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THESIS

CHANGES IN THE DISTRIBUTION AND PREDICTIVE MODELING OF DOWNY BROME (*BROMUS TECTORUM* L.) AT HIGH ELEVATIONS

Submitted by

James Bromberg

Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

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COLORADO STATE UNIVERSITY

May 6, 2010

WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY JAMES BROMBERG ENTITLED CHANGES IN THE DISTRIBUTION AND PREDICTIVE MODELING OF DOWNY BROME (*BROMUS TECTORUM* L.) AT HIGH ELEVATIONS BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

CHANGES IN THE DISTRIBUTION AND PREDICTIVE MODELING OF DOWNY BROME (*BROMUS TECTORUM* L.) AT HIGH ELEVATIONS

Downy brome (*Bromus tectorum* L.), an invasive winter annual grass, may be increasing in extent and abundance at high elevations in the western United States. This may pose a threat to high elevation plant communities and resources. Anecdotal information suggested this range expansion in the Rocky Mountains, but data to confirm it was limited.

The initial goal of my project was to examine whether downy brome was increasing at elevations above its typical range of up to 2440 m by resampling prior field studies. I further expanded my goals to make predictions about future range expansion using Maxent, a habitat matching model. I also evaluated how well the model predicted the future distribution of downy brome through additional field sampling.

Two vegetation surveys in Rocky Mountain National Park (RMNP) conducted in 1993 and 1999 were resampled in 2007. Although these surveys were not initially established to examine downy brome specifically, they were useful in tracking changes in downy brome presence, abundance, and distribution. Statistical analyses were used to examine presence and abundance of downy brome, while the predictive modeling explored the potential distribution throughout RMNP. Stratified random sampling throughout RMNP in 2008 was used to validate how well the model predicted the distribution of downy brome.

Results of the studies confirm suspicions that downy brome is spreading within RMNP. Analyses of the field sampling indicate that expansion of downy brome is likely occurring both in abundance and frequency at elevations ranging from 2470 m to 3080 m. Predictive modeling also indicates that further range expansion is likely within RMNP as new incidence of downy brome tend to be found within areas with a high predicted probability of occurrence. The stratified random points sampled throughout RMNP confirmed that the model performed well over a larger spatial scale despite the limited extent of the initial samples.

Because downy brome appears to be increasing, managers of high elevation lands may need to consider taking a more active role in preventing further spread. The accurate model predictions made with a relatively small sample size indicate that Maxent can be an extremely useful tool for land managers who have limited time and resources. Predictive models, however, are just one of many types of information to be considered in making management decisions and should be used in conjunction with other resources.

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CHAPTER I

Distributional Changes and Range Predictions of Downy Brome in Rocky Mountain National Park

Abstract

Downy brome (*Bromus tectorum* L.), an invasive winter annual grass, may be increasing in extent and abundance at high elevations in the western United States. This would pose a great threat to high elevation plant communities and resources. However, data to track this species in high elevation environments are limited. To address changes in the distribution and abundance of downy brome and the factors most associated with its occurrence, I used field sampling and statistical methods, and niche modeling. I re-sampled plots from two vegetation surveys established in 1993 and 1996 in Rocky Mountain National Park (RMNP) for presence and cover of downy brome. While not all comparisons between years demonstrated significant changes in downy brome abundance, its mean cover increased nearly five-fold from 1993 (0.7%) to 2007 (3.6%) in one of the two vegetation surveys (P=0.06). The average cover of downy brome within a second survey more than doubled from 1996 (0.5%) to 2007 (1.2%), although this change was not statistically significant (P=0.24). Downy brome was present in 50% more plots in 1999 than in 1993 (P=0.02) in the first survey. In the second survey, downy brome was present in 30% more plots in 2007 than in 1996 (P=0.08). Maxent, a species-environmental matching model, was generally able to predict occurrences of downy brome, as new locations were in the ranges predicted by models generated earlier. The model found that distance to roads, elevation and vegetation community influenced the predictions most. The strong response of downy brome to interannual environmental variability makes detecting change challenging, especially with small sample sizes. However, results suggest that the area in which downy brome occurs is likely increasing

in RMNP. Field surveys along with predictive modeling will be vital in directing efforts to manage this highly invasive species.

Introduction

Invasive species have altered ecosystem function and vastly changed vegetation communities worldwide (Hobbs and Mooney 1986; Mack and D'Antonio 1998; Dukes and Mooney 1999; Sax et al. 2007). The ranges of many invasive species have continued to expand as environmental conditions change. Most studies have examined biological invasions at lower elevations where anthropogenic influences on disturbance and seed dispersal are greatest (Dietz and Edwards 2006). High elevation habitats may now be at increased risk of invasion due to climate change and the increased use of mountain ranges by human populations (Pauchard et al. 2009).

Downy brome (*Bromus tectorum* L.) is one species that may be increasing in abundance at high elevation in the Rocky Mountains. It has spread rampantly and altered ecosystems throughout the western United States (Morrow and Stahlman 1984; Knapp 1996; Evans et al. 2001). It is a winter annual grass that takes advantage of the autumn rains for germination. Since it germinates before the winter arrives, it is much farther along in its growth by the time cool season native perennial seedlings emerge in the spring, which gives it a competitive advantage in its introduced range (Harris 1967).

Downy brome has been present in the United State since the late nineteenth century and is thought to have reached its 1981 distribution by around 1928 (Mack 1981). During the early 1900s, the species' range expanded so rapidly that it had become the dominant grass in much of the arid west (Mack and Pyke 1983; Mack 1981). More recent studies have shown the potential for further range expansion of downy brome throughout the western United States (Bradford and Lauenroth 2006; Bradley 2009). The grass may continue to expand its range in the United States at both high elevations and latitude (Rice and Mack 1991a). Although Chambers et al. (2007) reported that downy brome is limited by low temperatures at high elevation, land managers have recently observed it increasing in these habitats (J. Connor, Rocky Mountain National Park, pers. Comm.; Ramakrishnan et al. 2006). Because of the rate with which this species grows and alters ecosystem function (Rummell 1946; Melgoza et al. 1990; Humphrey and Schupp 2004; Sperry et al. 2006), concerns have surfaced that downy brome may threaten high elevation plant communities.

With the continued spread of downy brome into novel habitats, there is an urgent need to model its potential distribution (Stohlgren and Schnase 2006) to direct management efforts. Often the potential distribution of a species has been determined by pairing the habitats in which it currently occurs with those that have similar characteristics, but have not yet been invaded (Mack 1996; Stohlgren et al. 2005). This approach of matching habitats by modeling ecological niches has become more prevalent in predicting the potential ranges of invasive species in recent years (Peterson 2003). Statistical models, such as logistic regression, boosted regression trees, and classification regression trees (Friedman et al. 2000; Hastie et al. 2001; Elith et al. 2008), have also been used to predict species distributions. They use presence and absence data for a species, but predictions may be biased since absence points do not preclude that the species could occur there. Presence only models, such as the genetic algorithm for rule-set production (GARP) (Stockwell and Noble 1992; Stockwell and Peters 1999) and Maxent (Phillips et al. 2006), have demonstrated an increased ability to predict a species range since they allow the possibility of occurrence of a species even where it has not been found (Evangelista et al. 2008; Kumar et al. 2009).

In its native range of Eurasia, downy brome occurs from sea level up to 1525 m (Young 2000). Studies in the United States have shown it occurring from near sea level to about 1220 m in California (Rice and Mack 1991b) and occurring at the highest densities between 1220 m and 1525 m in the Great Basin (Hunter 1991). Records from the Rocky Mountain Herbarium in Wyoming show downy brome occurring in Colorado from 1370 m to near 2990 m throughout the 1990s, with most accessions collected between 1525 m and 2440 m. An accession of the Rocky Mountain Herbarium was collected from 3050 m in 2004. There are limitations to herbaria data since the locations from which specimens came are often not verified. Additionally, herbaria specimens are often concentrated in locations that botanists frequent, and thus such specimens may not be a representative sample of that species' distribution.

Few quantitative datasets exist on the abundance and distribution of downy brome over time and at high elevations. Since little has been done to document possible changes, I investigated the anecdotal accounts of its spread at high elevation and at multiple scales as proposed in the comprehensive research agenda of Pauchard et al. (2009). First, I examined whether downy brome has increased in either cover or frequency, or both, within Rocky Mountain National Park, a high elevation region of the southern Rocky Mountains. Second, I predicted the potential range of downy brome in the Park using the environmental matching model Maxent. Third, I examined what environmental variables were most strongly associated with the occurrence of downy brome within the study region. Knowing where downy brome is spreading and where it will likely invade in the future will help land managers at the Park and other high elevation areas make informed decisions on management of this invasive grass.

Methods and Materials

Study area. The study was conducted in Rocky Mountain National Park, which sits above the Colorado Front Range in the southern region of the Rocky Mountains. The elevation ranges from approximately 2300 m in Estes Park to over 4300 m on Longs Peak. The Park is situated at latitudes of approximately 40°10′N to 40°32′N, which influence the range of many species occurring in the park along with elevation, temperature and precipitation. One main road transverses the park generally from east to west, while additional roads run along the eastern border of the park. Three hundred and fifty nine miles of trails provide backcountry access as they meander throughout the park. Grasslands, shrublands and forested communities are all included in the study region. All of the study sites occurred within the eastern region of the park with elevation ranging from 2470 m to 3080 m.

The region near Estes Park at the east entrance of Rocky Mountain National Park typically experiences an arid climate with average annual precipitation of approximately 35.6 cm. The growing season is short with snow often occurring into early June and returning in September, and there is the potential for snow any month of the year. Average high temperatures in July are 25.7 °C with lows around 7.8 °C. Average temperatures for the month of January range from -8.7 °C to 3.5 °C. Extremely rapid changes in weather are a common occurrence in Rocky Mountain National Park.

Field Methods. Two previously developed surveys were re-sampled for the current study. These surveys were chosen because they each contained data on all plant species that occurred within the plots, including downy brome, if it was present. They also are two of the few long-term vegetation surveys available to resample in Rocky Mountain National Park. One of the surveys was originally set up to study secondary successional changes in vegetation. Plots were paired such that each plot within a disturbed site had a corresponding nearby site in an undisturbed similar vegetation community. This will be referred to as the Succession Study. The other study was originally set up to look at forest ecotones. Each site consisted of three plots along an elevation gradient, such that the middle plot was positioned on the border between two forest types. This will be referred to as the Ecotone Study. Both of these studies were incorporated into the current study to examine changes in the distribution of downy brome at these high elevation sites.

The Succession Study plots were re-sampled as close as possible to the original sampling design (Elzinga et al. 1998; McLendon and Redente 1993; Zadeh 2001). This study consisted of 17 sites in previously disturbed areas, with all but one having a corresponding reference site in undisturbed vegetation for a total of 33 plots. Because plots had been marked with rebar, a global positioning unit was used to relocate all of the plots based on previously recorded UTM coordinates in NAD83 datum. Each plot started from a coordinate from which a base line ran. A baseline extended from a coordinate that marked the plot location. Multiple transects extended perpendicular from the baseline at 1 meter intervals, and were 6 m to 13 m in length. Depending on the particular plot, data were collected every 1 to 2 m along each transect for the length of each plot. A pointer was placed vertically at each location along the transect and all vegetation in contact with the pointer was recorded.

The Ecotone Study plots were also re-sampled as closely as possible to the original study design. These consisted of 14 randomly selected transects along which three plots were located for a total of 42 plots (Stohlgren et al. 2000). These plots were set up using a modified Whittaker design (Stohlgren et al. 1995; Barnett and Stohlgren 2003) with the lengthwise direction of the 1000 m^2 plots heading uphill and three plots positioned along a transect such that the middle plot fell within the forest ecotone. Plots were relocated using a global positioning unit based on previously recorded UTM coordinates in NAD27 datum. The UTM coordinate represented the lower right corner of the plot from which measuring tapes extended 20 m to the left and 50 m uphill. Ocular estimates of cover classes used in the initial survey (Stohlgren et al. 2000) were recorded for all plant species present within the 1m^2 subplots. Data on cover of all species present within ten 1 m^2 subplots were recorded. Species presence for all species within two 10 m^2 subplots, one 100 m^2 subplot and the entire 1000 m^2 plot was also recorded.

Statistical Analyses of Field Data. I initially combined field data from the two surveys to see if I could increase the sample size when analyzing the data set. Only plots from each survey in which downy brome occurred in at least one of the sampling periods were included in the analysis. This eliminated skewing the data too strongly with the abundance of absence records. These preliminary analyses suggested that the survey being examined had a significant effect on the cover of downy brome ($F_{1,29}$=4.39 P=0.045) as well as on the frequency of downy brome ($F_{1,29}$=4.45 P=0.044). Furthermore, the variance of the two surveys differed drastically: covariance parameter estimates of cover were 3.2 for the Ecotone Study compared to 15.9 for the Succession Study, nearly five times greater variance. I therefore could not legitimately combine the analysis of the Succession Study plots and the Ecotone study plots without violating the assumption of equal variances, and analyzed the two surveys separately. Separate analyses were also more appropriate due to differences in data collection methods and the number of plots in each of the two surveys.

I used analysis of variance (ANOVA) to examine the effect of year on frequency of downy brome using PROC GLIMMIX (SAS 9.2, SAS Institute Inc., Cary, NC, USA) and on cover using PROC MIXED on each individual survey. The year of sampling and the survey sampled were fixed effects, while plots within each survey were random effects. I used paired t-tests of least square means to analyze cover and frequency of downy brome between specific years using these same two procedures in SAS.

Potential Distribution Modeling. Potential distribution of downy brome was predicted using Maxent (Phillips et al. 2006), a species environmental matching model. I chose to use Maxent because it has been found to perform best among many other modeling techniques (Elith et al. 2006; Evalgelista et al. 2008; Ortega-Huerta and Peterson 2008; Kumar et al. 2009) and can handle both continuous and categorical variables, incorporate interactions, and model non-linearities (Phillips et al. 2006). Field-collected occurrence data for downy brome from three time periods (1993, 1999 and 2007) were transferred from GPS to Excel (Microsoft 2007) spreadsheets and used in Maxent modeling to test how the additional data in each new time period affected the predictions of the model. Environmental variables that could potentially affect downy brome occurrence were gathered in GIS (geographic information system) Grid format (30 m spatial resolution) and included topographic (slope, aspect, and elevation), anthropogenic (e.g., distance from roads), and remotely sensed (e.g., Normalized Difference Vegetation Index [NDVI]) variables that were chosen based on their use in previously published studies (e.g., Rew et al. 2005; Kumar et al. 2006; Evangelista et al. 2008; Mortensen et al. 2009). Downy brome occurrence data were integrated with these environmental variable layers using Maxent to generate potential distribution maps. The three models generated with data from the three time periods were compared to one another based on the top environmental predictors and the area covered by each of the predicted probability levels. I also examined how many of the new downy brome locations were predicted by the models generated from earlier time periods. I used the three Maxent generated predictions to determine whether the models indicated a changing distribution of downy brome over time.

A two-tailed Wilcoxon-signed rank test (Randin et al. 2006; Phillips et al. 2009) was used to test whether the probability of occurrence values for downy brome predicted by the Maxent model for three different time periods differed from each other. One thousand random points throughout the Park were generated and the probability values of each were extracted from the three models to run the above test.

Results

Field sampling. The frequency of downy brome within plots was variable from year to year. Only plots in which downy brome was currently present or had been present at one time were used for analyses, because other plots may had been unsuitable habitat. In the 14 Succession Study plots used for analysis, downy brome occurred within 29% of the plots in 1993 and increased to 79% of the plots in 1999 (P=0.02) (Figure 1a). In 2007, downy brome occurred in 50% of the Succession Study plots. Although it occurred in more plots than the original survey, this was not a significant increase from 1993 (P=0.26). There was also no detectable change in the frequency of downy brome when evaluating the observational period from 1999 to 2007 (P=0.13).

In the 17 Ecotone Study plots analyzed (Figure 1b), there was a marginally significant increase in the frequency of downy brome between 1996 and 2007 (P=0.08). Downy brome occurred within 58% of these plots in 1996 and 88% of the plots in 2007. Thus, the only significant differences in the frequency of downy brome were an increase from 1993 to 1999 in the Succession Study plots and a marginally significant increase from 1996 to 2007 in the Ecotone Study plots. All other differences in frequency of downy brome, whether in an increasing or decreasing direction, were not significant.

Cover of downy brome within plots consistently increased from 1993 to 2007. The average cover of downy brome in the Succession Study plots in 1993 was 0.7% (Figure 2a), and in 1999 was 1.0%, however this was not a significant increase (P=0.88). Average cover further increased to 3.6% within these plots in 2007. This was a marginally significant increase from both 1993 (P=0.06) and 1999 (P=0.08). The maximum cover in any of our high elevation plots was 20.4%, but cover was generally much lower than that.

The Ecotone Study plots showed a similarly increasing trend (Figure 2b). Cover of downy brome was 0.5% in 1996 and increased to 1.2% in 2007. Although cover more than doubled, this was not statistically significant (P=0.24) because of the variance in cover within the same plots across the two years and the small sample sizes.

Distribution modeling. The area predicted to have probabilities of downy brome occurrence of 30 to 50%, 50 to 80% and 80 to 100% increased by only 1 to 2 km^2 between the 1996 and 2007 models (Figure 3). The predicted area of the lowest probability class (less than 10%) also increased from 984 km^2 in 1996 to 997 km^2 in 2007. Only the 10 to 30% probability class demonstrated a decrease in predicted area from 59 km^2 in 1996 to 43 km^2 in 2007. The areas determined to fall within probability classes by the Maxent model cannot be compared by statistical tests in the software package. It appears that there were only minimal changes in the predicted areas from the model, and thus the general predicted area of downy brome seems consistent over the modeling periods. However, the model predictions based on data from 1996, 1999, and 2007 were significantly different from each other after Bonferroni correction for multiple comparisons ($P<0.001$, two tailed Wilcoxon-signed rank test, paired by model).

The environmental variables that were most influential in predicting the occurrence of downy brome for all three models were the distance of the sampling site from the nearest road, the elevation of the sampling site, and the vegetation community within the sampling site (Table 1). However, the relative importance of these three environmental variables shifted among the models (Table 1). The vegetation community was the most influential predictor variable in the model in 1996 accounting for 40.4% of the predicted occurrence of downy brome. This dropped to 23.5% in 1999 and 17.7% in 2007. Distance to the nearest road was the next most influential predictor variable in the 1996 model accounting for 23.6% of the predicted occurrences. Distance to the nearest road was the most influential variable in 1999, accounting for 31.8%, and increased further to account for 35.9% of the variation in the 2007 model. Elevation was the third most influential predictor variable in the 1996 model accounting for 15.2% of the variation in the predicted range. This variable also increased in influence accounting for 24% in the 1999 model and 29.1% in the 2007 model.

I compared 1996 and 1999 model predictions with the 2007 model predictions to evaluate whether including more data points to parameterize the model improved its predictive ability. The threshold for predicting downy brome was set at greater than 10% because I found downy brome in the field only in areas with this probability classification and higher. I determined that a predicted probability above 10% coincided with the potential for downy brome occurrence. A predicted probability below 10% in the model was considered to have a very low likelihood of downy brome occurrence. Forty percent of the field-sampled downy brome locations in 2007 were predicted by the model based on 1996 and earlier data. Using 1999 and earlier data, 60% of the same 2007 downy brome locations were predicted by the model. Thus, most new downy brome locations using this model are occurring where the models predicted high habitat suitability. Because the 2007 model was generated using the new 2007 sample locations, all points where downy brome was found in 2007 were predicted to occur by the 2007 model, as would be expected.

Discussion

The results indicate that downy brome likely increased in cover and frequency in Rocky Mountain National Park over the decade and a half between 1993 and 2007. Although not all comparisons between years showed an increase, all significant and marginally significant differences were in an increasing direction. Because this species shows annual variability in its distribution due to interannual environmental variability, we would expect to see decreases in downy brome some years and increases in other years. It is remarkable that only increases in both cover and frequency were detected given this annual variability. In addition to the increases in downy brome, it is also worth mentioning that average cover more than doubled in the Ecotone Study plots from 1996 to 2007. However, this is not statistically significant and a change in cover from 0.5% to 1.2% may also have little ecological significance. Cover at high elevations was still relatively low in most plots; the greatest average cover of downy brome was 3.6% in the Succession Study plots in 2007, with the greatest cover of nearly 20% found in an individual plot in that same year. For comparison, downy brome has the potential for much greater cover as demonstrated in a study conducted in the Great Basin where nearly 100% cover was found (Booth et al. 2003).

Sample sizes of the two surveys were small because I was limited to using plots established for previous studies. However, even with these small sample sizes and great variability within and between plots, I was able to demonstrate an increase in downy brome at high elevations. It is likely that had the sample sizes been larger, I would have seen an even more significant increase in cover and frequency of downy brome. However, considering that many of the plots were in disturbed sites and not a random sampling of the entire Park, this may have also skewed the study towards areas of greater likelihood of downy brome occurrence. The increased disturbance present in the Succession Study plots may also explain why significant increases in cover were only seen in this study and not in the Ecotone Study plots. I was unable to detect an increase in suitable habitat of downy brome from the different years' model predictions, which may be because Maxent is able to make predictions of species habitat based on fewer points.

Each model generated using Maxent included additional sample locations to address the second study question of whether including more data changed the predicted distribution of downy brome. Chronological model predictions from 1996, 1999 and 2007 were significantly different from each other in terms of the distribution of suitable habitat for downy brome, but did not demonstrate increases in the areas predicted to have high suitability. Approximately the same acreage was predicted to be infested with downy brome in all three of the models. Minor changes in the location of the predicted areas and the probability of occurrence existed, but were of little consequence. Six of the ten new occurrences of downy brome found in 2007 field samples were predicted by the 1999 model. Downy brome mostly increased within the area of probable occurrence predicted by the earlier models. Because more than half of the new locations found were predicted by the earlier models, the models with fewer data points were able to predict the potential range reasonably well, although far from perfectly. It appears that only a small sample of presence locations is necessary to generate a model prediction using Maxent, because the model prediction changed minimally as new sample points were added. My results are consistent with other small sample studies using Maxent (Kumar and Stohlgren 2009). One such study used a sample size of four geckos to successfully predict where the fifth one would likely occur (Pearson et al. 2007). With each successive study, modelers are gaining confidence that Maxent works well with small sample sizes.

The final research objective was to determine what factors were most associated with the occurrence of downy brome in the Park. Elevation, distance to roads, and the vegetation community were the most influential environmental variables in predicting where downy brome would occur. Downy brome probability of occurrence was highest in shrublands and grasslands, and decreased with elevation and the distance away from roads and trails. Even using the smallest data-set, these same three environmental variables were identified as being the most correlated with occurrence of downy brome. However, the environmental variables shifted in their relative importance as I added more data to the models. I do not believe that the shift was due to actual changes in the influence of these environmental factors. A more likely explanation is that adding more data allowed the model to identify stronger relationships to these environmental factors simply due to the larger sample size. It was not at all surprising that these three environmental factors were determined to be highly correlated with downy brome occurrence. Downy brome has previously been shown to occur at specific elevation ranges. A study in the Great Basin showed downy brome occurring only up to 1900 m (Hunter 1991). I found it occurring at 2884 m in 2008 which is the highest known occurrence within Rocky Mountain National Park. Roads have been identified as a common pathway of dispersal and are disturbed sites that support many invasive plant species (Getz and Baker 2008). Downy brome in particular is common in disturbed areas such as roadways and pastures (Upadhyaya et al. 1986). The grass can colonize both steppe and forest vegetation communities even with vast differences in soil type, climate, and community structure (Daubenmire 1968). However, it is more likely to occur in grass and shrubland communities than in forested areas (Pierson et al. 1990). The limited tolerance of downy brome to shade influences what vegetation types can support this grass. Forests with more open canopies, either naturally or due to disturbance, are more likely to support downy brome than closed canopy forests due to amounts of light available on the forest floor (Pierson et al. 1990), although neither forest type supports it in great abundance.

Many mechanisms for the increase in distribution and abundance of downy brome have been proposed. Factors such as propagule pressure, local adaptation, and environmental change have been suggested as means of range expansion for invasive species.

Often a species may not occupy an area with suitable growing conditions simply due to absence of propagules (Richardson et al. 2000). The chance dispersal of downy brome seed appears to be high within the Park due to the presence of roads and abundance of wildlife that regularly transport seeds (Pierson and Mack 1990). Although the grass seems to have the potential for dispersal throughout the Park, environmental restrictions may still limit its range at these high elevations (Pierson and Mack 1990).

Local adaptation of downy brome has also been proposed as a mechanism for the expansion into high elevation communities. Great genetic variation has been found in downy brome both within and among populations in the intermountain region (Rice and Mack 1991a). However, the genetic variation between high and low elevation populations of the Rocky Mountain Front Range appears limited (Kao et al. 2008). The limited traits that have been examined do not indicate that local adaptation to high elevation conditions has occurred in this region, but this mechanism for range expansion cannot be ruled out.

Climate change is having ecological impacts on ecosystems world wide (Walther et al. 2002) and may play a role in the spread of downy brome at high elevations. It is one of the major driving factors expected to decrease biodiversity over the next century with shifts in species distributions and abundance (Sala et al. 2000; Thomas et al. 2004). It is also expected to lead to shifts in altitude and latitude of species ranges (McCarty 2001). The atmospheric carbon dioxide concentration is increasing, temperatures are increasing, and the timing and intensity of precipitation are being altered (IPCC 2001). These changes can facilitate the spread of invasive species such as downy brome. Growth rates of downy brome have been shown to increase under elevated carbon dioxide levels (Smith et al. 1987; Smith et al. 2000), which has been seen with many other non-native invaders as well (Sasek and Strain 1988; Sasek and Strain 1991). Temperature and precipitation patterns also greatly affect the growth and distribution of downy brome (Bradley 2009). It is not clear how these environmental factors will change to impact the distribution of downy brome. Major concern exists due to the potential spread of downy brome under certain climatic scenarios (Bradley 2009).

Nitrogen deposition in the Rocky Mountains is likely another environmental change encouraging the range expansion of downy brome. Nitrogen deposition has been correlated with increased fire frequency, habitat alteration, and increased invasion of non-native plant species (Fenn et al. 2003). The addition of nitrogen to soils can tip the balance toward an abundance of non-native species because native species are often adapted to lower levels of nutrients (Ostertag and Verville 2002; Brooks 2003). Nitrogen addition has been shown to increase the competitive effects of downy brome (Lowe et al. 2003), and reducing nitrogen in the soil can limit growth of downy brome (Beckstead and

Augspurger 2004). The Rocky Mountains receive elevated levels of nitrogen (Williams et al. 1996), which has been more pronounced on the east side of the mountain range than the west (Baron et al. 2000). Increased nitrogen in the Colorado Rocky Mountains is likely contributing to the range expansion of downy brome that I have documented.

With the potential spread of downy brome throughout the Rocky Mountains, it is imperative that land managers be able to make quick and effective use of the available information. I have documented that downy brome is likely expanding into these high elevation communities. The Maxent model also indicates that there is the potential for much greater expansion at high elevation. I detected new locations of downy brome occurring where the model predicted it might be found, demonstrating that it may be filling in the areas predicted by the model to have medium to high probabilities of occurrence. If all of the predicted areas within Rocky Mountain National Park become infested with downy brome, there is a much larger problem on their hands. Without management, downy brome has the potential to contribute to the loss of native plant communities by increasing fire frequency and resultant further invasions (Beatley 1966; Yensen 1981; Knapp 1996). Further exacerbating the issue is devastating lodgepole pine mortality caused by mountain pine beetles in the Rocky Mountains (Jenkins et al. 2008), which creates the potential for much more habitat to become vulnerable to downy brome invasion.

My study indicates that downy brome is likely increasing in cover, and that the model informs us where continued range expansion is likely to occur. Land managers can use the model predictions in developing their management plans for the control of invasive species. The models inform managers where species are likely to occur. With the limited resources of time and money available to most land managers, models will help them focus and prioritize their efforts to areas where these resources are needed most. There are many benefits of such environmental matching models to land managers. First, there is no need to waste efforts looking for a species where it is very unlikely to occur. Second, model predictions will hone in on areas with likely occurrence of a species where it is not yet present. Monitoring and management of invasive plant species will be of the utmost importance in these areas to prevent invasions into new habitats. Third, early control before invasion occurs will reduce the financial burden and resource input of land managers. One final benefit to managers is that even a very small number of samples can be used to develop a fairly accurate prediction model with Maxent (Pearson et al. 2007; Wisz et al. 2008; Kumar and Stohlgren 2009) provided the samples capture the environmental variation associated with the species occurrence. Few land managers have the resources to conduct a thorough survey on which to base management decisions. With models like Maxent, managers may not need to conduct a thorough survey of an invasive species on their land to predict its likely future occurrence. A little data may go a long way toward increasing the efficacy of invasive plant management efforts.

Interpretive Summary

The data from field study plots sampled over the last 15 years suggest that downy brome is spreading at high elevations in Rocky Mountain National Park. I applied a model that used environmental conditions where downy brome is found in the Park to predict where the plant was likely to spread. All three generated models showed a similar predicted distribution that was greater than the current distribution of downy brome in Rocky Mountain National Park. Many of the new locations of downy brome occurred where the earlier models predicted they would occur. This indicates that downy brome may likely continue spreading within this high elevation region.

The models suggest that areas close to roads and trails, at lower elevations, and in shrubland plant communities in the park are most likely to be invaded by downy brome. Knowledge of both the high risk areas and environmental factors that support the growth and spread of downy brome can greatly increase the effectiveness of management efforts. Land managers generally have limited time and money available for on-the-ground management. Because Maxent is a geospatial model, its mapping images can help focus weed management and control on areas with a high probability of spread as well as areas of high resource value. Using this or similar models can reduce the time and effort managers spend searching for weeds in areas of high priority but low probability of occurrence, thus more effectively using their limited resources.

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Table 1.1. Contribution of the top environmental variables to the predicted distribution of downy brome in the three prediction years.

Environmental variable	Prediction Year 1996	1999	2007	Effect
Distance to nearest road	23.6%	31.8%	35.9%	Negative*
Elevation	15.2%	24.0%	29.1%	Negative*
Vegetation community	40.4%	23.5%	17.7%	Shrublands and grasslands were most invaded

* Probability of occurrence decreased with increasing distance from roads/trails and increasing elevation

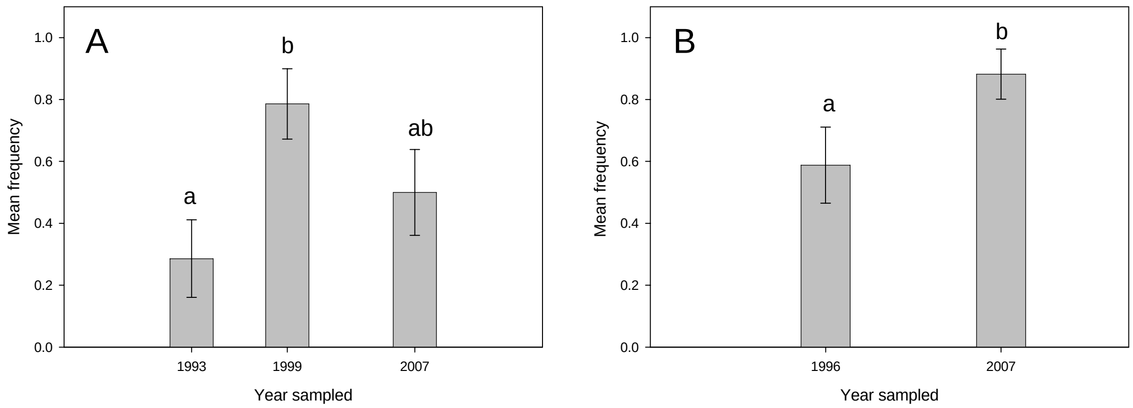

Figure 1.1. The mean frequency of downy brome in (A) the Succession Plots and (B) the Ecotone Plots over the course of the study. Error bars are the standard error of the means (α=0.05).

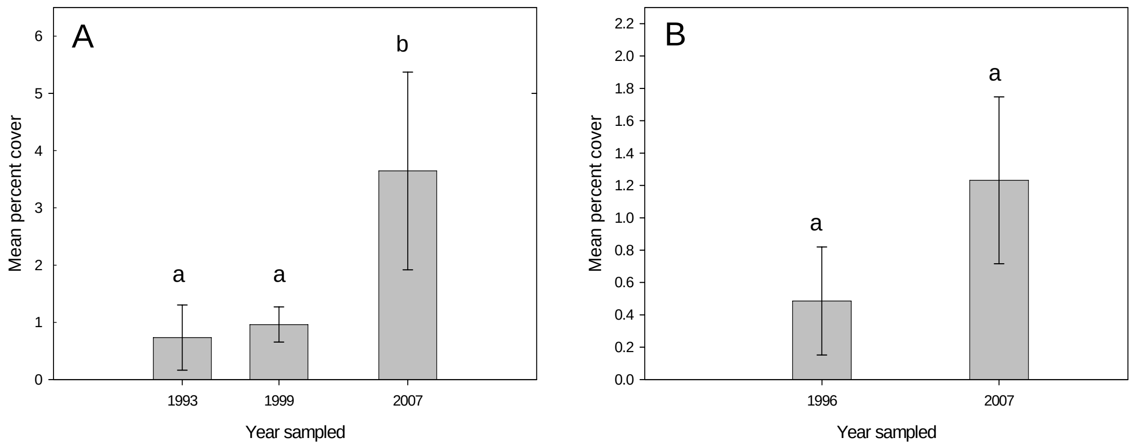

Figure 1.2. The mean cover of downy brome expressed as a percentage of the area sampled in (A) the Succession Plots and (B) the Ecotone Plots over the course of the study. Error bars are the standard error of the means (α=0.05).

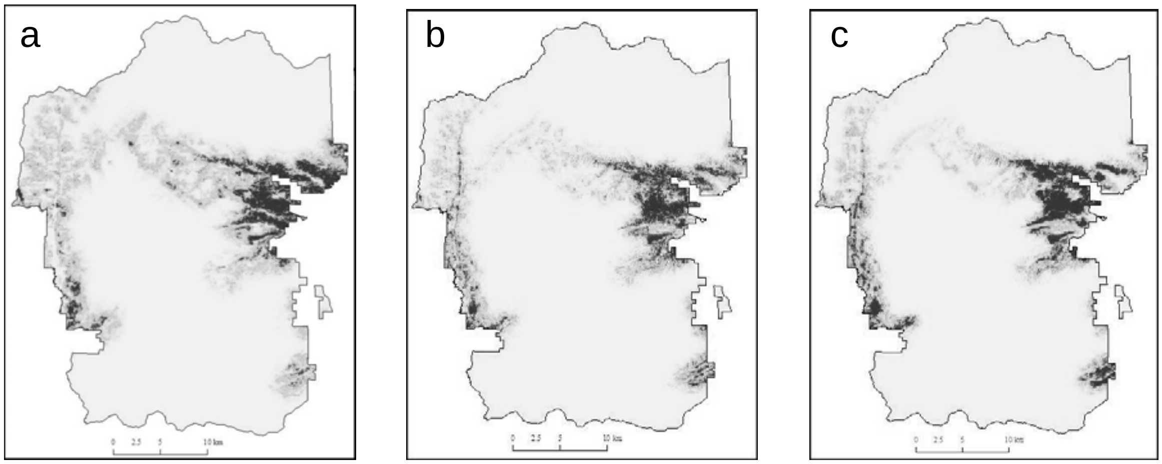

Figure 1.3. Predicted probabilities of downy brome occurrence in Rocky Mountain National Park using data from (a) 1996 and earlier, (b) 1999 and earlier, and (c) 2007 and earlier. Black indicates a high predicted probability of downy brome occurrence. Lighter shades of grey indicate a decreased probability of occurrence of downy brome.

CHAPTER II

Maxent Model Validation Using Random Stratified Field Locations in Rocky Mountain National Park

Abstract

Researcher and land managers need tools available to them to easily access the potential distributions of species such as those that are either rare or invasive. Maxent is one such predictive tool that has become more widely used in the last five years. Predictive models have internal mechanisms for determining accuracy. However, little work has been done to field-test these models, especially when making predictions at a different scale than the training data used in building the model. Based on predictions of downy brome distribution using Maxent, I sampled random points throughout Rocky Mountain National Park that were stratified among influential predictor variables and probability classes. Ninety three sites were evaluated for presence or absence of downy brome.

Logistic regression confirmed that the most influential predictor variables in the model including elevation, distance to roads and trails, and vegetation type, strongly influenced the distribution of downy brome. Further results showed that the probabilities of downy brome occurrence matched the proportion of occurrences found in the field. Proportions were generally on the lower side of the probability classes probably because downy brome has not yet reached its full potential range. Field sampling also detected occurrences of downy brome in Lumpy Ridge and Wild Basin. Both areas were predicted to have a high likelihood of downy brome, but it was previously not known to occur there.

With field validation, it is evident how well the model predicted downy brome occurrence in Rocky Mountain National Park. If this model can perform as well with

other species, it has the potential to be very useful not only to researchers, but to land managers as well. Although predictive models should not be the sole guide for management decisions, they can help to focus management efforts in the areas of greatest need and to allocate limited time and resources most effectively.

Introduction

The importance of predicting species distributions is increasing, especially with rapid environmental change. Scientists and land managers may need to locate and protect populations of a rare species or identify habitat that may be threatened by an invasive species. These are merely two of many reasons accurate predictive tools are important. Distributions of species vary according to an array of biological and physical conditions. Scientists often attempt to predict the ranges of species based on various environmental factors known to be associated with particular species.

Many models have been used to predict species ranges. A species' potential distribution has frequently been determined by locating habitats similar to those in which the species occurs (Mack 1996; Stohlgren et al. 2005). This approach of modeling ecological niches has become more prevalent in predicting the potential ranges of invasive species in recent years (Peterson 2003; Stohlgren et al. 2010). Models that use known locations of a species (i.e., presence-only models), such as DOMAIN (Carpenter et al. 1993), genetic algorithm for rule-set production (GARP) (Stockwell and Noble 1992; Stockwell and Peters 1999), and Maxent (Phillips et al. 2006), have demonstrated improved ability to predict a species' range over models that use both locations where the species is known to occur and known not to occur (i.e., presence-absence models). Presence only models do not assume that absence precludes the possibility of occurrence (Evangelista et al. 2008; Kumar et al. 2009). Much uncertainty exists with absences, because they may indicate either unsuitable habitat or suitable habitat into which the species has not yet dispersed.

Although many of these models effectively predict where species are likely to occur, they may not be rigorously validated. Many species habitat models use a subset of the original data to validate the model (Fielding and Bell 1997; Elith et al. 2006). In such cases, the data are partitioned into training data to generate model predictions and testing data that are used to assess the accuracy of the model predictions. If the testing data are sufficiently predicted correctly by the model, then the model is considered to accurately predict the species' range. Because the testing data are a random sub-sample of the original data-set, information can not be obtained on the accuracy of the model when applied to a larger region than that from which the original data came. Improved model evaluation can be obtained by incorporating independent field-based presence and absence data, but this method is rarely used (see Costa et al. 2010 for a recent example using this method with reptiles).

Model comparisons are often used to determine which model is the best predictor of a species' range. The area under the curve (AUC) is often used for comparisons of species presence and absence data (Elith 2006; Evangelista 2008), although there are other criteria that are useful for this purpose. The AUC of a receiver operating curve explains how different the data are from random by discriminating between the likelihood that the model will predict higher probabilities in presence locations than in absence locations (Hosmer and Lemeshow 2000). Models with a higher AUC are generally considered to have greater predictive power because more of the distribution of the data is explained by variation in the factors affecting the data. However, the use of AUC has its drawbacks. A low AUC value may indicate low discrimination between presences and absences even with a model that fits the data accurately (Lobo et al. 2008). AUC values also provide no information on the spatial distribution of incorrectly predicted presences and absences of a species (Lobo et al. 2008). Thus, AUC is useful in measuring how well presence locations can be discriminated from absences based on predictor variables, while providing little information about how well the model predictions fit the species distribution.

Although AUC provides the ability of a model to discriminate between presences and “current” absences, calibration gives additional information about the numerical accuracy of the predictions (Harell et al. 1996). Calibration quantifies the real chance of occurrence of a species at different predicted probabilities. Thus, it examines how accurately the model is predicting the likelihood of occurrence. Studies rarely quantify the calibration of predictions (Caroll et al. 1999; Vaughan and Ormerod 2005), providing limited information about the accuracy of models.

The focus of this study was to examine how well an environmental matching model predicted the distribution of a species. I modeled the distribution of downy brome because of the concern land managers have about spread of this non-native species throughout high elevation plant communities (see Chapter 1). Although modeling potential ranges of other species may be of interest as well, downy brome was of high priority to land managers. I used Maxent for modeling this species because it is considered to have high predictive capabilities with small sample sizes (Phillips et al. 2006). Comparison studies with other similar models such as GARP, DOMAIN and regression trees have found Maxent to be one of the top performing models (Elith et al. 2006; Evangelista et al. 2008). However, these studies draw their main conclusions of model performance based on the AUC values without considering other criteria that provide further information on predictive capabilities. A combination of variance analysis, discriminatory analysis (AUC values), and model calibration were examined in my study to determine Maxent's efficacy in predicting the downy brome distribution in Rocky Mountain National Park. Of interest to me was whether the predicted model probabilities were strong indicators of where downy brome would occur in previously unsurveyed areas. I also wanted to confirm that the top environmental predictors determined by the model were the most influential variables on the distribution on downy brome. Applying an independent field sample to the Maxent model predictions will bring forth new information that can not be obtained from partitioning the original data into training and testing subsets.

Methods and Materials

Study area. The model validation study was conducted in Rocky Mountain National Park, which sits above the Colorado Front Range in the southern region of the Rocky Mountains. The elevation of the Park ranges from approximately 2,300 m (7,500 ft) in Estes Park to over 4,300 m (14,100 ft) on Longs Peak. The Park is situated at latitudes of approximately 40°10´N to 40°32´N and longitude of 105°31'W to 105°41' W (Peet 1981). One main road traverses the park running generally east to west, and additional roads run along the eastern border of the park. The backcountry is accessible through three hundred fifty nine miles of trails as they meander throughout the park. Grasslands, shrub lands, and forests as well as rocky, non-vegetated areas were included in the study region. All of the sampling sites occurred within Rocky Mountain National Park and ranged in elevation from 2490 m to 3540 m.

Rocky Mountain National Park experiences an arid climate east of the continental divide with average annual precipitation of approximately 400 mm in Estes Park at the east side of the park (WRCC 2009). Approximately 480 mm of precipitation fall annually in Grand Lake at the west side of the Park (WRCC 2009). Most of the total precipitation comes in the form of summer rain although the west side of the park receives much more winter snow fall (WRCC 2009). The growing season is short with snow often occurring into early June and returning in September and the potential for snow any month of the year. Average high temperatures in July are 25.7 °C with lows around 7.8 °C (WRCC 2009). Average temperatures for the month of January range from a high of 3.5 °C to a low around -8.7 °C (WRCC 2009). Extremely rapid changes in weather are a common occurrence in Rocky Mountain National Park.

Field Methods. Random UTM coordinates were generated in ArcGIS 9.2 (ESRI Inc., Redlands, CA, USA) and stratified among five probability classes (<0.1, 0.1-0.3, 0.3-0.5,0.5-0.8, and ≥0.8) of downy brome occurrence. The probabilities of occurrence were generated in Maxent, a species environmental matching model (Phillips et al. 2006), using downy brome occurrence data in Rocky Mountain National Park collected between 1993 and 2007. The coordinates were also stratified among vegetation communities and elevation, which were two of the most influential environmental predictors from the 2007 Maxent model of downy brome. Distance to the nearest road, which also included distance to trails, was also one of the most influential environmental predictors, but was not used for stratifying sample locations. An array of distances from roads and trails would automatically be captured in the randomness of the stratified sampling. Elevation was grouped into six classes (<2500 m, 2500- 2700 m, 2700- 2900 m, 2900- 3100 m, 3100- 3300 m, >3300 m) for the purpose of stratifying site locations. Elevation of randomly generated sites ranged from 2396 m to 4023 m. Sites actually visited ranged from 2490 m to 3540 m in elevation. Missing occurrences of downy brome at higher elevations was not a concern, because the highest recorded specimen in Colorado was collected in 2004 at approximately 3050 m (Rocky Mountain Herbarium). That is substantially lower in elevation than many of the highest sites visited in this study. Distance to the nearest road or trail of randomly generated sites ranged from 30 m to 12046 m with the farthest site visited at 8574 m from a road or trail. The sites were stratified among six vegetation communities, which included non-vegetated, shrubland, grassland, deciduous forest, coniferous forest, and tundra.

Sites were visited in the summer of 2008 from early July to early September. Although over 200 random sites within Rocky Mountain National Park were generated as potential locations to visit for ground truthing the model, I was only able to visit 93 sites during the summer of 2008. Time constraints and difficultly of access such as steep cliffs prevented me from visiting all possible sites. Although many of the randomly generated sites were never surveyed, I made certain that I visited at least some sites within all probability classes. Each site required hiking along trails or roads to get as close to the location as possible and then navigating to the exact site location. I used a Garmin ETrex Vista GPS unit to navigate to the UTM coordinates using NAD83 datum to match the reference system in which the locations were originally generated. Once at a particular UTM coordinate, I searched for any downy brome within a 30 x 30 meter area because that was the resolution of the environmental variable layers used in Maxent to generate the 2007 model. I spent approximately 10 to 20 minutes at each plot to thoroughly scour for signs of downy brome within the plot. Sites with minimal vegetation required less time to search for the grass than those is dense grasslands and shrub lands. Plots significantly infested with downy brome also required much less time to determine if the grass was present. Because the Maxent model generates the probability of occurrence of species, I recorded the presence or absence of downy brome, but not abundance at each site.

Analysis. I compared the probability of occurrence generated by the 2007 Maxent model to the actual occurrences I found in the field within each probability class in 2008. This allowed me to examine the numbers and percentages of occurrences of downy brome in 2008 that fell within each probability class from the 2007 model. This provided a general calibration of the model in predicting occurrences at various probabilities.

Using Proc GLIMMIX (SAS 9.2., SAS Institute Inc., Cary, NC, USA), I regressed the predicted model probabilities against the 2008 occurrences of downy brome. I used this method to access the influence of predicted probabilities on determining true occurrences.

To examine the effect of each of the top environmental predictor variables (elevation, distance to roads/trails, and vegetation community) on downy brome occurrence, I conducted ANOVA using the procedure GLIMMIX (SAS 9.2, SAS Institute Inc., Cary, NC, USA). Because these environmental variables were predicted to have the greatest influence on predicting downy brome occurrence, I looked for relationships between occurrence of downy brome and each of these environmental variables. One location occurred in the tundra vegetation community and was removed from the analysis because variance cannot be determined without replication. In addition, it was known that downy brome is highly unlikely to occur in this vegetation type due to the extreme elevation of tundra communities. Thus, it was ecologically appropriate to remove this visited location from the analysis.

I ran logistic regressions using the procedure GLIMMIX (SAS 9.2, SAS Institute Inc., Cary, NC, USA) to determine the best model of the top three environmental variables to fit the Maxent predictions. I removed the single tundra location from the analyses for the same reasons I did with the ANOVAs. Several combinations of the variables and their interaction terms were examined. I compared type III tests of fixed effects and Akaike's information criterion (AIC) to find the best logistic model. To be certain the model chosen was the best fit, I also conducted a backwards model selection using PROC LOGISTIC (SAS 9.2, SAS Institute Inc., Cary, NC, USA) including all environmental variables that made up the Maxent predictions (see Table 1). This model should be the same as the one selected using PROC GLIMMIX.

Using the procedure LOGISTIC (SAS 9.2, SAS Institute Inc., Cary, NC, USA), I generated a receiver operating curve (ROC) to examine how well the logistic regression models were correctly predicting true occurrences of downy brome. The area under the ROC curve (AUC) is often used as a measure of the overall accuracy of the model (Fielding and Bell 1997; Manel et al. 2008). An AUC value ≥ 0.9 is an indication of extremely high model performance (Swets 1988), and lower values indicate less optimal predictive capabilities of a model. I used the AUC value to access the performance level of the best fit logistic regression.

Results

More occurrences of downy brome were detected in 2008 in locations predicted by the 2007 Maxent model to have higher probabilities of occurrence. The number of occurrences increased consistently with each successive probability class (Figure 2.1A). Even though the lowest probability class (<0.1) was more thoroughly sampled than others (Figure 2.1A), no occurrences of downy brome were found within the random stratified sampling points for this probability class. In the highest probability class (≥0.8), a total of 13 occurrences were detected, which was the most out of any probability class. The proportion of sites visited within each probability class showed a very similar trend. As probabilities increased by class, the proportion of plots containing downy brome also increased (Figure 2.1B).

Elevation, distance to roads and trails, and vegetation type all strongly affected where downy brome occurred in 2008. Elevation was the strongest effect when conducting ANOVA and logistic regression analysis (AIC=68.99, $F_{1,90}$=17.56, $P<0.0001$). Distance to roads was the next most influential predictor of the occurrence of downy brome (AIC=100.11, $F_{1,90}$=7.86, $P=0.006$). Vegetation community, still significantly influential on downy brome occurrence, was a weaker effect than the other two predictor variables tested (AIC=111.92, $F_{4,87}$=2.78, $P=0.032$).

Logistic regression of 2008 downy brome occurrence demonstrated that 2007 predicted probabilities strongly influenced where downy brome occurred (AIC=84.88, $F_{1,90}$=22.76, $P<0.0001$). The ROC analysis gave an area under the curve of 0.86. From the characteristics table generated in the statistical output, a threshold probability of approximately 0.31 would predict the most correct presences and absences of downy brome. This threshold is determined by the value at which sensitivity (the percent of correctly predicted occurrences) and specificity (the percent of correctly predicted absences) are equal.

Logistic regressions of the top environmental predictors resulted in a best fit model including the variables for elevation and distance to roads and trails as well as the interaction between distance and elevation (Figure 2.2). This model had an AIC value of 69.13, which was the lowest AIC value of any logistic regression model tested, except for testing elevation alone (AIC= 68.99). All effects were significant in this model: elevation (parameter estimate=-0.018, $F_{1,89}$=14.55, P=0.0003), distance to roads and trails (parameter estimate=-0.011, $F_{1, 89}$=4.22, P=0.043), and the interaction between elevation and distance to roads and trails (parameter estimate=3.62E-6, $F_{1, 89}$=4.26, P=0.042). Figure 2.2 depicts the relationship of the regressed variables with respect to the probability of downy brome occurrence. An ROC analysis generated from the logistic regression resulted in an AUC of 0.92 (Figure 2.3). The backwards model selection including all possible environmental variables (Table 2.1) confirmed that the logistic regression with elevation, distance from roads, and the interaction between the two was in fact the best fit model to the data.

The 2008 random stratified points generated for validating the 2007 Maxent model covered a much greater extent in Rocky Mountain National Park than the locations sampled in 2007 and earlier. New regions of the park where data had not previously been collected were predicted to have high probability of downy brome occurrence. As predicted, downy brome was found in many of these high probability regions sampled in

2008. Two new regions predicted to have high probabilities of occurrence were Lumpy Ridge north of the Estes Park entrance and the Wild Basin entrance, both on the east side of the park. I found downy brome in both of these regions (Figure 2.4). A third area that was predicted to have a high probability of occurrence was the Kawauneechee Valley on the west side of the park, but I did not find downy brome at any of the random stratified points from the survey in 2008. However, park staff found downy brome within the west side high probability area of the Park near the Kawauneechee Visitor Center (pers comm., Dyan Hardin, Rocky Mountain National Park, 13T 0428662 4457565 NAD83).

Discussion

After testing the accuracy of the Maxent model, the downy brome predictions were generally quite good. More occurrences of downy brome were found at higher probabilities using the random stratified design, which was an initial indication that higher predicted probabilities do in fact correlate with greater likelihood of occurrence. A higher proportion of sites visited with downy brome occurred at higher probabilities, also providing evidence that increased predicted probabilities indicate a realized increased chance of occurrence on the ground. The calibration of the data demonstrated that the proportions of sites visited containing downy brome in fact matched the expected ranges within each probability class. The only exception was in the highest probability class in which the proportion of sites found to have downy brome was slightly lower than the expected probability range. It is likely that downy brome has not yet fully expanded into its suitable habitat range at Rocky Mountain National Park, which resulted in lower occurrences than expected.

The environmental predictor variables that Maxent chose as most influential on downy brome distribution were also the strongest variables based on the field validation data collected. The Maxent model identified elevation, distance to nearest road, and vegetation type as being influential on predicting where downy brome would occur. All of these variables did have strong effects on the occurrence of downy brome when using other analysis methods as well. When including all of the environmental variables from the Maxent model used, backward model selection also chose two of those top three environmental variables in the best logistic model explaining the distribution of downy brome. Regression analysis and the Maxent model predictions thus came up with very similar outcomes in what variables to use to predict downy brome occurrence. It is possible that limiting the Maxent model to only these most influential variables may still have generated accurate predictions (Parolo et al. 2008). Because the area under the ROC curve was very high (>0.9), this validated the strength of these variables in predicting occurrence.

Stratified random sampling was useful for the field validation because it allowed for sampling a much larger area than from where the original data were collected. Because the Maxent predictions were projected at a larger spatial scale, it was critical that the field sampling captured the range of areas within the projection. Scaling issues could arise in the initial model, because the survey data used to generate the Maxent predictions may not have captured the environmental variability of the entire Park. My random stratified sampling was designed to capture that variability. Most species distribution models partition the original data into training data to make model predictions and test data to assess the predictive accuracy. Spatial autocorrelation also inflates the model accuracy when using data from a non-independent sample to test the model (Veloz 2009). Because the random stratified sampling covered a much greater extent of the Park, it picked up occurrences in areas of the Park where downy brome was not previously known to occur, but where the model predicted it would be. Although the Maxent predictions may have had spatial autocorrelation and scaling issues, field validation using the random stratified sampling indicated that the model still performed well for the entire Park.

Stratified sampling methods did not work perfectly. Some of the areas of the Park with a high predicted probability of downy brome occurrence were not found to have downy brome. This may have either been due to scaling issues with the model not being able to predict areas far from the initial survey area, or simply lower propagule pressure and dispersal in these areas. The western road corridor in the park was predicted to have high occurrence of downy brome. Most of the downy brome in the Colorado Rockies appears to be spreading into the Park from the foothills and plains to the east. It may not have reached the western side of the park yet, where only one occurrence of downy brome was found (Figure 2.4). Although the sample size was not small, a larger sample may have been able to detect more downy brome occurrences throughout the Park. Thorough mapping of downy brome along roads and trails picked up additional occurrence locations that the random stratified sampling did not detect (Appendix A).

Although Maxent has been used by researchers to make predictions about species distributions, it can be a valuable tool for land managers. Maxent predicted the likelihood of occurrence for downy brome based on a small initial set of data. The field validation of the model demonstrated that the predictions were quite good from this initial small data set. With the limited time and resources that land managers often have for data collection, Maxent may help them determine species ranges based on a quick initial assessment of a species. For downy brome, land managers can make inferences about occurrence based on model probabilities and environmental factors such as elevation. Such information is useful to managers in helping prioritize the allocation of time and resources. There are always uncertainties in any model predictions, which is evident from the probability classes and proportions of sites found with downy brome in those classes. With such uncertainties, land managers should not solely base their decisions on models, but rather use them to help guide their management efforts.

Maxent predictions have been made for other species, but similar field based validations have not been performed. It is possible that other species with widespread distributions but apparent environmental constraints may also be predicted well by the model, but this information is not known. Prior studies have compared species with limited distributions to those that can thrive in a greater range of environmental conditions (Evangelista et al. 2008; Hernandez et al. 2008). Even a widespread species such as downy brome will have constrained distributions in less desirable environments. Downy brome is widespread throughout the Great Basin (Mack 1981; Knapp 1996), but it appears to be more constrained in a high elevation range such as Rocky Mountain National Park. The model should be validated in various physical and climatic conditions to see if it can consistently make correct predictions in numerous types of environments. In addition to testing the model in different environments, other similar generalist as well as specialist species should be included in model validations to determine what types of species best fit the model predictions.

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Table 2.1. Environmental variable GIS layers included in the Maxent analysis of downy brome in Rocky Mountain National Park

Environmental Variable	**Spatial resolution**	**Data Source**
Elevation (DEM)*	30m	NED seamless data
Slope	30m	Derived from the DEM
Eastness	30m	Derived from the DEM
Northness	30m	Derived from the DEM
Flow accumulation	30m	Derived from the DEM
Flow direction	30m	Derived from the DEM
Geologic type	30m	USGS
Geologic age	30m	USGS
Soil type	30m	Soil data mart **
Vegetation type	30m	Landfire data **
NDVI (2001)***	30m	Landsat ETM+ (GLCF)
Brightness Index (2001)	30m	Landsat ETM+ (GLCF)
Greenness Index (2001)	30m	Landsat ETM+ (GLCF)
Moistness Index (2001)	30m	Landsat ETM+ (GLCF)
Wetness	30m	
Mean MODIS EVI ****	250m	NASA
Peak MODIS EVI	250m	NASA
Range in MODIS EVI	250m	NASA
Distance from Roads*****	30m	created in ArcGIS
Distance from Streams*****	30m	created in ArcGIS
Overland distance to water*****	30m	Flows Tools (Theobald et al. 2006)
Radiation*****	30m	created in ArcGIS
Snow potential index*****	30m	created in ArcGIS

* Digital Elevation Model (NED or National Elevation Dataset is the primary elevation dataset used by the USGS, http://ned.usgs.gov/)
** Soil data mart is online data accessible through the Natural Resources Conservation Service (NRCS), http://soildatamart.nrcs.usda.gov/
Landfire data is online data provided by the United States Geological Survey (USGS), http://www.landfire.gov/datatool.php
*** NDVI (Normalized Difference Vegetation Index) is a measure between -1.0 and +1.0 based on ratios of spatial reflectances in the infrared
and near infrared light frequencies. Sourced from Landsat Enhanced Thematic Mapper Plus,

http://eros.usgs.gov/#/Find_Data/Products_and_Data_Available/
ETM
**** Moderate Resolution Imaging Spectroradiometer,
http://modis.gsfc.nasa.gov/
***** variables created in GIS based on spatial data layers provided by Rocky Mountain National Park

(table adapted from information provided by Dr. Sunil Kumar, NREL, Colorado State University, 2009)

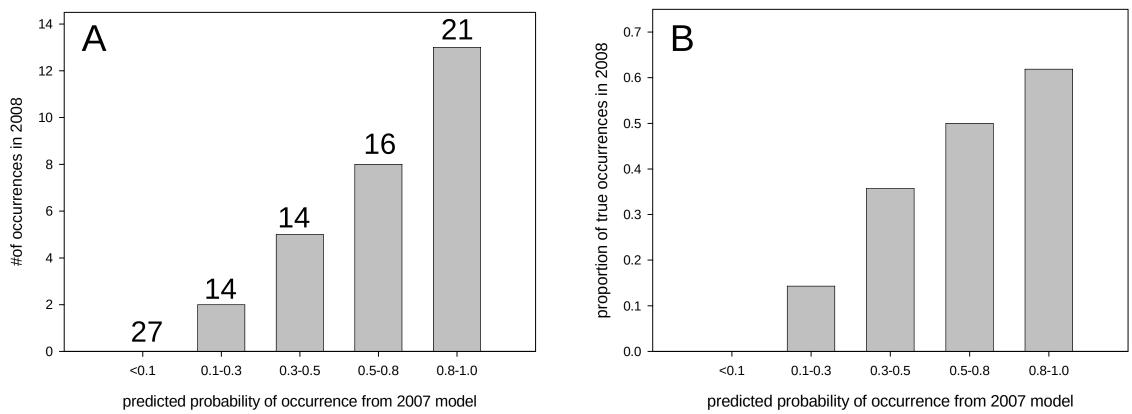

Figure 2.1. (A) Bars represent the number of sites visited within each probability class from the 2008 random stratified sampling that had downy brome present. Probability classes were generated from the probabilities of the 2007 Maxent model. The numbers above each bar are the number of sites visited within each probability class. (B) Bars represent the proportion of sites with downy brome present within each probability class.

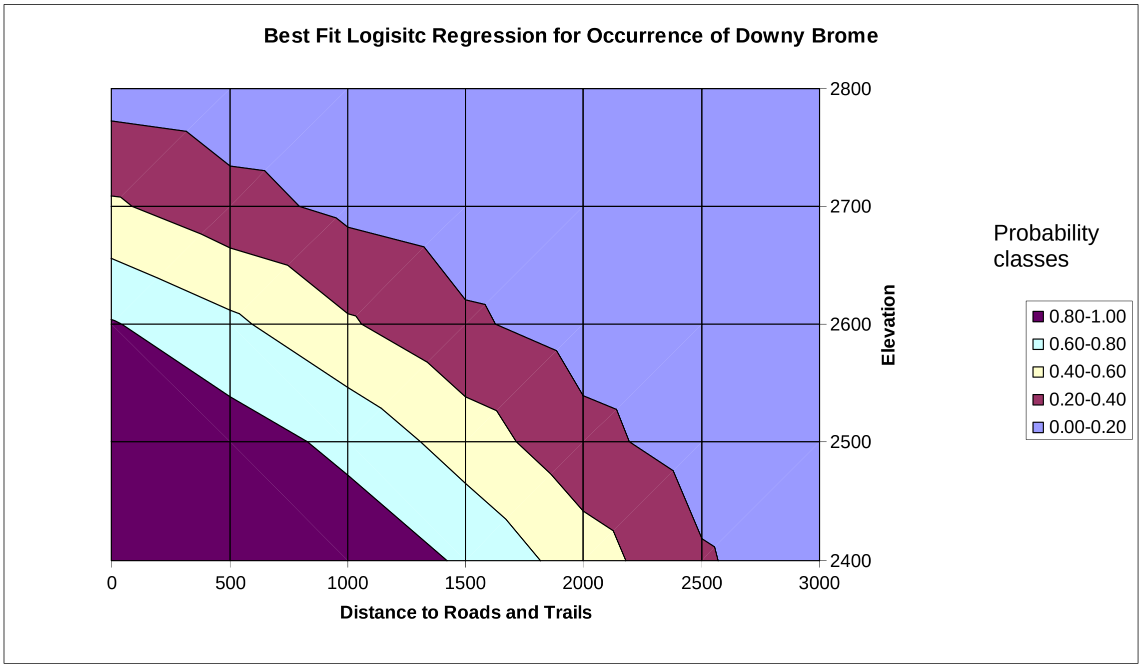

Figure 2.2. The regressed relationship of elevation and distance to roads and trails. Based on the regression model that best fit the 2008 presence and absence data for downy brome, probability classes are plotted with respect to these environmental variables. Very high probabilities of occurrence occur at lower elevations and closer to roads and trails. Very low probabilities of occurrence occur at higher elevations and farther from roads and trails.

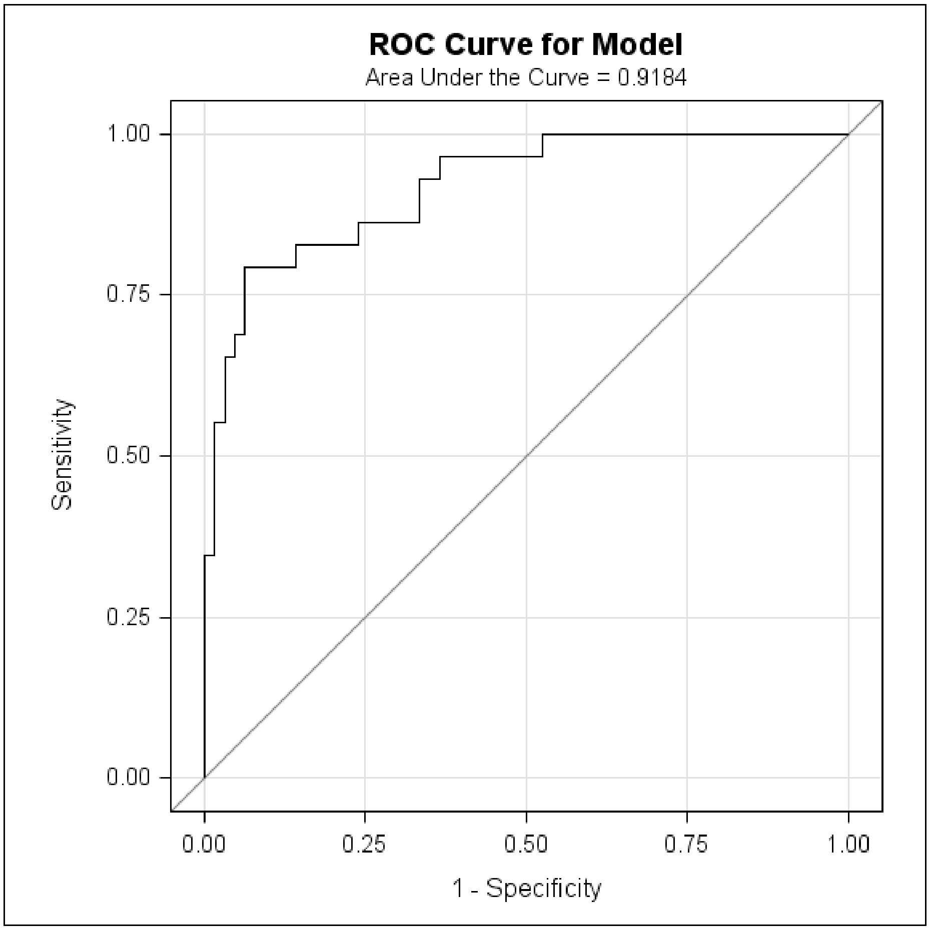

Figure 2.3. Receiver Operating Curve (ROC) for the best fit logistic regression for downy brome occurrence. Sensitivity is the probability of finding downy brome where it is predicted to occur (true positives). Specificity is the probability of not finding downy brome when it is predicted to be absent (true negatives). The area under the curve (AUC) describes the strength of the model by demonstrating how different the data are from random. Thus, a high AUC (≥0.90) is representative of a model with very good fit.

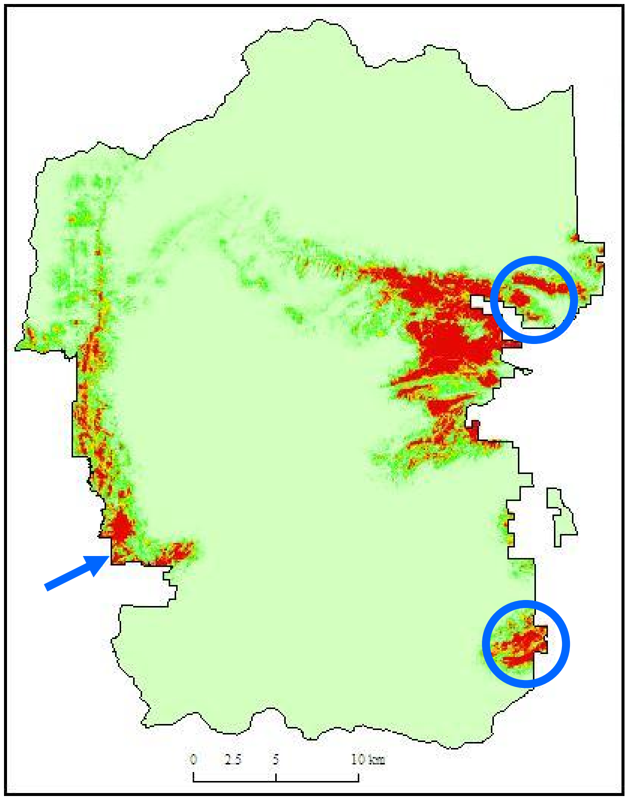

Figure 2.4. Map of 2007 probability of downy brome occurrence with red representing very high probabilities and light green representing low probabilities. Areas circled on the map are Lumpy Ridge and Wild Basin, both with high probability areas where downy brome was found. The arrow represents an area of high probability of occurrence where downy brome was not detected by the 2008 sampling, but was detected by staff of Rocky Mountain National Park.

APPENDIX A

Opportunistic Sampling of Downy Brome

In the summer of 2008, I conducted a survey of downy brome for Rocky Mountain National Park, separate from the random sampling points used to validate the Maxent model. This consisted of surveying along all roads and many of the trails within the park. The model had already suggested an increased chance of downy brome occurrence along roads and trails within certain elevation ranges. Location (UTM coordinate), vegetation community, dominant species, elevation, size of site and ocular estimate of downy brome cover were recorded for the park. In this survey from June to August 2008, I recorded sites in 47 grassland locations, 32 shrub land communities, and 42 forested sites (Table A1). The total area of downy brome detected was 146.3 acres in grasslands, 87.4 acres in shrub lands, and 60.6 acres in forests.

I combined these survey occurrences with the data from the random stratified sampling points (Chapter 2) to examine the number of occurrences within each predicted probability class from the three Maxent models run for 1996, 1999, and 2007 (Chapter 1). The number of opportunistic survey locations and randomly sampled occurrences are summarized in table A2. Interestingly, the highest number of occurrences was within the lowest probability class, and the lowest number of occurrences was within the highest probability class (Figure A1). I also looked at the percentage of occurrences in each probability class with these combined data. Because the only absences recorded were from the random stratified sampling (Chapter 2), I had many more absences at low probabilities than at high probabilities. Thus, the percentages of occurrences across the probability classes were more similar than were the counts of occurrences, but still did not show the increasing trend that I expected (Figure A2).

Looking across the three model years, the 1996 model showed more occurrences at very low probability and fewer occurrences at very high probability than the more recent 1999 and 2007 models (Figure A1). The 1999 and 2007 models may be making only slightly better predictions of the 2008 downy brome data. However, using the opportunistic downy brome locations mapped for the park would appear to show poor model performance for all model years when compared to the random stratified sampling locations. It should also be noted that the number of occurrences for the 1999 and 2007 models are very similar within each probability class. Thus, the additional data added in 2007 does not appear to have much effect on increasing the predictive power of the model. Although none of these models were generated from large data sets, this might indicate that only a small amount of data is necessary to generate a strong predictive model. Additional data may not increase the predictive capabilities of the model.

It is important to address why the opportunistic sampling demonstrated drastically different results from the random stratified sampling. Low probability opportunistic locations were much greater than the number of high probability locations, which is the opposite pattern shown by random sampling. For the random sampling, 30m x 30m areas were thoroughly searched for downy brome as this was the same pixel size used by the Maxent model. Opportunistic patch sizes varied greatly from less than 0.001 acres up to approximately 35 acres. Many of these patches were greater than the 30m x 30m pixel size used by the Maxent model. Only a single coordinate would represent the entire infested patch of downy brome. Due to variation on the landscape, many of the coordinates recorded may have fallen within a low probability pixel by chance. Ultimately, the pattern evident from the opportunistic sampling may be an issue of recording measurements at a much larger scale than that of the original model. Random stratified points demonstrated that sampling at the same scale will give much better results when accessing the validity of the model.

These data do not dispute that the model is a good predictor of downy brome in Rocky Mountain National Park. Even at very low probabilities, there is still a predicted chance of occurrence that is greater than zero. Although the random stratified sampling did not detect any downy brome in the lowest probability class, a more thorough survey along roads and trails within the park did detect downy brome. Downy brome has the potential to occur at most predicted probabilities. It is much more likely to occur in areas with the highest predicted probability, as seen from the random stratified sampling conducted for the model validation. Because roads and trails are closely associated with the distribution of downy brome, it is possible to find it in these areas even at low predicted probabilities.

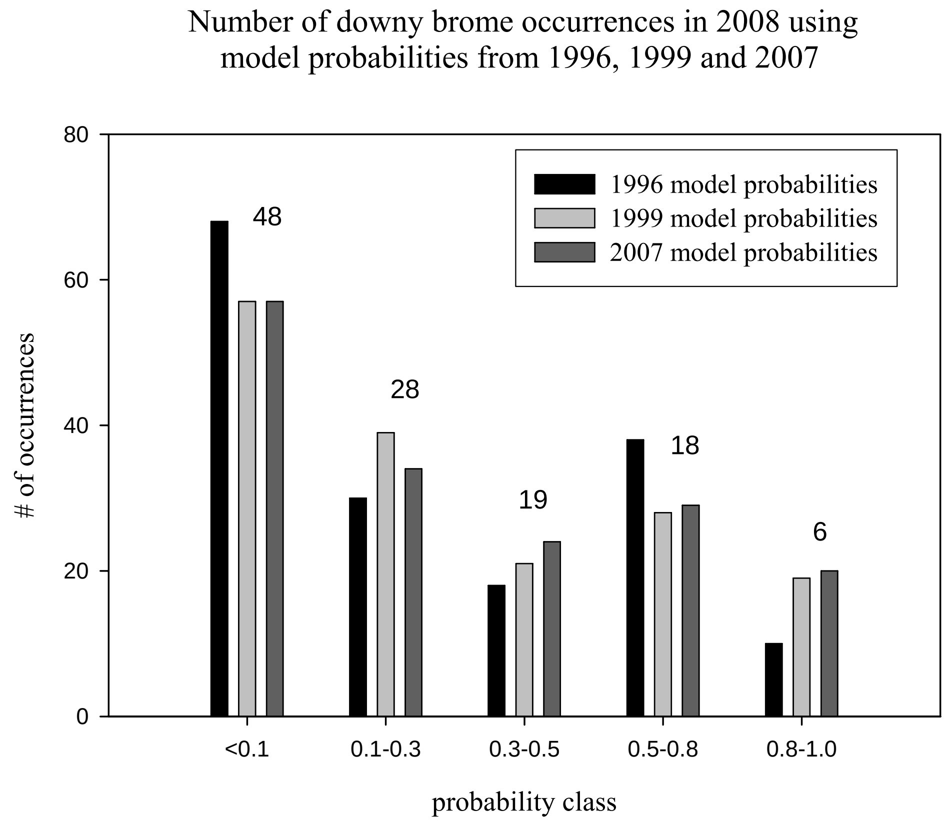

Figure A1. The number of downy brome occurrences from the 2008 sampling including both random stratified points and opportunistic surveying for Rocky Mountain National Park. 2008 downy brome occurrences within each probability class are shown across 1996, 1999 and 2007 model predictions. The numbers of opportunistic points included in each 2007 probability class are shown above the bars.

Percentage of downy brome occurrences in 2008
using probabilities from 1996, 1999 and 2007 models

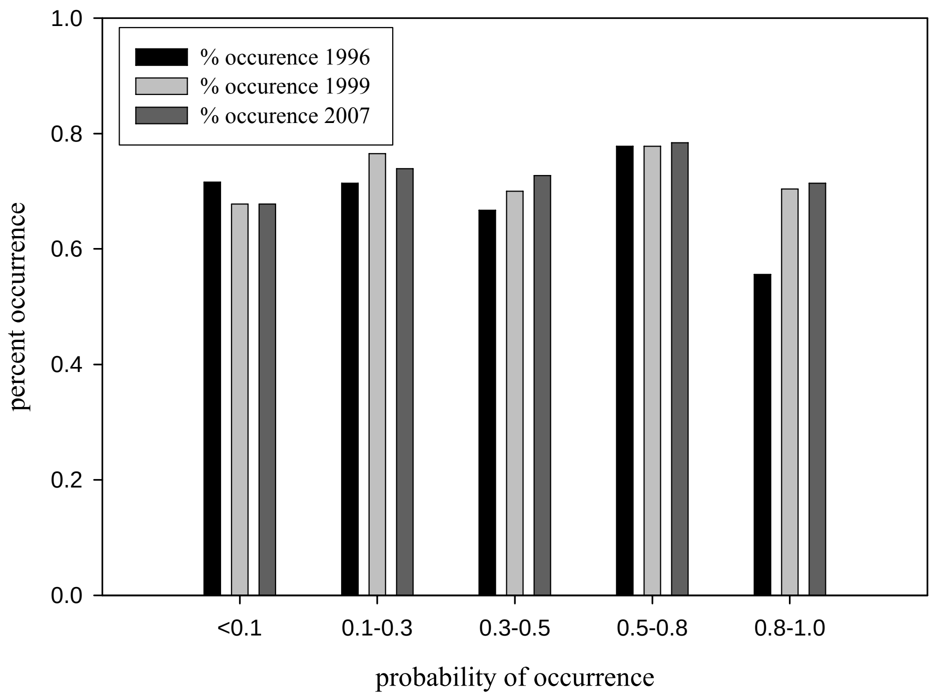

Figure A2. The percentage of downy brome occurrences within each probability class from the 2008 sampling including both random stratified points and surveying for Rocky Mountain National Park. Percentages are the number of downy brome occurrences over the total number of sample locations within each probability class. 2008 percent downy brome occurrences are shown across 1996, 1999 and 2007 model predictions.

Table A1. 2008 survey locations along roads and trails for Rocky Mountain National Park downy brome mapping project with elevation, patch size, and probabilities predicted in each of the three Maxent modeling years for those locations.

Veg type	Easting	Northing	Elev (ft)	Size (ac)	prob2007	prob1999	prob1996
GRASSLAND	449703	4472130	NA	0	0.0955	0.2236	0.4442
GRASSLAND	446922	4472899	8560	0	0.3751	0.1620	0.0580
GRASSLAND	455719	4475120	8113	0.001	0.0113	0.0257	0.1845
GRASSLAND	454609	4475140	8254	0.002	0.0045	0.0061	0.0018
GRASSLAND	454523	4475210	8287	0.002	0.0019	0.0055	0.0045
GRASSLAND	454428	4475252	8310	0.002	0.0165	0.0317	0.0050
GRASSLAND	447489	4469851	8890	0.002	0.3288	0.4900	0.5725
GRASSLAND	448289	4470579	8907	0.005	0.8743	0.8070	0.5003
GRASSLAND	446654	4467158	8132	0.006	0.1752	0.0567	0.0420
GRASSLAND	449424	4464343	8642	0.0064	0.3557	0.0997	0.1669
GRASSLAND	446426	4467935	9205	0.01	0.1591	0.0814	0.0312
GRASSLAND	447901	4472557	8400	0.01	0.3816	0.0551	0.0202
GRASSLAND	447858	4468929	8448	0.01	0.8076	0.8446	0.5428
GRASSLAND	445931	4466482	8477	0.014	0.1377	0.2549	0.0227
GRASSLAND	449054	4471618	8648	0.014	0.1555	0.2860	0.1521
GRASSLAND	447422	4465060	8808	0.0188	0.0075	0.0153	0.0166
GRASSLAND	449353	4464290	8640	0.05	0.1166	0.1240	0.2492
GRASSLAND	445613	4473315	8587	0.06	0.2331	0.0110	0.0474
GRASSLAND	456606	4475326	7969	0.08	0.0041	0.0147	0.4055
GRASSLAND	457186	4475540	7896	0.084	0.0026	0.0036	0.0611
GRASSLAND	449329	4464921	8675	0.1	0.1054	0.3438	0.2220
GRASSLAND	457333	4475557	7910	0.11	0.0014	0.0060	0.0945
GRASSLAND	448101	4469069	8476	0.12	0.3702	0.2275	0.0851
GRASSLAND	448888	4467353	8126	0.17	0.0223	0.0041	0.0127
GRASSLAND	450981	4466325	7938	0.23	0.0186	0.0476	0.2988
GRASSLAND	454457	4451972	8369	0.24	0.3524	0.5918	0.0310
GRASSLAND	457045	4475523	7903	0.43	0.0089	0.0043	0.0109
GRASSLAND	447627	4468746	8543	0.463	0.0547	0.1012	0.1389
GRASSLAND	449366	4468590	8306	0.52	0.5522	0.3701	0.0218
GRASSLAND	447272	4465112	8785	0.569	0.0377	0.0903	0.0458
GRASSLAND	448901	4471429	8661	1.09	0.6177	0.5897	0.6379
GRASSLAND	449072	4467328	8106	1.14	0.1791	0.0213	0.0318
GRASSLAND	446452	4465082	9058	1.163	0.0028	0.0000	0.0001
GRASSLAND	447952	4468570	8576	2.28	0.5471	0.6188	0.4751
GRASSLAND	448536	4463810	8720	3.23	0.0616	0.2773	0.0927

Table A1. 2008 survey locations along roads and trails for Rocky Mountain National Park downy brome mapping project with elevation, patch size, and probabilities predicted in each of the three Maxent modeling years for those locations. (continued)

Veg type	Easting	Northing	Elev (ft)	Size (ac)	prob2007	prob1999	prob1996
GRASSLAND	449956	4468528	8276	3.64	0.1658	0.1493	0.3174
GRASSLAND	447470	4467336	8110	4.65	0.0894	0.2522	0.0792
GRASSLAND	449918	4468794	8389	5.02	0.7467	0.1629	0.0778
GRASSLAND	449196	4468392	8398	7.7	0.3364	0.3187	0.3200
GRASSLAND	447744	4466570	8136	9.66	0.0490	0.0260	0.0076
GRASSLAND	451320	4468666	8179	9.95	0.4652	0.6751	0.8397
GRASSLAND	451528	4471099	8454	12.2772	0.7829	0.6260	0.4118
GRASSLAND	449083	4471799	8576	16.1	0.3199	0.4170	0.0225
GRASSLAND	449619	4465992	8280	28	0.2945	0.2292	0.1236
GRASSLAND	451461	4469167	8221	32.956	0.4675	0.5830	0.8987

Table A1. 2008 survey locations along roads and trails for Rocky Mountain National Park downy brome mapping project with elevation, patch size, and probabilities predicted in each of the three Maxent modeling years for those locations. (continued)

Veg type	Easting	Northing	Elev (ft)	Size (ac)	prob2007	prob1999	prob1996
SHRUBLAND	448443	4470284	8733	0	0.4753	0.5595	0.2629
SHRUBLAND	445496	4466910	8192	0.001	0.2769	0.1771	0.0180
SHRUBLAND	451225	4467926	8159	0.001	0.6770	0.6819	0.1845
SHRUBLAND	447941	4469296	8536	0.002	0.7813	0.7906	0.3470
SHRUBLAND	448393	4469596	8539	0.002	0.8486	0.8395	0.5586
SHRUBLAND	446837	4465180	9005	0.004	0.0061	0.0077	0.0436
SHRUBLAND	445070	4473569	8567	0.005	0.5479	0.3299	0.1319
SHRUBLAND	455689	4472318	7985	0.01	0.0072	0.0250	0.8455
SHRUBLAND	444287	4473811	8694	0.012	0.0514	0.1032	0.0828
SHRUBLAND	450712	4469373	9099	0.02	0.7673	0.7313	0.7191
SHRUBLAND	447075	4468685	9022	0.056	0.2436	0.1253	0.0988
SHRUBLAND	449041	4465770	8369	0.12	0.1726	0.0904	0.0929
SHRUBLAND	444618	4473677	8536	0.16	0.2076	0.1073	0.0792
SHRUBLAND	445911	4467054	8218	0.175	0.0649	0.0062	0.0034
SHRUBLAND	451439	4467924	8083	0.219	0.5901	0.4196	0.3189
SHRUBLAND	447666	4464986	8664	0.255	0.0099	0.0193	0.0096
SHRUBLAND	456214	4472230	8093	0.33	0.0043	0.0132	0.2849
SHRUBLAND	450787	4469389	9092	0.35498	0.7008	0.8284	0.8619
SHRUBLAND	448317	4465557	8428	0.489	0.5617	0.1584	0.0030
SHRUBLAND	450459	4463876	8562	0.848	0.3550	0.4822	0.1577
SHRUBLAND	450356	4469364	9199	0.853	0.8159	0.7232	0.7591
SHRUBLAND	450534	4464102	8579	0.897	0.2382	0.1916	0.1629
SHRUBLAND	450564	4469336	9110	1.39685	0.7124	0.6347	0.9633
SHRUBLAND	455637	4472248	7913	2.15	0.0268	0.0510	0.5297
SHRUBLAND	450396	4466145	8095	2.29	0.0152	0.0069	0.0317
SHRUBLAND	450660	4468695	8320	3.7016	0.5683	0.7360	0.6820
SHRUBLAND	447007	4469416	8835	4.01	0.0339	0.1021	0.0540
SHRUBLAND	447102	4463500	9051	4.4	0.0530	0.0474	0.0356
SHRUBLAND	448094	4467367	8132	6.28	0.0815	0.0127	0.0106
SHRUBLAND	451546	4468919	8082	12.5814	0.2051	0.4501	0.6694
SHRUBLAND	448722	4465790	8454	17.8	0.6702	0.8947	0.7499
SHRUBLAND	447325	4469523	8644	27.95	0.1039	0.4943	0.3674

Table A1. 2008 survey locations along roads and trails for Rocky Mountain National Park downy brome mapping project with elevation, patch size, and probabilities predicted in each of the three Maxent modeling years for those locations. (continued)

Veg type	Easting	Northing	Elev (ft)	Size (ac)	prob2007	prob1999	prob1996
FOREST	449418	4472319	8137	0	0.5194	0.3717	0.0617
FOREST	455648	4472359	8110	0.001	0.0083	0.0255	0.7750
FOREST	447923	4468641	8536	0.001	0.5447	0.1211	0.1339
FOREST	447785	4466468	8110	0.002	0.1267	0.1388	0.1228
FOREST	446480	4467875	9261	0.002	0.2977	0.1573	0.1053
FOREST	449457	4472377	8190	0.002	0.2577	0.1970	0.2661
FOREST	447598	4469132	8602	0.002	0.3884	0.2730	0.1737
FOREST	446600	4468230	9245	0.004	0.0077	0.0334	0.0241
FOREST	446685	4466590	8224	0.004	0.3696	0.2353	0.0396
FOREST	448237	4469690	8638	0.005	0.1560	0.5048	0.5521
FOREST	449052	4465625	8385	0.006	0.0353	0.0052	0.2330
FOREST	445994	4462373	9043	0.008	0.1420	0.2723	0.0144
FOREST	453787	4475024	8549	0.01	0.0023	0.0078	0.0042
FOREST	445681	4466899	8218	0.014	0.1749	0.1305	0.0255
FOREST	445010	4473294	8588	0.02	0.0945	0.0693	0.0006
FOREST	448300	4470270	8690	0.0375	0.2939	0.5285	0.2406
FOREST	451025	4469561	9035	0.03866	0.8458	0.5819	0.6342
FOREST	450742	4469459	9141	0.04188	0.4984	0.3991	0.8012
FOREST	448018	4465087	8510	0.052	0.0297	0.0497	0.0397
FOREST	448211	4466350	8060	0.08	0.1320	0.0768	0.0077
FOREST	450791	4471412	8480	0.12	0.2741	0.1763	0.2706
FOREST	449214	4472125	8457	0.127	0.5989	0.4265	0.3215
FOREST	446047	4466533	8336	0.139	0.0643	0.0864	0.1044
FOREST	447133	4466688	8162	0.15	0.0241	0.0718	0.0575
FOREST	448080	4465158	8434	0.182	0.0534	0.0681	0.0259
FOREST	443726	4473823	8854	0.2	0.0910	0.1872	0.1134
FOREST	446970	4468053	NA	0.223	0.4788	0.1199	0.1519
FOREST	449104	4464333	8635	0.27	0.0500	0.4247	0.0654
FOREST	445656	4462249	9155	0.34	0.0775	0.0020	0.0020
FOREST	446419	4473295	8598	0.47	0.1115	0.0342	0.0477
FOREST	446824	4468240	9143	0.528	0.0389	0.0403	0.0053
FOREST	448315	4463305	8733	0.66	0.0294	0.0122	0.0725
FOREST	447086	4463316	8886	0.73	0.0361	0.0360	0.0058
FOREST	449396	4471984	8445	0.87	0.2101	0.2503	0.0993
FOREST	449369	4470318	9151	0.90695	0.8707	0.8760	0.6206
FOREST	454587	4452113	8368	1.34	0.0000	0.0000	0.0000
FOREST	447381	4466684	8179	1.38	0.0500	0.1444	0.0541
FOREST	448638	4463578	8722	2.32	0.1016	0.0089	0.0863
FOREST	451667	4469774	8707	2.83381	0.4440	0.4635	0.6298
FOREST	454066	4475074	8425	4.59	0.0089	0.0079	0.0067
FOREST	447276	4468389	8713	6.23	0.3379	0.4030	0.1638
FOREST	449689	4467521	8128	35.68	0.0278	0.0118	0.0981

Table A2. The number of downy brome sites visited in each probability class for each of the three Maxent model years. All opportunistic locations indicate presence of downy brome. Random stratified sites visited are broken down into those containing occurrences and those in which downy brome was absent.

Model year	Probability class	Opportunistic locations	Random occurrences	Random absences
1996	0- 0.1	61	2	41
	0.1-0.3	26	1	7
	0.3-0.5	10	5	3
	0.5-0.8	16	16	10
	0.8-1.0	6	5	2
1999	0-0.1	49	0	39
	0.1-0.3	32	3	6
	0.3-0.5	16	4	10
	0.5-0.8	16	9	6
	0.8-1.0	6	12	3
2007	0-0.1	48	0	27
	0.1-0.3	28	2	12
	0.3-0.5	19	5	9
	0.5-0.8	18	8	8
	0.8-1.0	6	13	8

APPENDIX B

Survey locations of 2007 field sampling

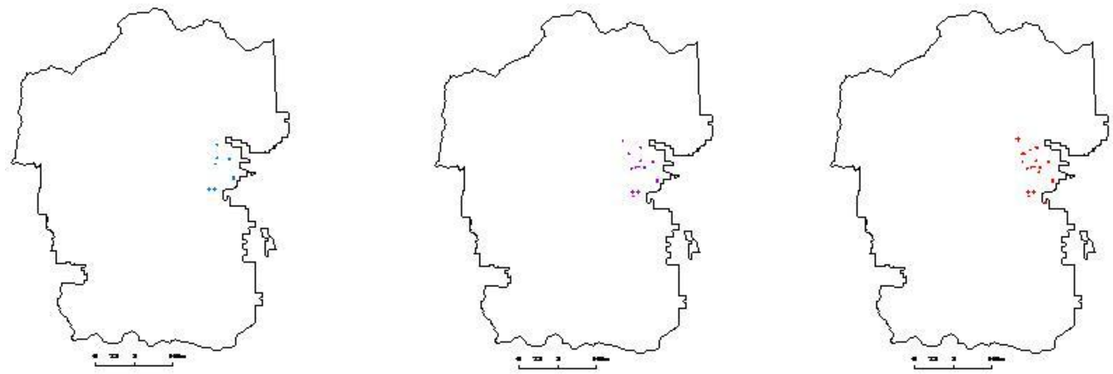

Figure B1. Locations of sampled downy brome from the Ecotone study and Succession study plots in 1996, 1999, and 2007. The map on the left shows the locations within Rocky Mountain National Park of the 14 occurrence of downy brome sampled in 1996 on which the 1996 Maxent model was generated. The middle map shows 21 occurrences on which the 1999 Maxent model was generated. The map on the left shows 31 occurrences on which the 2007 Maxent model was generated. Note that all sample locations represented by small dots are in the central eastern region of the Park.

Table B1. UTM coordinates of Ecotone study plots surveyed for downy brome in Rocky Mountain National Park.

	Easting	Northing
1	447159.97	4469634.23
2	447231.13	4469794.77
3	444990.34	4462323.95
4	445210.14	4462323.35
5	445110.14	4462323.75
6	447202.54	4470837.76
7	426792.59	4475888.06
8	426732.55	4475888.81
9	426652.15	4475891.63
10	446217.33	4475368.44
11	446417.4	4475368.39
12	446297.08	4475368.70
13	449351.82	4468681.59
14	449351.73	4468581.19
15	449351.39	4468501.01
16	452449.3	4452166.43
17	452449.44	4451901.19
18	452449.74	4452026.57
19	453814.66	4461087.80
20	453874.08	4461088.17
21	453934.52	4461086.99

	Easting	Northing
22	449465.51	4471628.28
23	449245.13	4471628.53
24	448985.06	4471628.07
25	451101.07	4467266.32
26	451100.49	4467426.31
27	451100.48	4467565.01
28	450217.67	4464572.18
29	450217.75	4464631.40
30	450217.41	4464491.46
31	450662.03	4469823.22
32	450582.15	4469824.49
33	450501.77	4469824.75
34	451643.45	4455136.99
35	451443.25	4455136.79
36	451543.34	4455136.31
37	448679.89	4465885.67
38	448680.28	4465826.84
39	448680.67	4465945.28
40	452690.5	4463226.37
41	452629.78	4463225.66
42	452570.5	4463225.18

Table B2. UTM coordinates of Succession study plots surveyed for downy brome in Rocky Mountain National Park.

	(disturbed sites)			(reference sites)	
	Easting	Northing		Easting	Northing
1	448800	4468978		448359	4468950
2	447909	4468800		447823	4468749
3	446765	4472611		446442	4472557
4	446724	4472339		N/A	N/A
5	448250	4471180		448290	4471090
6	449607	4468974		449497	4468906
7	449520	4468954		N/A	N/A
8	448054	4465673		447982	4465726
9	448032	4465349		448073	4465269
10	448993	4469734		449050	4469798
11	447501	4470633		447497	4470681
12	448055	4465150		448092	4465116
13	447740	4464923		447748	4464913
14	448042	4471547		448007	4471568
15	445298	4472362		445218	4472417
16	445292	4462589		445259	4462603
17	442720	4465247		442705	4465205

APPENDIX C

2008 field sampling for model validation

Table C1. UTM coordinates of random stratified locations visited in Rocky Mountain National Park in 2008.

Site ID	Easting	Northing	Elevation (m)	Road dist. (m)	Vegetation type	Prob. class	Brome present
1	448201	4469359	2582	283	Conifer	5	Y
4	450416	4471176	2815	799	Deciduous	5	N
5	450269	4469590	2799	663	Grassland	5	N
6	450402	4469180	2603	342	Conifer	5	Y
7	448963	4470361	2657	524	Shrubland	5	N
8	428801	4457750	2655	201	Shrubland	5	N
9	450820	4471620	2561	212	Deciduous	5	Y
10	428460	4458627	2647	457	Conifer	5	N
11	448792	4470571	2707	459	Shrubland	5	Y
12	448817	4469764	2593	379	Shrubland	5	Y
14	451117	4469127	2553	323	Conifer	5	Y
15	448144	4471157	2694	335	Deciduous	5	N
16	449293	4469112	2539	258	Shrubland	5	Y
17	449116	4469200	2545	90	Shrubland	5	Y
18	448219	4466096	2640	892	Conifer	5	Y
20	449104	4469717	2590	150	Shrubland	5	Y
21	450422	4469063	2566	283	Grassland	5	Y
24	453145	4451790	2593	295	Conifer	5	N
26	427024	4469339	2709	67	Grassland	5	N
27	444468	4474136	2757	551	Conifer	5	Y
28	454488	4451818	2578	426	Conifer	5	Y
29	450511	4464174	2556	192	Shrubland	5	Y
34	451253	4468995	2501	180	Conifer	4	Y
37	451083	4470957	2766	811	Deciduous	4	N
38	448799	4472039	2614	474	Grassland	4	Y
39	448249	4470464	2654	201	Conifer	4	Y
40	447857	4469502	2591	402	Deciduous	4	Y
41	448600	4470849	2739	324	Shrubland	4	Y
43	426908	4466498	2684	446	Grassland	4	N
44	447259	4468118	2621	721	Shrubland	4	N
47	450100	4472719	2520	242	Conifer	4	Y
49	427040	4472869	2980	886	Grassland	4	N
50	453594	4456678	2763	95	Grassland	4	N
52	451250	4450889	2660	842	Deciduous	4	N
54	449724	4466378	2527	242	Conifer	4	Y
55	426970	4469586	2715	300	Conifer	4	N
57	427664	4461706	2660	726	Non-Vegetated	4	N
60	446885	4463690	2761	1677	Shrubland	4	Y
65	450375	4468542	2505	309	Conifer	3	Y
66	444520	4472021	2920	931	Deciduous	3	N
67	448255	4465661	2557	824	Non-Vegetated	3	Y
68	448945	4471873	2637	582	Deciduous	3	Y
69	427490	4461801	2660	900	Deciduous	3	N
71	448772	4468226	2494	323	Deciduous	3	Y
72	426584	4465051	2681	570	Deciduous	3	N
77	450226	4463682	2635	531	Deciduous	3	N
78	427450	4463025	2664	576	Non-Vegetated	3	N

Table C1. UTM coordinates of random stratified locations visited in Rocky Mountain National Park in 2008. (continued)

Site ID	Easting	Northing	Elevation (m)	Road dist. (m)	Vegetation type	Prob. class	Brome present
79	450571	4467524	2490	124	Shrubland	3	Y
82	452234	4458953	2897	324	Deciduous	3	N
83	453683	4456675	2758	108	Conifer	3	N
88	439845	4471273	3310	306	Deciduous	3	N
89	427609	4475247	2791	750	Deciduous	3	N
91	453993	4452345	2594	514	Deciduous	2	N
95	444298	4471560	2879	658	Grassland	2	N
97	446973	4462934	2756	1256	Deciduous	2	N
98	445890	4467390	2582	693	Shrubland	2	N
103	426825	4464988	2678	543	Conifer	2	N
105	449428	4468040	2498	404	Conifer	2	Y
106	452483	4452616	2959	1357	Deciduous	2	N
107	448361	4470478	2655	182	Shrubland	2	Y
108	453011	4469824	2533	430	Conifer	2	N
113	428241	4462836	2672	216	Conifer	2	N
114	452564	4457639	2903	384	Deciduous	2	N
116	427703	4473370	2765	573	Conifer	2	N
119	439680	4471182	3221	408	Grassland	2	N
120	432396	4476401	3240	577	Grassland	2	N
122	443118	4468475	3201	2210	Conifer	1	N
125	428200	4464316	2727	949	Conifer	1	N
137	442963	4470831	3258	30	Conifer	1	N
139	452206	4459106	2887	446	Conifer	1	N
141	430913	4465156	2927	3336	Conifer	1	N
142	438396	4453086	3444	6638	Conifer	1	N
146	452392	4454592	2840	2239	Deciduous	1	N
148	440428	4470535	3119	994	Conifer	1	N
152	444897	4460958	3067	1304	Grassland	1	N
159	432884	4475747	3435	242	Conifer	1	N
167	430523	4459953	2910	1825	Conifer	1	N
176	433039	4475853	3440	228	Tundra	1	N
179	428660	4451994	2560	1361	Deciduous	1	N
185	430416	4460595	3041	2014	Conifer	1	N
186	449447	4449794	2781	2876	Conifer	1	N
193	432579	4453412	2773	1129	Conifer	1	N
195	442852	4471807	3307	153	Conifer	1	N
198	442853	4472035	3326	95	Non-Vegetated	1	N
203	434533	4454113	2646	2644	Deciduous	1	N
205	440457	4453551	3389	8574	Non-Vegetated	1	N
220	426819	4470097	2774	819	Conifer	1	N
221	447080	4451195	2980	5013	Conifer	1	N
225	435261	4454710	3080	3335	Conifer	1	N
254	428822	4464665	2772	1426	Conifer	1	N
261	442318	4470271	3540	892	Conifer	1	N
274	442963	4463492	3327	2699	Conifer	1	N
284	445288	4453008	3275	7100	Conifer	1	N

APPENDIX D

Maps of downy brome locations in

Rocky Mountain National Park

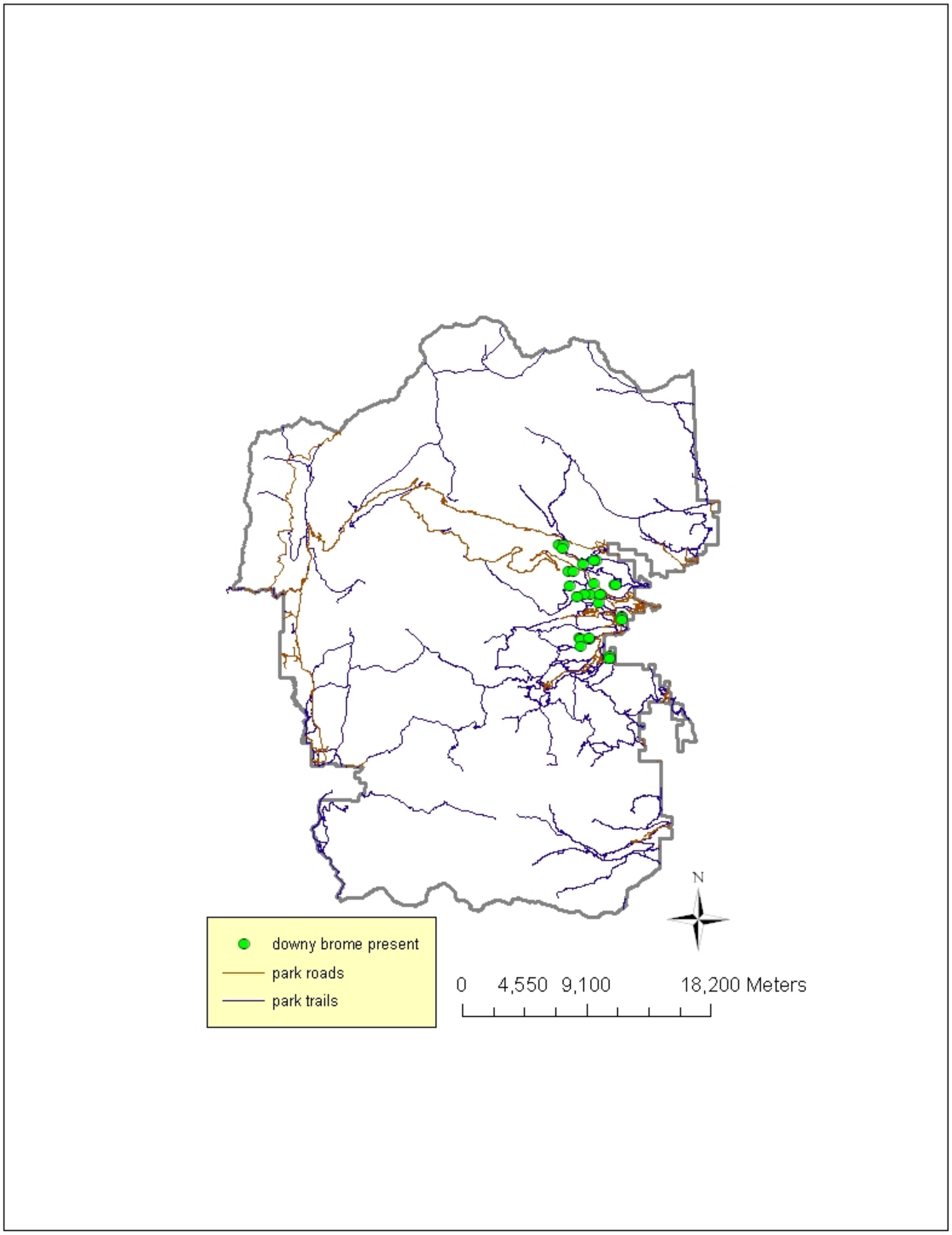

Figure D1. Map of downy brome locations in Rocky Mountain National Park from 2007 field sampling of Ecotone study plots and Succession study plots.

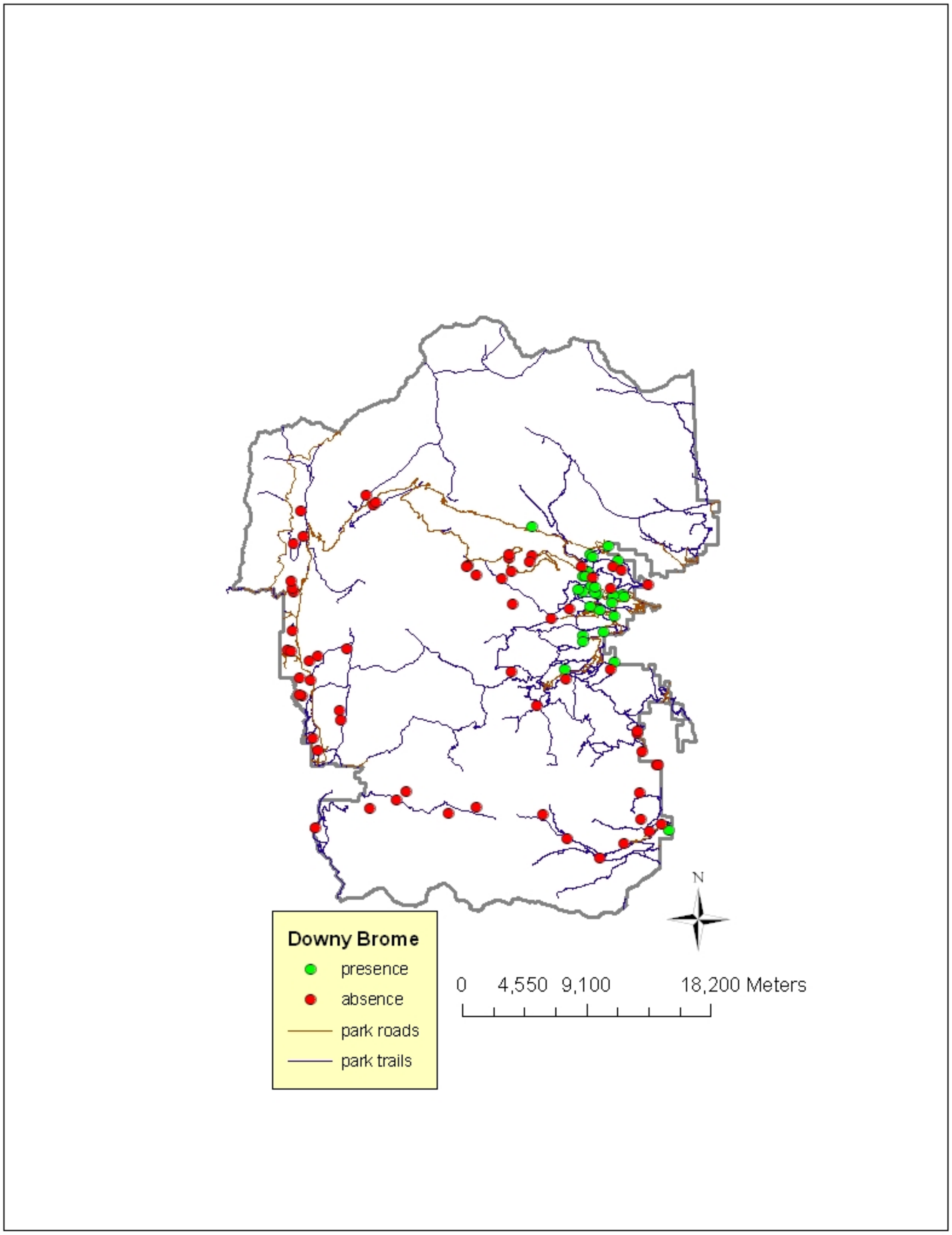

Figure D2. Random stratified sites surveyed for downy brome in Rocky Mountain National Park in 2008.

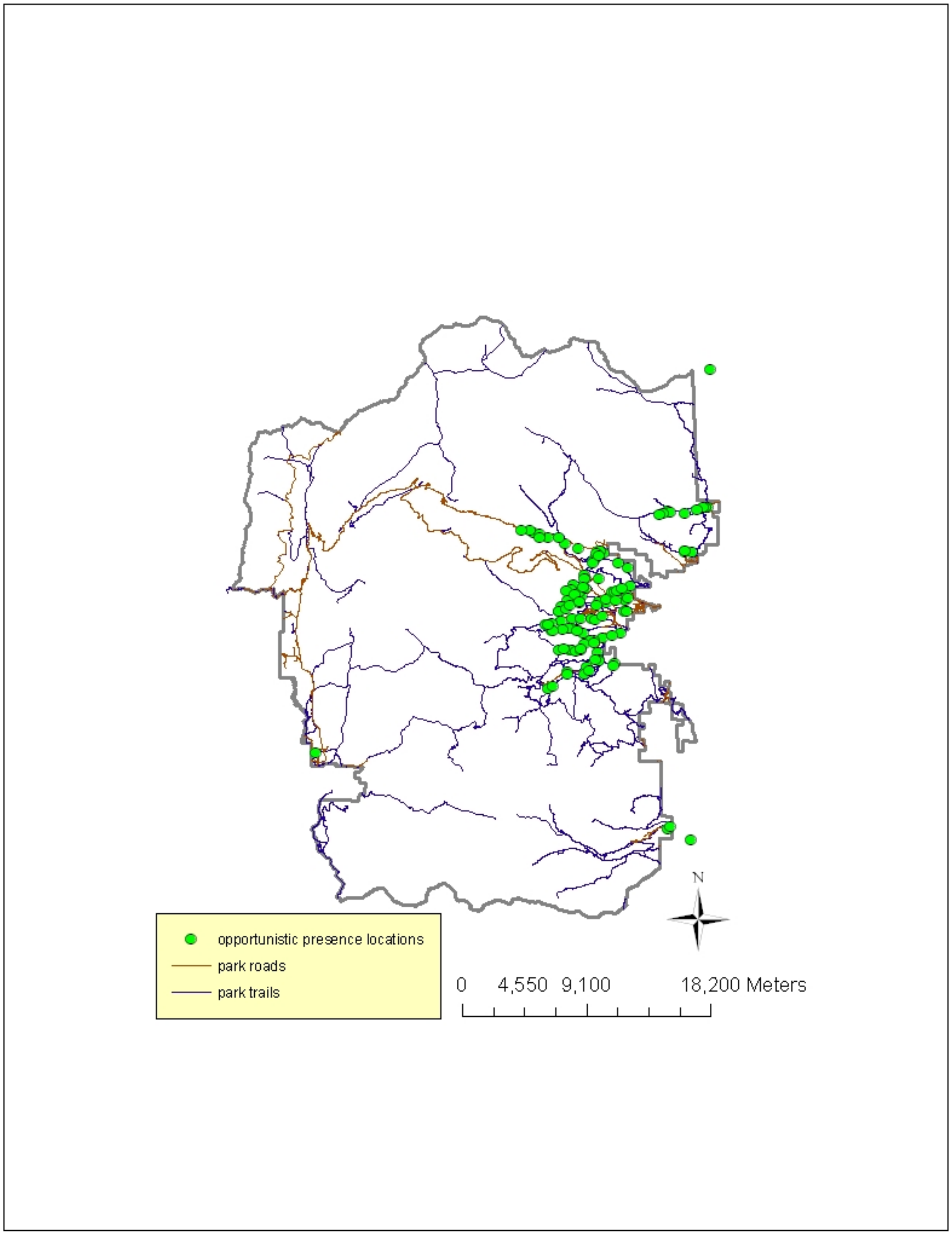

Figure D3. Opportunistic locations found in 2008 from mapping of downy brome along roads and trails in Rocky Mountain National Park.

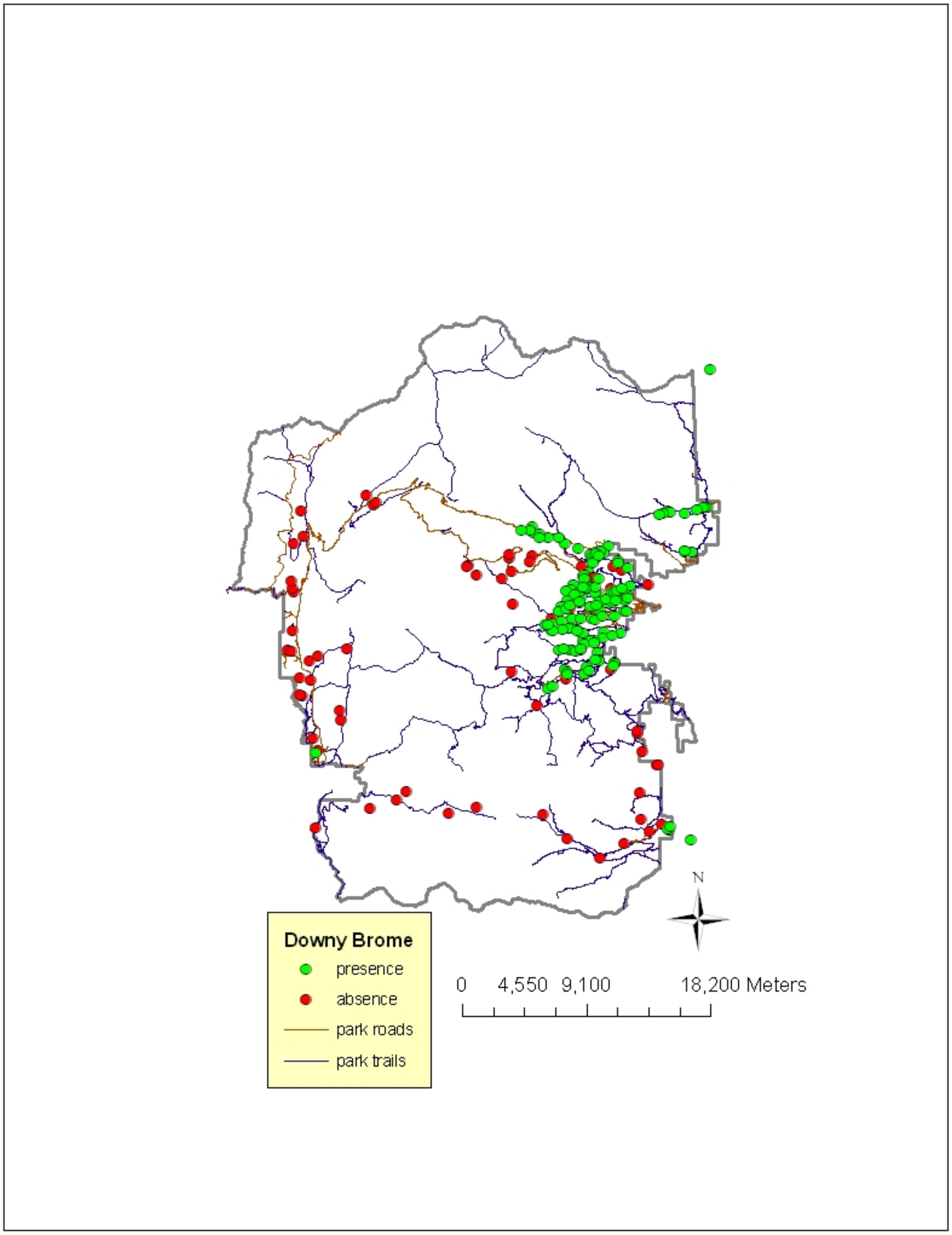

Figure D4. All sites visited in Rocky Mountain National Park in 2008 including both the random stratified locations for the Maxent model validation and opportunistic locations collect for the downy brome mapping project.