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# Non-native plant invasions in managed and protected ponderosa pine/Douglas-fir forests of the Colorado Front Range☆

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## Abstract

We examined patterns of non-native plant diversity in protected and managed ponderosa pine/Douglas-fir forests of the Colorado Front Range. Cheesman Lake, a protected landscape, and Turkey Creek, a managed landscape, appear to have had similar natural disturbance histories prior to European settlement and fire protection during the last century. However, Turkey Creek has experienced logging, grazing, prescribed burning, and recreation since the late 1800s, while Cheesman Lake has not.

Using the modified-Whittaker plot design to sample understory species richness and cover, we collected data for 30 0.1 ha plots in each landscape. Topographic position greatly influenced results, while management history did not. At both Cheesman Lake and Turkey Creek, low/riparian plots had highest native and non-native species richness and cover; upland plots (especially east/west-facing, south-facing and flat, high plots) had the lowest. However, there were no significant differences between Cheesman Lake and Turkey Creek for native species richness, native species cover, non-native species richness, or non-native species cover for any topographic category. In general, non-native species richness and cover were highly positively correlated with native species richness and/or cover (among other variables). In total, 16 non-native species were recorded at Cheesman Lake and Turkey Creek; none of the 16 non-native species were more common at one site than another.

These findings suggest that: (1) areas that are high in native species diversity also contain more non-native species; (2) both protected and managed areas can be invaded by non-native plant species, and at similar intensities; and (3) logging, grazing, and other similar disturbances may have less of an impact on non-native species establishment and growth than topographic position (i.e., in lowland and riparian zones versus upland zones).
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## 1. Introduction

Non-native species can adversely affect natural communities by changing native community structure, altering fire regimes, increasing water use in riparian areas, and impacting wildlife habitat (e.g., Robinson,



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1965; Smith, 1985; Hughes et al., 1991; Billings, 1994; Trammell and Butler, 1995; Walker and Smith, 1997; Mack et al., 2000). Land managers are becoming increasingly aware of problems created by non-native species invasions. In the western United States, there is a general concern that high-impact disturbances such as logging, grazing, fire (both prescribed and natural), recreational use, and other activities may increase the number of non-natives on the landscape (Pettit et al., 1995; Young and Allen, 1997). However, it is often difficult to determine the degree to which human activities have influenced understory plant communities because few reference ecosystems exist for observation, and historical ecosystems were not adequately described.

Lower montane forests on the eastern slopes of the Colorado Front Range Mountains have experienced intense logging, grazing, fire suppression, and recreation since Euro-American settlement began in the 1870s (General Land Office field notes, 1879, 1882; Jack, 1900). Increased forest densities and occurrences of severe wildfires are intensifying the need for forest restoration over large areas, by methods such as mechanical thinning and/or prescribed burning. Consequently, there is a growing concern that these restoration actions may create opportunities for non-native plant species to become difficult management problems. The Cheesman Lake landscape is a lower montane forest in the Upper South Platte Watershed that has been well-protected from logging, grazing, prescribed fires, and recreation. Cheesman Lake and nearby managed forests provide a rare opportunity to examine the effects of management on non-native species introduction and establishment.

Our objective is to examine the patterns of non-native species diversity in the Cheesman Lake and adjacent managed landscapes. These landscapes appear to have had a similar natural disturbance history before Euro-American settlement (Brown et al., 1999). Their similar topographic complexity but different post-settlement histories provide opportunities to relate non-native species invasion to both topography and management history. Specifically, we address the following questions about the vulnerability of native plant communities to non-native species invasion:

(1) Are managed landscapes more heavily invaded by non-native species than protected ones?
(2) Which areas in each of these landscapes are most vulnerable to non-native plant invasions?
(3) How do biotic and abiotic factors, such as native species cover and species richness, overstory characteristics, disturbance history, and proximity to water and roads, influence patterns of non-native species invasion?
(4) Are certain non-native species more apt to invade one landscape (i.e., managed or protected) than another?

Answers to these questions will be useful to land managers who are trying to assess the impacts of forest restoration, which will include disturbances such as logging, prescribed fire, and increased motor vehicle travel, on the understory species composition in ponderosa pine ecosystems of the Colorado Front Range. Researchers and others who are interested in predicting and explaining the vulnerability of forest communities to non-native species invasion may also find the results of this study useful.

## 2. Methods

### 2.1. Study areas

Our study areas are in the Upper South Platte Watershed of central Colorado, USA, approximately 60 km southwest of Denver (Fig. 1). Soils in the Upper South Platte Watershed, which are gravely coarse sandy loams derived from weathered Pikes Peak granite (USDA Forest Service, 1992), are very well drained and erosive. Average annual precipitation is around 40 cm, and there is no persistent winter snowpack. Summer precipitation comes mainly in the form of erratic thunderstorms. Elevations in the portion of the Upper South Platte Watershed we sampled ranged from 2100 to 2400 m.

The overstory forest vegetation in the Upper South Platte Watershed is dry ponderosa pine/Douglas-fir forest (*Pinus ponderosa*/*Pseudotsuga menziesii*; Peet, 1981). Understory vegetation is typically grassy or shrubby or both. Historically, both overstory and understory densities were spatially heterogeneous across the landscape (Kaufmann et al., 2000; Kaufmann et al., 2001). Because of this high spatial heterogeneity, the landscape historically burned as a

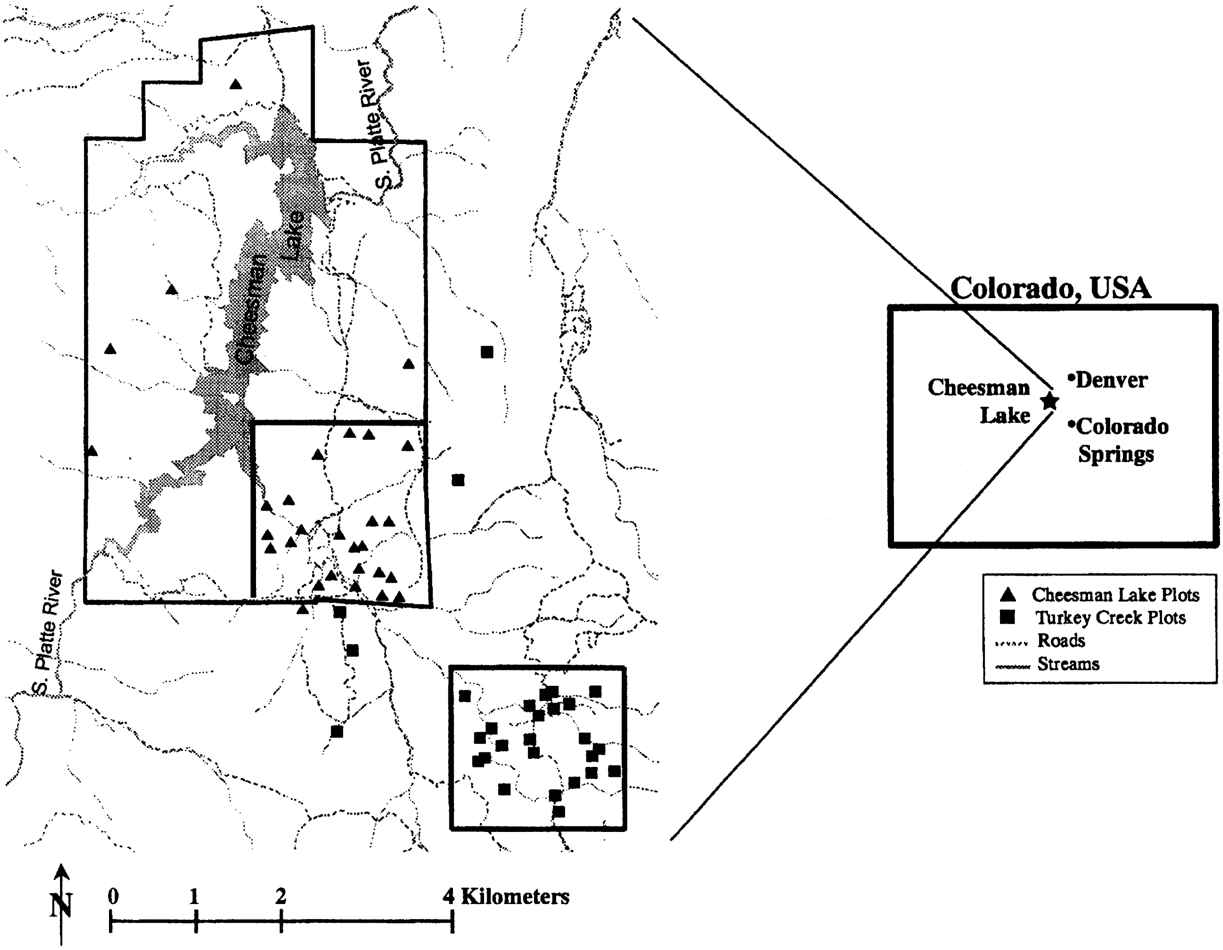


Fig. 1. Map of the study area in the Upper South Platte Watershed, 60 km southwest of Denver, Colorado. The Cheesman Lake landscape boundary and the 4-km$^2$ areas at Cheesman Lake and Turkey Creek are delineated.

mixed-severity fire regime, where both surface and stand-replacing fires were probable (Brown et al., 1999). Forest management practices since Euro-American settlement have resulted in a more homogeneous and dense overstory in many areas of the watershed, which favors crown fire regimes.

The Cheesman Lake landscape is a 35 km$^2$ forested area in the Upper South Platte Watershed that has been protected from forest management (Fig. 1). Cheesman Lake, a reservoir created on the South Platte River at the beginning of the 20th century, and the surrounding land are owned and managed by Denver Water. Unlike most montane forests in the Colorado Front Range, the land surrounding Cheesman Lake is relatively undisturbed. The land has experienced only minimal, localized logging (mostly below the current water line of the reservoir) prior to the time of dam completion. At the time of dam completion in 1905, a six-strand fence was erected around the property, which has excluded logging and domestic grazing. Cheesman Lake and the surrounding property are not open to public recreation, except for shoreline fishing and limited hiking. Wildfires, however, have been suppressed since the early 1900s. We will refer to the Cheesman Lake landscape as a 'protected' landscape because of the general lack of logging, grazing, and recreational pressures that are common outside Cheesman Lake.

The 'managed' study area, the Turkey Creek landscape, is also within the Upper South Platte Watershed and is adjacent to the Cheesman Lake landscape

(Fig. 1). This area, on the South Platte Ranger District of the Pike National Forest, has experienced periodic logging since the 1890s, grazing from 1880s to 1940s, and prescribed burning; naturally ignited fires have also been suppressed during the 20th century (Jack, 1900; General Land Office field notes, 1879 and 1882; DeLay, T.J., unpublished data).

To minimize environmental differences between Cheesman Lake and Turkey Creek, we established two 4 $km^2$ (2 km $\times$ 2 km) areas, one at Cheesman Lake and one at Turkey Creek (Fig. 1). Kaufmann et al. (2000) provide detailed information about the 4 $km^2$ areas and sampling methods, which we summarize here. The 4 $km^2$ areas are similar in elevation, topography and soils, and are separated by a distance of only 1 km. Within each 4 $km^2$ area, five plots were established in each of five topographic categories, for a total of 25 plots: north-facing slopes, south-facing slopes, east- or west-facing slopes, flat high areas (i.e. ridge tops), and low or riparian areas. Five additional plots were also established at Cheesman Lake and Turkey Creek outside the 4 $km^2$ areas to represent a larger, landscape scale; one plot was located in each topographic category. To obtain unbiased plot locations within each topographic category, we overlaid a grid on USGS topographic maps, and used random grid coordinate tables and plot selection rules to select grid cells for plot sites. Plot selection rules specified that for north, south, and east/west plots, plot azimuth had to be within 20° of each cardinal direction, and slope must be between 15 and 35%. For flat/high plots, plot azimuth could be any value, but slope must be <10%. Low/riparian plots were located above the banks of permanent streams, but could cross-intermittent streams; plot aspect could vary, but slope had to be <15%. We located all plots in forested areas, so that each plot contained at least 20 trees (seven of the early plots did not quite meet this requirement, but were still considered forested). All plots were 0.1 ha (20 m $\times$ 50 m), with the long axis aligned down the fall line on north, south, east and west plots.

Plots were further lumped to examine the effects of water availability on non-native species. Two categories were created: upland (north, south, east/west, and flat/high plots) and low/riparian plots. We felt comfortable combining plots in this fashion because plots on north, south, east/west and flat/high sites are much drier than low/riparian plots, which are adjacent to an intermittent or perennial water source or are located in low areas where the water table is relatively close to the surface (M.R. Kaufmann, personal observation).

### 2.2. Understory sampling

The modified-Whittaker plot design (Stohlgren et al., 1995) was used for sampling forest understory vegetation. This design provides nested spatial sampling at scales of 1, 10, 100, and 1000 $m^2$ (0.1 ha total plot size). Ten 1 $m^2$ subplots were located around the perimeter of the 20 m $\times$ 50 m plot. Two 10 $m^2$ subplots were located in diagonally opposite corners of the plot, and one 100 $m^2$ subplot was located in the center of the plot. Percent foliar cover was recorded for each species in the 10 1 $m^2$ plots. Cumulative additional species were recorded for each of the 10 $m^2$ plots, the 100 $m^2$ plot, and the remainder of the 1000 $m^2$ plot. This nested sampling approach avoids most of the problems associated with spatial auto-correlation among samples, and it captures a significantly higher percentage of total species richness than other techniques (Stohlgren et al., 1995). Data were collected for 60 plots (five plots per topographic type in each 4 $km^2$ area, plus the five additional plots outside the 4 $km^2$ areas at Cheesman Lake and Turkey Creek) during June 1996 and June to July 1997. An analysis of precipitation data collected by a Remote Automated Weather Station (RAWS) at Cheesman Lake indicated that there were no differences in monthly precipitation between 1996 and 1997 for the growing season (April to July; unpublished data).

Considerable attention was paid to quality assurance and quality control for plant identification and cover estimates. Plant identification was monitored carefully to assure that species lists were accurate. While phenological changes during the field season could not be avoided, we sampled plots for both the managed and protected sites in random order to minimize their effects on data quality. Three field crew members were experienced botanists and were familiar with the local flora. For species that could not be identified in the field, careful notes were recorded about the specimen's location and vegetative features, and samples were collected and pressed for laboratory identification. While most 'unknowns' could be later identified at the Colorado State University and University of Wyoming herbaria, an average of 6.8% of the species in each plot could not be identified. Unknown species were disregarded in all statistical analyses.

All species that could be identified were classified as either native or non-native according to Weber and Wittmann (1996) and the USDA NRCS Plants Database (2001); in the case of a discrepancy, we deferred to Weber and Wittmann.

### 2.3. Overstory sampling and plot attribute data

Forest overstory data also were collected in each modified-Whittaker plot. For each tree taller than breast height (1.37 m), tree diameter at breast height (DBH), species, and live or dead status were recorded. From these data, we calculated basal area and trees per hectare (both total and by species) of live and dead trees.

We recorded the UTM coordinates of the upper right and lower left corners of each plot with a hand-held GPS unit. We also obtained GIS coverages of streams, roads, and property ownership for the Cheesman Lake and Turkey Creek study areas. The stream coverage contained all streams (perennial or intermittent) in the study areas. The road coverage depicted every road in our two study areas; all of these roads were unpaved private or Forest Service roads, and none were heavily traveled. The property ownership coverage outlined the Cheesman Lake property line. Using the plot coordinate data and the GIS coverages, we calculated the distance of each plot from perennial or intermittent streams, roads, and the six-strand fence around the Cheesman property. These variables were selected because of their potential effects on the introduction of non-native species.

We relied upon the ages of the oldest trees in each plot and the fire history for the study area to estimate the year of the last fire (either surface or stand-replacing) and the last stand-replacing fire in each plot. In each plot, 20 randomly selected live trees were cored for age; every tree in the plot that appeared to be over 200 years old was also cored and its age was determined by cross-dating (Kaufmann et al., 2000). Next, we used the fire scar data collected by Brown et al. (1999) to estimate fire disturbance dates for each plot. We screened fire scar data for sample(s) within 200 m of each plot, and the most recent fire recorded by a fire scar was used as the year of the last fire in the plot. In Turkey Creek, we also had maps of two prescribed fires that burned in 1987 and 1995, each of which covered about one-third of the 4 $km^2$ area; when plots fell in those areas, these dates were used as the year of the most recent fire. To determine the year of the last stand-replacing fire, we compared the ages of the five oldest trees sampled in the plot (which included the oldest cohort in the plot) with the nearby fire dates. The first fire date preceding the date of the initiation of the oldest cohort was assumed to be the year of the last stand-replacing fire.

Basal area, trees per hectare, year of the last fire and last stand-replacing fire, and the distance from water, roads, and the property line were used for assessing the effects of stand density, disturbance history, proximity to water, and degree of remoteness on understory plant diversity and non-native species invasion.

### 2.4. Statistical analysis

We conducted statistical analyses with SYSTAT (versions 9.0 and 10.0, SPSS Inc.). We used an analysis of variance to test for significant differences in native species richness, non-native species richness, native species cover, and non-native species cover by topographic category and management history (Cheesman Lake v. Turkey Creek). To compare native species richness, non-native species richness, and native species cover for all upland plots versus low/riparian plots, we used a linear contrast. To compare non-native species cover for all upland plots versus low/riparian plots, we used a permutation test, because assumptions of normality and homogeneous variance were violated. Fisher's exact test was used to test for differences in the presence or absence of an individual non-native species between Cheesman Lake and Turkey Creek; an analysis of variance was used to test for differences in the percent cover of an individual non-native species between Cheesman Lake and Turkey Creek. These statistical tests were evaluated at the $\alpha = 0.05$ level.

We used path coefficient analyses (Dewey and Lu, 1959; Stohlgren et al., 2001a) to evaluate the direct and indirect relationships of environmental variables to non-native species richness and cover. Path coefficient analysis displays the standardized partial-regression coefficient (direct influence) of an environmental factor on the dependent variable, with significant ($P < 0.05$) simple correlations (indirect influences) shown among environmental variables. To determine direct influences, we ran forward stepwise regressions to estimate the correlation between each variable and non-native species richness and cover at our two study sites. Only variables that were significant at the $\alpha = 0.15$ level were retained in the forward regression model. Indirect influences were determined by looking for correlations between each pair of significant variables. Eleven predictor variables were used for all analyses (with the exception of distance from the property line at Turkey Creek, which is not meaningful for these tests):

- distance to (1) the closest perennial or intermittent stream, (2) the property line, and (3) the closest road;
- year of (4) the last stand-replacing fire and (5) the last fire (stand-replacing or not);
- live ponderosa pine (6) basal area ($m^2$/ha) and (7) trees/ha;
- live Douglas-fir (8) basal area ($m^2$/ha) and (9) trees/ha;
- (10) native species richness/plot, and (11) percent native cover.

Two predictor variables were transformed prior to the regression analyses to correct for non-linear relationships between the predictor variable and non-native species richness and cover: a $\log_{10}$ transformation was used on distance to closest perennial or intermittent stream, and native species richness was squared.

## 3. Results

### 3.1. Native and non-native species richness and cover in protected and managed landscapes

The cumulative numbers of native and non-native species were strikingly similar at Cheesman Lake and Turkey Creek. In the 30 plots located at Cheesman Lake, 190 known species were recorded, of which 176 were native and 14 were non-native. Twenty-five out of 30 plots at Cheesman Lake contained at least one non-native species; many plots contained several (range: 0–9 non-native species per plot). The 30 plots in Turkey Creek contained 196 known species; 182 species were native, and 14 were not native. The number of non-native species per plot at Turkey Creek ranged from 0 to 10, with 26 of 30 plots containing at least one non-native species. At both Cheesman Lake and Turkey Creek, all of the plots that contained only native species were in the drier, upland sites; non-native species were found in all low/riparian plots. Overall, Cheesman Lake and Turkey Creek did not differ in native species richness, native species cover, non-native species richness, or non-native species cover (Table 1).

While management history did not affect richness and cover of plant species, topographic position did (Table 1). At Cheesman Lake, low/riparian plots contained the highest native and non-native species richness and cover; south slopes generally contained the lowest native and non-native richness and cover. At Turkey Creek, low/riparian plots also contained the highest native and non-native richness and cover, as observed at Cheesman Lake. In contrast with Cheesman Lake, at Turkey Creek east/west and flat/high plots recorded the lowest native and non-native species richness and cover.

When plots were classified as either upland or low/riparian, differences between upland and lowland/riparian plots within each study area were also apparent (Table 2). At Cheesman Lake and Turkey Creek, native species richness and non-native species richness were significantly higher in the low/riparian plots than the upland plots. Native species cover was also significantly higher in the low/riparian plots than the upland plots at Cheesman Lake and Turkey Creek (although only marginally significant at Cheesman Lake, and consistent with other trends; $P = 0.051$). Non-native species cover was significantly higher in the low/riparian plots than the upland plots at Cheesman Lake, but not at Turkey Creek ($P = 0.176$).

### 3.2. Predictors of non-native species richness and cover

At Cheesman Lake, 76% of the variation in non-native species richness can be explained by distance from the closest perennial or intermittent stream, percent native species cover, distance from the property line, and Douglas-fir basal area (Fig. 2). Of these variables, percent native species cover had a direct, positive effect on non-native species richness, while

Table 1
Two-way analysis of variance results for native and non-native species richness and cover at Cheesman Lake and Turkey Creek, by topographic category

| | Cheesman Lake | | | Turkey Creek | | | P value[a] | | |
|---|---|---|---|---|---|---|---|---|---|
| | $n$ | Mean | S.E. | $n$ | Mean | S.E. | Site | Topo | Site × topo |
| Native species richness/plot | | | | | | | 0.430 | <0.001 | 0.111 |
| E/W | 6 | 40.7 | (2.0) | 6 | 36.8 | (3.4) | | | |
| F/H | 6 | 42.5 | (2.6) | 7 | 41.4 | (1.7) | | | |
| L/R | 6 | 59.5 | (3.6) | 6 | 68.2 | (4.8) | | | |
| N | 6 | 41.5 | (3.6) | 5 | 38.0 | (2.2) | | | |
| S | 6 | 32.8 | (2.2) | 6 | 40.2 | (2.8) | | | |
| Native species cover (%) | | | | | | | 0.070 | <0.001 | 0.501 |
| E/W | 6 | 18.3 | (2.4) | 6 | 19.4 | (2.8) | | | |
| F/H | 6 | 24.2 | (6.0) | 7 | 25.1 | (2.9) | | | |
| L/R | 6 | 31.2 | (6.5) | 6 | 43.5 | (6.2) | | | |
| N | 6 | 24.1 | (3.1) | 5 | 25.2 | (6.7) | | | |
| S | 6 | 11.1 | (2.2) | 6 | 21.5 | (2.0) | | | |
| Non-native species richness/plot | | | | | | | 0.992 | <0.001 | 0.524 |
| E/W | 6 | 2.3 | (0.6) | 6 | 1.7 | (0.6) | | | |
| F/H | 6 | 1.7 | (0.6) | 7 | 1.1 | (0.4) | | | |
| L/R | 6 | 5.5 | (1.0) | 6 | 4.7 | (1.2) | | | |
| N | 6 | 1.8 | (0.7) | 5 | 3.0 | (0.7) | | | |
| S | 6 | 1.5 | (0.4) | 6 | 2.3 | (0.7) | | | |
| Non-native species cover (%) | | | | | | | 0.281 | 0.002 | 0.466 |
| E/W | 6 | 0.7 | (0.3) | 6 | 0.0 | (0.0) | | | |
| F/H | 6 | 0.1 | (0.1) | 7 | 0.2 | (0.1) | | | |
| L/R | 6 | 3.9 | (1.8) | 6 | 1.7 | (1.5) | | | |
| N | 6 | 0.0 | (0.0) | 5 | 0.1 | (0.1) | | | |
| S | 6 | 0.1 | (0.0) | 6 | 0.3 | (0.2) | | | |

Topographic categories are abbreviated as follows: E/W, east- or west-facing plots; F/H, flat/high plots; L/R, low/riparian plots; N, north-facing plots; S, south-facing plots.

[a] $P$ value categories are as follows: 'site' compares Cheesman Lake and Turkey Creek across all topographic categories; 'topo' compares topographic categories across all sites; 'site × topo' compares site by topographic category interactions.

distance from perennial/intermittent stream, distance from the property line, and Douglas-fir basal area had direct, negative effects. There was also an indirect effect of distance from the property line and Douglas-fir basal area on non-native species richness because of the negative correlation between these two predictors.

Sixty-two percent of the variation in the percent non-native cover at Cheesman Lake could be explained by native species richness, percent native cover, distance from the property line, and Douglas-fir basal area (Fig. 2). Native species richness and percent native cover had direct, positive effects on non-native species cover, while distance from the property line and Douglas-fir basal area had direct, negative effects. There is also a strong, positive relationship between native species richness and native species cover that is indirectly influencing non-native species cover. Non-native species cover is also indirectly influenced by the negative relationship between distance from the property line and Douglas-fir basal area.

At Turkey Creek, 32% of the variation in non-native species richness and 33% of the variation in percent non-native cover can be explained by native species richness (Fig. 3). No other variables were significant in predicting non-native species richness or cover at Turkey Creek.

### 3.3. Non-native species composition in protected and managed landscapes

In total, 16 non-native species were recorded in the plots at Cheesman Lake and Turkey Creek (Table 3).

Table 2
Linear contrast results of native and non-native species richness and native species cover for upland plots versus low/riparian plots, and permutation test results for non-native species cover for upland versus low/riparian plots

| | Upland plots | | Low/riparian plots | | P value |
|---|---|---|---|---|---|
| | Mean | S.E. | Mean | S.E. | |
| Native species richness/plot | | | | | |
| Cheesman Lake | 39.4 | 1.4 | 59.5 | 2.8 | <0.001 |
| Turkey Creek | 39.1 | 1.6 | 68.2 | 3.2 | <0.001 |
| Native species cover (%) | | | | | |
| Cheesman Lake | 19.4 | 2.2 | 31.2 | 4.4 | 0.051 |
| Turkey Creek | 22.8 | 2.2 | 43.5 | 4.3 | <0.001 |
| Non-native species richness/plot | | | | | |
| Cheesman Lake | 1.8 | 0.3 | 5.5 | 0.7 | <0.001 |
| Turkey Creek | 2.0 | 0.4 | 4.7 | 0.8 | 0.010 |
| Non-native species cover (%) | | | | | |
| Cheesman Lake | 0.2 | 0.1 | 3.9 | 1.8 | <0.001 |
| Turkey Creek | 0.1 | 0.1 | 1.7 | 1.4 | 0.176 |

We used a permutation test for non-native species cover because assumptions of normality and homogeneous variance were violated. Upland plots (east- or west-facing, flat/high, north-facing and south-facing) have an overall $n = 24$, and low/riparian plots have an $n$ of 6. $P$ values were Bonferroni-adjusted because multiple tests were performed (Miller, 1981).

Twelve of the non-native species were common to both Cheesman Lake and Turkey Creek; two species were unique to each study area. Of the 16 non-native species, 12 were forbs and four were grasses; no non-native trees, shrubs or succulents were detected. Six non-native species were annuals, two were biennials, and eight were perennials.

In general, each non-native species occurred in only a handful of the 30 Cheesman Lake or Turkey Creek plots. Only four species, *Chenopodium album*, *Taraxacum officinale*, *Thlaspi montanum*, and *Verbascum thapsus*, occurred in >10 plots at either Cheesman Lake or Turkey Creek. At Cheesman Lake, *V. thapsus* was the most common (13 of 30 plots), and at Turkey Creek, *T. officinale* occurred in the most plots (15 of 30 plots). Interestingly, cheatgrass (*Bromus tectorum*) was not observed in any plots at Cheesman Lake or Turkey Creek, although its presence was observed outside the west boundary of the Cheesman Lake property. None of the non-native species was more common at one site versus the other.

Percent cover of each non-native species within a plot was generally low. Of all the species, *Poa pratensis* had the highest percent cover in both Cheesman Lake and Turkey Creek; there was no significant difference in percent cover for *P. pratensis* between the two study areas (2.3 and 4.6%, respectively; $P = 0.33$). In fact, for all 16 non-native species found in Cheesman Lake and Turkey Creek, only percent cover of *V. thapsus* was significantly different between the study areas ($P < 0.001$); percent cover of *V. thapsus* was higher at Turkey Creek than at Cheesman Lake.

## 4. Discussion

### *4.1. Native and non-native species richness and cover in protected and managed landscapes*

Our studies at Cheesman Lake and Turkey Creek provide insight into the influence of land use management on non-native species invasion and into the potential role of preserves in sustaining vegetative communities that are free of non-native species. We anticipated that disturbed, heavily managed landscapes might contain lower native plant diversity and greater non-native species diversity than protected landscapes. This was not the case. Our results indicate that Cheesman Lake and Turkey Creek generally have been invaded by non-native plant species at the same intensity and by the same species. These findings contradict the general and long-held paradigm that areas that have been disturbed by humans are more readily invaded than undisturbed areas (Elton, 1958; Fox and Fox, 1986; Orians, 1986; Rejmánek, 1989). Our results do not determine, however, if the initial rates of invasion differed.

Our protected landscape at Cheesman Lake contained 14 non-native species, which represented 7.4% of the cumulative number of species sampled on this landscape. Twenty-five of 30 plots contained at least one exotic, with an average of 2.6 non-native species per plot. Non-native species were found even in sampled plots on the west side of the reservoir where there are no roads and access is very restricted. Similar invasions into protected areas have been seen elsewhere. In the United States, non-native plant species have spread throughout most, if not all, of the nation's

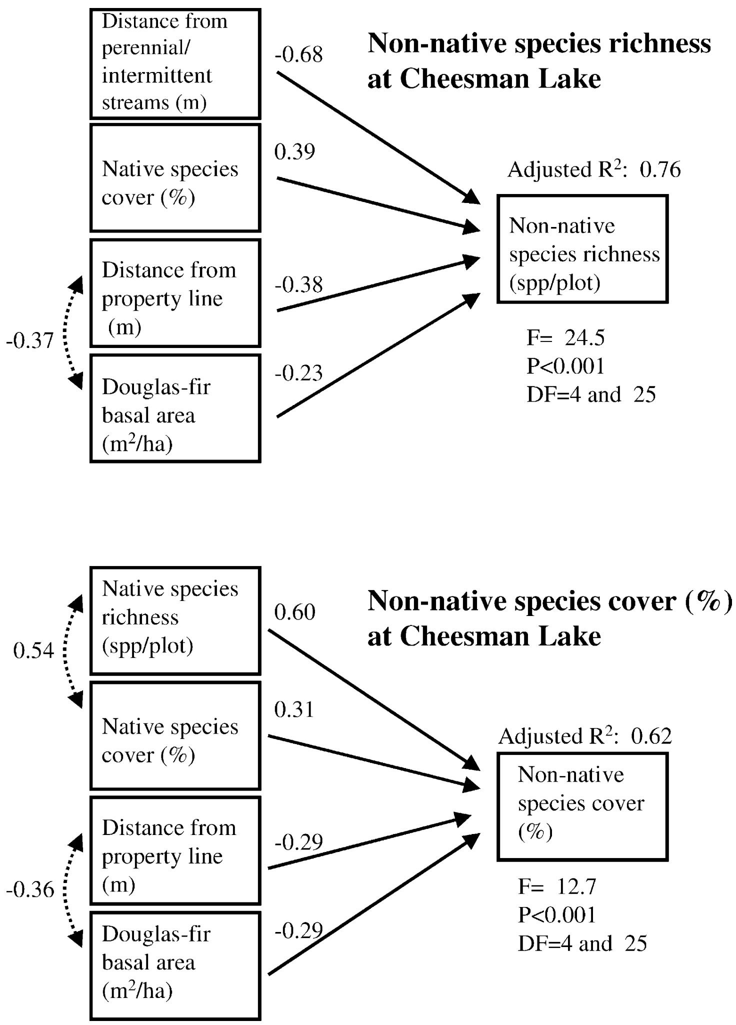


Fig. 2. Path analysis for non-native species richness (top) and percent cover (bottom) at Cheesman Lake. Two predictor variables were transformed prior to the forward stepwise regression analyses to correct for non-linear relationships between the predictor variable and non-native species richness and cover: a $\log_{10}$ transformation was used on distance to closest perennial or intermittent stream, and native species richness was squared. Solid arrows, with the standardized partial-regression coefficient reported above them, indicate direct effects. Dashed arrows indicate indirect effects, with simple correlation values reported alongside the arrows.

wilderness areas (Marion et al., 1986) and many National Parks (Goigel and Bratton, 1983; Stohlgren et al., 1999; Whipple, 2001). In a relic stand of *Pinus edulis*/*Juniperus osteosperma* in Utah that has had little or no human and livestock use, the non-native cheatgrass (*B. tectorum*) was by far the most frequent species in the understory (Goodrich and Gale, 1999).

While land management did not have an effect on non-native species, water availability did. At both Cheesman Lake and Turkey Creek, plots in low/riparian areas had significantly higher non-native species richness than plots in upland areas. Plots in low/riparian areas also had significantly higher native species richness than plots in upland areas. Our results do not support the theory that species-rich communities are more able to resist invasion by non-native species (Elton, 1958; Case, 1990; Tilman, 1997; Fox and Fox, 1986). On the contrary, many other studies have found that areas that are 'hotspots' of native plant species richness also have high non-native richness

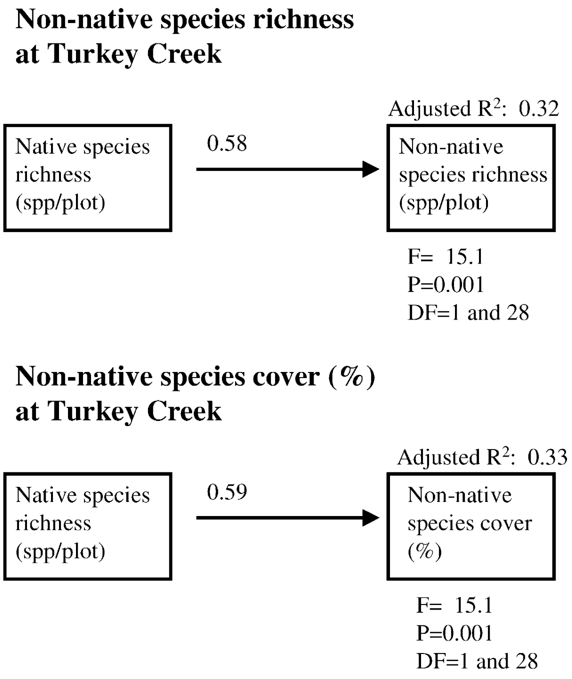


Fig. 3. Path analysis for non-native species richness (top) and percent cover (bottom) at Turkey Creek. Two predictor variables were transformed prior to the forward stepwise regression analyses to correct for non-linear relationships between the predictor variable and non-native species richness and cover: a $\log_{10}$ transformation was used on distance to closest perennial or intermittent stream, and native species richness was squared. Solid arrows, with the standardized partial-regression coefficient reported above them, indicate direct effects.

(e.g. Stohlgren et al., 1998, 1999, 2001a, 2002). This may be because the high resource levels (water, light soil nutrients, etc.) that are available for native plant species are also available for non-native species (Stohlgren et al., 2001a, 2002).

Overall, the number of native and non-native plant species recorded at Cheesman Lake and Turkey Creek is low. We suspect that the harsh growing environment of the Upper South Platte Watershed, with low precipitation, undeveloped and well-drained soils, and relatively high summer temperatures may constrain both native species diversity and non-native species invasion (Baker, 1986; Stohlgren et al., 2002). Our observed values of native and non-native species richness and cover are comparable with those observed in other studies in similar environments. For example, Stohlgren et al. (1999), studying in the ponderosa pine zone of Rocky Mountain National Park, Colorado, reported an average of 37.0 native species and 2.0 non-native species per modified-Whittaker plot; native cover averaged 14.7% and non-native cover was 0.2%. By comparison, our results indicated that, across all sites and topographic categories, average native species per modified-Whittaker plot was 44.2 and average non-native species per plot was 2.5. Native cover averaged 24.4% and non-native cover averaged 0.7%.

### *4.2. Predictors of non-native species richness and cover*

In our analysis, native species richness and cover were two of the strongest predictors of non-native species richness and cover, and they were positively correlated. This reinforces our previously stated finding that areas high in native species diversity are also high in non-native species diversity. Only native species richness was statistically significant at Turkey Creek; other significant predictors at Cheesman Lake included distance from perennial or intermittent stream, distance from property lines, and Douglas-fir basal area.

Path analysis showed that as distance from perennial or intermittent streams increased in Cheesman Lake, non-native species richness decreased. This result is also supported by our finding that plots in low/riparian areas had significantly higher non-native species than plots in upland areas.

Path analysis also showed that the Cheesman Lake plots closest to the property line (which is marked with a six-strand fence) have more non-native species. This suggests an edge effect between the managed and protected landscapes. However, exotics are even found in the remote plots on the west side of the reservoir, where access is severely limited. Perhaps Cheesman is too small, with too much edge, to be safe from invasions.

At Cheesman Lake, forests with more Douglas-fir have lower non-native species richness and cover. This may be because an increase in Douglas-fir basal area also indicates an increase in total basal area. As basal area increases, available light is limited and understory plant richness and cover would be expected to decrease.

Although the year of the last fire and year of the last stand-replacing fire were entered into the multivariate models, they were not significant predictors of non-native species richness and cover at either Cheesman

Table 3
Number of plots (out of 30 plots per site) containing a given non-native species (1000 $m^2$ plots), and percent cover of a given non-native species (1 $m^2$ plots) when it was found in a plot

| Species | Life form[a] | Number of 1000 $m^2$ plots | | Mean percent cover and (S.E.) in the 1 $m^2$ plots | |
|---|---|---|---|---|---|
| | | Cheesman Lake | Turkey Creek | Cheesman Lake | Turkey Creek |
| Forbs | | | | | |
| *Carduus nutans* (nodding plumeless thistle) | B | 1 | 1 | 0.0 (–) | 0.0 (–) |
| *Cerastium fontanum* (common chickweed) | P | 1 | 0 | 0.0 (–) | 0.0 (–) |
| *Chenopodium album* (lambsquarters) | A | 11 | 11 | 0.6 (–) | 0.3 (0.3) |
| *Cirsium arvense* (Canadian thistle) | P | 1 | 1 | 0.0 (–) | 0.9 (–) |
| *Crepis capillaries* (Hawksbeard) | A | 1 | 1 | 0.0 (–) | 0.0 (–) |
| *Kochia scoparia* (ironweed) | A | 0 | 1 | 0.0 (–) | 0.0 (–) |
| *Lactuca serriola* (prickly lettuce) | A | 1 | 0 | 0.7 (–) | 0.0 (–) |
| *Linaria vulgaris* (butter and eggs) | P | 6 | 3 | 1.5 (0.5) | 0.2 (0.2) |
| *Taraxacum officinale* (common dandelion) | P | 9 | 15 | 0.2 (0.1) | 0.3 (0.3) |
| *Thlaspi montanum* (alpine pennycress) | P | 11 | 14 | 0.6 (0.5) | 0.1 (0.0) |
| *Tragopogon dubius* (yellow salsify) | A | 9 | 3 | 0.3 (–) | 0.0 (–) |
| *Verbascum thapsus* (common mullein) | B | 13 | 10 | 0.1 (0.0) | 0.6 (0.1) |
| Grasses | | | | | |
| *Bromus inermis* (smooth brome) | P | 2 | 3 | 0.3 (0.2) | 1.7 (–) |
| *Festuca ovina* (sheep fescue) | P | 6 | 4 | 1.4 (0.5) | 0.4 (0.2) |
| *Poa annua* (annual bluegrass) | A | 0 | 1 | 0.0 (–) | 0.0 (–) |
| *Poa pratensis* (Kentucky bluegrass) | P | 5 | 7 | 2.3 (0.9) | 4.6 (–) |

There were no significant differences in the number of plots containing a given non-native between Cheesman Lake and Turkey Creek. *Verbascum thapsus* had significantly higher percent cover in Turkey Creek ($P < 0.001$); no other differences in percent cover were significant.
[a] Life form: A, annual; B, biennial; P, perennial.

Lake or Turkey Creek. This suggests that these fires may have occurred too long ago for them to still be having a significant impact on non-native species diversity (the year of the last stand-replacing fire recorded by fire scars ranged from 1496 to 1851, and the year of the last known fire ranged from 1587 to 1995). Perhaps patterns of non-native species invasion may be different immediately following such disturbances (i.e., 1 or 2 years after a fire). Distance from the plot to the nearest road was also not a significant predictor of non-native species richness and cover. Perhaps our roads are too lightly traveled to have an impact on exotic species spread. Or, perhaps roads only influence species composition on a very localized spatial scale (i.e., roadsides).

### 4.3. Non-native species composition in protected and managed landscapes

In general, the non-native species invading the managed landscape also are invading the protected landscape. Twelve of the 16 non-native species occurred at both sites. All of the 16 species occurred in a similar number of plots in Cheesman Lake and Turkey Creek. Only one species, *V. thapsus*, had a significantly higher percent cover in Turkey Creek than in Cheesman Lake. This suggests that the species pool of non-natives may be very similar at both sites and that these species are responding to similar environmental factors in establishment and cover.

### 4.4. Implications for management

As the need for restoration of ponderosa pine/Douglas-fir forests in the western United States becomes apparent, the effects of restoration actions (which may include activities such as thinning and prescribed burning) on non-native species invasion are still largely unknown. Results here indicate that perhaps disturbances (including disturbances similar to those used in restoration projects) may not increase plant invasions on a landscape over the long-term. The immediate effects of disturbances in these ecosystems over the short-term (e.g., 1 to 5 years) still need to be investigated.

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