different from all other meadows at P < 0.10

** M3 and M4 were significantly different from M2 meadows at P < 0.05

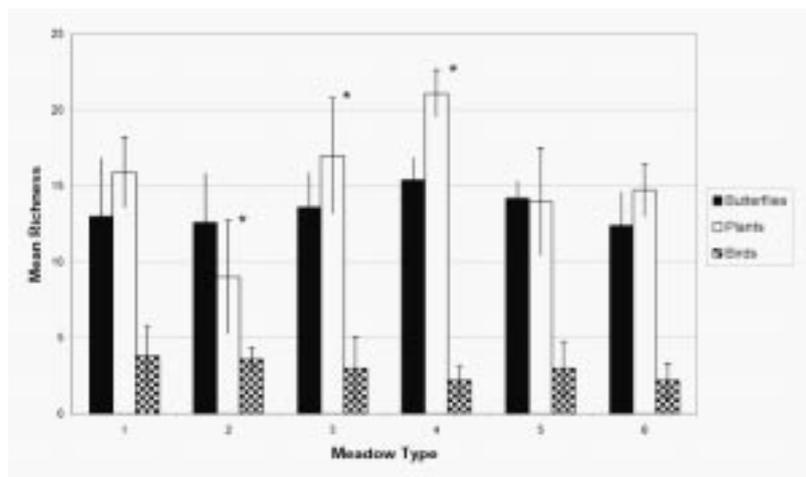


Figure 1. Comparison of species richness among plants, birds and butterflies in each of the six remotely sensed meadow types. Bars indicate 95% confidence interval. Asterisks denote a significant difference in plant richness in M3 and M4 meadows as compared with M2 meadows.

easier to detect significant differences in more species rich taxa (e.g., plants) than taxa that are represented by fewer species (e.g., butterflies and birds).

3.3 SEASONAL AND INTERANNUAL VARIATION IN NDVI

3.3.1 *Seasonal change*

Temperature and precipitation data obtained from the Western Regional Climate Center for Montana Climatological Division 2 indicate that above average temperatures and below average precipitation occurred throughout the summer and fall of 1994 (Table II). In contrast, warmer than average temperatures and higher than normal precipitation during spring and summer 1997 accelerated the rate of plant growth and development in the region. Significantly cooler and wetter than normal conditions in June 1998, however, led to delayed phenology and plant development during spring and early summer.

Table II
Summer temperature and precipitation, Montana Southwestern Division

	May		June		July		August	
Temperature (°C)								
1994	11.0	(+2.2)	13.8	(+0.8)	17.1	(-0.1)	17.8	(+1.6)
1997	10.4	(+1.6)	14.0	(+1.0)	16.3	(-0.8)	16.2	(0.0)
1998	9.6	(+0.7)	10.5	(-2.5)	18.8	(+1.6)	17.8	(+1.5)
1895–1998 mean	8.8		13.0		17.2		16.2	
Precipitation (cm)								
1994	4.6	(-1.2)	5.6	(-0.7)	3.8	(+0.2)	1.4	(-1.7)
1997	6.1	(+0.2)	8.7	(+2.3)	6.5	(+2.9)	4.7	(+1.6)
1998	5.4	(+0.4)	10.1	(+3.7)	3.6	(+0.1)	1.7	(-1.4)
1895–1998 mean	5.9		6.3		3.5		3.1	

(Numbers in parentheses denote departures from mean values)

Trends of seasonal change in greenness for all three years indicate that the mesic meadow types exhibit the greatest overall change between midsummer and fall, while xeric meadows exhibit little year-to-year variation in the summer-fall decrease in greenness (Figure 2). In 1994, below-average precipitation for the summer and early fall produced severe moisture stress across all meadow types and a high degree of greenness change for hydric meadow types and the mesic meadows. M4 meadows showed significantly more change in greenness compared to M5 meadows ($P < 0.05$, $F = 6.26$, $df = 5, 24$). In contrast, xeric meadows,

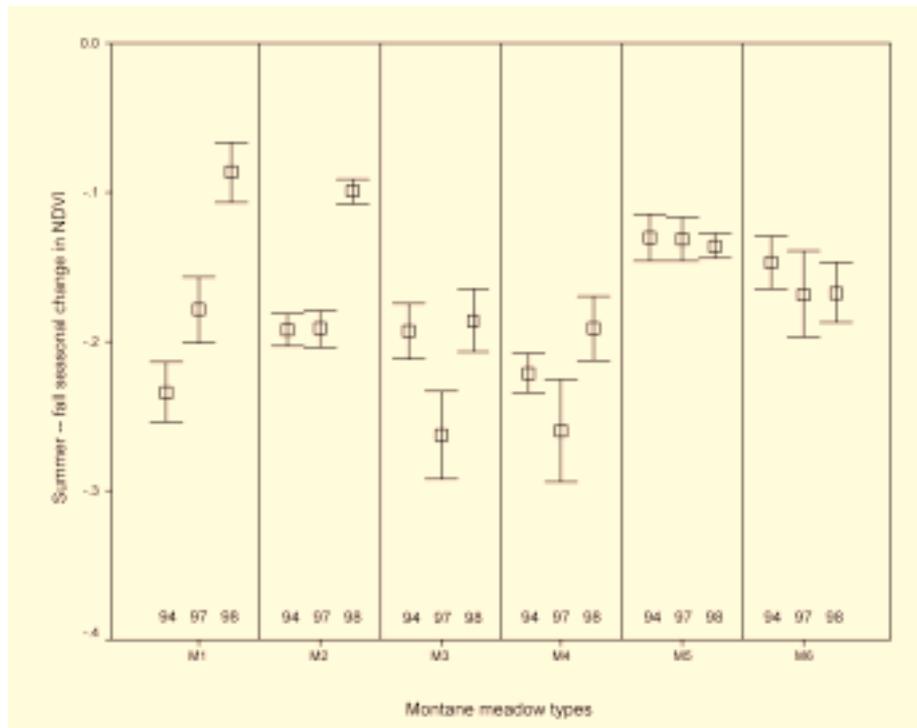


Figure 2. Seasonal change in NDVI (mean and standard error) for 1994, 1997, and 1998. More negative values indicated greater seasonal decreases in greenness from summer to fall.

with vegetation adapted to dry conditions, exhibited the least seasonal greenness change in 1994. Under wetter conditions (1997 and 1998), the hydric meadows showed less seasonal change, while the mesic meadows continued to exhibit large changes in summer-to-fall greenness values (Figure 2). In 1997, M3 and M4 meadows showed significantly more change in greenness compared to M5 meadows ($P < 0.05$, $F = 4.44$, $df = 5, 24$). In 1998, M3 and M4 meadows showed significantly more change in greenness compared to M1 meadows, and M4 meadows showed significantly more change in greenness compared to M2 meadows ($P < 0.05$, $F = 6.315$, $df = 5, 24$).

Differences between the three years are suggestive of strong environmental controls, particularly temperature and precipitation, on changes in meadow greenness. Hydric meadows in the study region tend to occur along streams and rivers that provide the vegetation with a constant source of moisture. Xeric meadows are typically on south-facing slopes, with near-constant moisture deficits producing sparse vegetation cover and little change in greenness. Mesic meadows, however, are dominated by a high percentage cover of grasses and forbs that are more dependent on precipitation for moisture.

3.3.2 Interannual change

Overall, the mesic M3 and M4 meadows exhibited the greatest range in interannual change in midsummer greenness of the six meadow types when comparing the periods 1994–1997 and 1997–98 (Figure 3). Comparing greenness values for midsummer 1994 to midsummer 1997, all meadows were substantially greener in 1997 than 1994. Of the mesic meadows, the M4 meadows exhibited a significantly larger interannual change in NDVI (1994–1997) than M1 and M2 meadows ($P < 0.05$, $F = 4.824$, $df = 5, 24$). We attribute these greenness changes to differences in early summer precipitation between the two years. Combined May–June precipitation for 1994 was 1.9 cm lower than normal; May–June precipitation for 1997 was 2.5 cm above normal (Table II). Temperatures for both periods were warmer than the long-term mean (mean May–June 1994: $+1.5^{\circ}\text{C}$; mean May–June 1997: $+1.3^{\circ}\text{C}$). Comparing greenness values for midsummer 1997 to midsummer 1998, however, the hydric and xeric meadows showed little difference in 1997 and 1998 midsummer greenness values (Figure 3). Mesic meadows exhibited lower greenness values in summer 1998 than summer 1997, which we attribute, based on field observations, to vegetation development occurring slightly later in the growing season, likely a result of cooler than normal temperatures and above-average rainfall in early summer (June) 1998 (Table II).

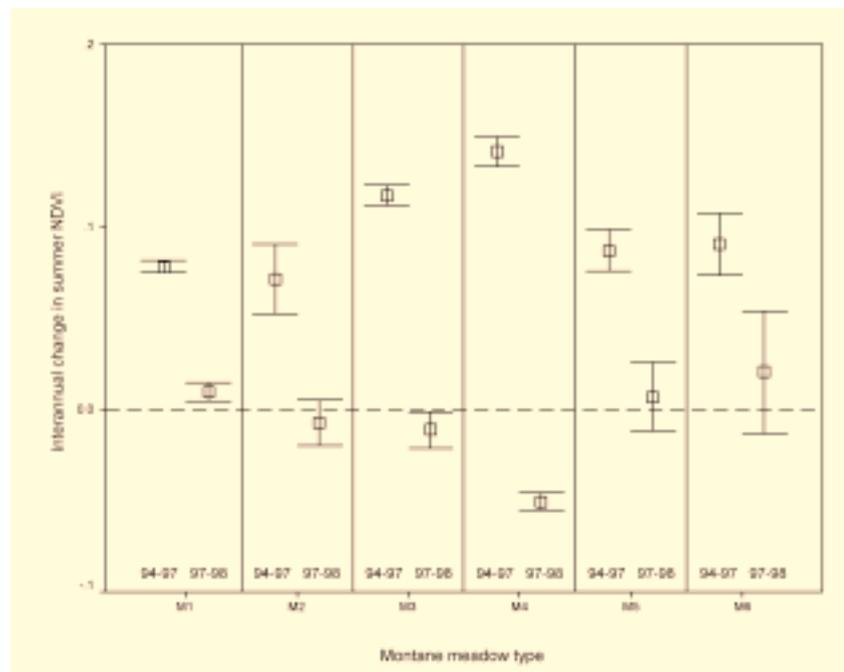


Figure 3. Interannual change in summer greenness, 1994–1997 and 1997–1998. Positive values indicate that all meadows were substantially greener in 1997 than 1994. With the exception of M4 meadows, meadows showed little difference between 1997 and 1998 midsummer NDVI values.

4. Conclusions

Satellite multispectral imagery can be used to identify spectrally and ecologically distinct montane meadow communities within the Greater Yellowstone Ecosystem along a moisture gradient from hydric to mesic to xeric. Mesic meadows supported the highest plant species diversity, although bird and butterfly communities did not show statistically significant differences in diversity among meadow types. Mesic meadows showed under both wet and dry years the most seasonal variation in vegetation greenness (as measured by NDVI). Interannual change similarly peaked in the mesic meadows. Because of their sensitivity to environmental conditions and specialized flora and fauna, mesic montane meadows may be important habitats to monitor with respect to degradation or loss of species in response to environmental and climatic stressors.

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