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Evaluating dominance as a component of non-native species invasions

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ABSTRACT

Many studies have quantified plant invasions by determining patterns of non-native species establishment (i.e. richness and absolute cover). Until recently, dominance has been largely overlooked as a significant component of invasion. Therefore, we re-examined a 6-year data set of 323 0.1 ha plots within 18 vegetation types collected in the Grand Staircase-Escalante National Monument from 1998 to 2003, including dominance (i.e. relative cover) in our analyses. We specifically focused on the non-native species *Bromus tectorum*, a notable dominant annual grass in this system. We found that non-native species establishment and dominance are both occurring in species-rich, mesic vegetation types. Therefore, non-native species dominance may result despite many equally abundant native species rather than a dominant few, and competitive exclusion does not seem to be a primary control on either non-native species establishment or dominance in this study. Unlike patterns observed for non-native species establishment, relative non-native species cover could not be predicted by native species richness across vegetation types ($R^2 < 0.001$; $P = 0.45$). However, non-native species richness was found to be positively correlated with relative non-native species cover and relative *B. tectorum* cover ($R^2 = 0.46$, $P < 0.01$; $R^2 = 0.17$, $P < 0.01$). Analyses within vegetation types revealed predominantly positive relationships among these variables for the correlations that were significant. Regression tree analyses across vegetation types that included additional biotic and abiotic variables were a little better at predicting non-native species dominance (PRE = 0.49) and *B. tectorum* dominance (PRE = 0.39) than at predicting establishment. Land managers will need to set priorities for control efforts on the more productive, species-rich vegetation types that appear to be susceptible to both components of invasion.

Keywords

Biological invasions, *Bromus tectorum*, cheatgrass, dominance, Grand Staircase-Escalante National Monument, non-native species.

INTRODUCTION

Contradictory findings among experimental and observational studies conducted across multiple spatial and temporal scales have hindered our ability to determine the major factors controlling species invasion patterns (Levine & D'Antonio, 1999; Stohlgren, 2002). Most small-scale experimental studies have shown species-rich plots to be more resistant to invasion (Robinson *et al.*, 1995; Tilman, 1997; Knops *et al.*, 1999; Levine, 2000; Naeem *et al.*, 2000; Prieur-Richard *et al.*, 2000; Hector *et al.*, 2001; Lyons & Schwartz, 2001; Troumbis *et al.*, 2002), but a lack of resistance in similar experiments has also been seen (Palmer & Maurer, 1997; Crawley *et al.*, 1999; Foster *et al.*, 2002). Few large-scale observational studies have shown a negative relationship between native and non-native species richness (Fox & Fox, 1986; Woods, 1993; Morgan, 1998), whereas a positive relationship has been seen in most cases (Pickard, 1984; Planty-Tabacchi *et al.*, 1996; Stohlgren *et al.*, 1998b, 1999, 2003; Wiser *et al.*, 1998; Lonsdale, 1999; Smith & Knapp, 1999; Levine, 2000; Brown & Peet, 2003). These contradictions may be the consequence of differences in primary controls on invasion at different scales.

At smaller spatial scales, native and non-native species richness may be negatively correlated because of competitive exclusion (Tilman, 1997; Kennedy *et al.*, 2002). At larger spatial scales, the effects of competition are likely masked because of increasing habitat heterogeneity that allows competitors with similar habitat requirements to coexist (Levine & D'Antonio, 1999; Stohlgren, 2002; Jiang & Morin, 2004). Other factors include disturbance, resource availability and productivity. Disturbance increases susceptibility to invasion (Fox & Fox, 1986; Hobbs, 1989; Hobbs

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& Huenneke, 1992); resource availability hinders and promotes invasion (Luken & Goessling, 1995; Hutchinson & Vankat, 1997; Stohlgren *et al.*, 1998b); and productivity, as measured by some of these other factors, also hinders and promotes invasion. It has even been suggested that differences among experimental and observational studies could be a result of differences in how invasion is measured (Cleland *et al.*, 2004). For example, many observational studies determine invasion by measuring non-native richness (i.e. a measure of establishment), whereas most experimental studies measure invasion by quantifying non-native species biomass (i.e. a measure of dominance).

Recently, several studies have emphasized the importance of including some measure of dominance and establishment in these types of analyses to better understand the invasion patterns we observe (Huston, 2004; Lundholm & Larson, 2004). The likelihood of a non-native species becoming dominant in a vegetation type is an even greater concern than a non-native establishing because dominance could result in a decline in native diversity. Analyses of establishment and dominance might also provide different insights as to the extent of an invasion because different controls on these parameters likely exist (Lundholm & Larson, 2004).

Including dominance as a measure of invasion success may provide valuable information to land managers seeking to control and manage ubiquitous non-native species across landscapes. Many non-native plant species have invaded regions to such an extent that they are impossible to control with limited resources (Rejmánek, 2000). Thus, it may be necessary to look beyond presence/absence predictions toward predictions of dominance for these species. Specifically, determining what factors allow a species to move from being a relatively rare, established species to a dominant member of a vegetation type could be important in guiding mitigation efforts to areas with conditions that promote dominance.

Native diversity theory suggests that dominance is most likely to occur in highly productive environments with limited disturbance. Species richness typically declines in these habitats where a superior competitor dominates (Grime, 1973a,b; Huston, 1979). Huston (2004) theorized that native and non-native species should respond similarly to environmental conditions and should have increased establishment and dominance in productive vegetation types. However, it is likely that analyses of dominance would also vary at different spatial and temporal scales and in different areas. For example, in arid regions with constrained productivity and frequent disturbances, species richness is highest in areas of greater productivity (i.e. mesic vegetation types; Stohlgren *et al.*, 2001; Waters, 2003).

Few studies have included a measure of dominance in their analyses of invasion patterns. De Gruchy *et al.* (2005) found that although non-native species biomass increased as habitat productivity increased, productivity could not predict non-native species dominance, and concluded that disturbance history might have more impact than diversity or productivity on invasion. Cleland *et al.* (2004) showed that native richness was negatively correlated with non-native abundance. While non-natives were more likely to establish in species-rich vegetation types, their success declined as a result of lowered resource availability in these communities. An experimental study in tallgrass prairie also concluded that dominance, not richness, had a greater effect on the invasibility of the community (Smith *et al.*, 2004).

To determine what additional insight non-native species dominance may provide to previously defined non-native species invasion patterns in the field, we re-examined a highly published data set collected from Grand Staircase-Escalante National Monument in southern Utah over a 6-year period from 1998 to 2003 (summarized in Stohlgren *et al.*, 2005). Analyses of the data set in previous studies focused primarily on non-native species establishment, examining patterns of non-native species richness and absolute cover. Patterns remained consistent across studies, with resource-rich, species-rich vegetation types having greater susceptibility to non-native species establishment. Our primary objectives were to: (1) investigate non-native species dominance (i.e. relative cover) in this arid landscape as a component of invasion and (2) to compare these findings to previous studies of establishment. *Bromus tectorum* was found in 68% (261 of 386) of our plots and represented > 80% of relative non-native cover in half of our vegetation types. Thus, focusing on this generalist invader provided a great way to quantify potential dominance of a single invading species.

Our hypotheses included: (1) Non-native species and *B. tectorum* dominance would be greatest in more productive, species-rich and mesic vegetation types. (2) Native species richness and non-native species richness would be positively correlated with relative non-native species cover across vegetation types (this relationship could be positive or negative within vegetation types). (3) Because *B. tectorum* is a dominant generalist in the Monument, a regression tree model would be able to predict *B. tectorum* dominance better than *B. tectorum* establishment. (4) Predictors of non-native and *B. tectorum* dominance would differ from those of establishment.

METHODS

Study area

The Grand Staircase-Escalante National Monument consists of 849,870 ha of remote land in southern Utah, ranging in elevation from 1372 to 2530 m (Grand Staircase-Escalante National Monument, 2000). The climate of the region is generally temperate and arid with average annual precipitation approaching 250 mm. Mean summer temperatures and winter temperatures range from 16 °C to 32 + °C and −9 °C to 4 °C, respectively (National Climatic Data Center, 2003).

Field sampling

From 1998 through 2003, 379 modified Whittaker vegetation plots were established within 18 vegetation types using a stratified random sampling design (Table 1; Stohlgren *et al.*, 1995, 1998a). Each modified Whittaker plot covers 1000 m^2 (20×50 m) and contains 10×1 m^2, 2×10 m^2 and 1×100 m^2 nested subplots.

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Table 1 Summary statistics (standard error in parentheses) by vegetation type. The final column gives the percentage of relative non-native species cover represented by *Bromus tectorum* (BRTE)

Vegetation type	*n*	Native richness	Relative native cover (%)	Non-native richness	Relative non-native cover (%)	Relative BRTE cover (%)	Relative BRTE cover/ Relative non-native cover (%)
Mountain shrub	11	30 (2.2)	97 (1.6)	1.2 (0.26)	3.4 (1.6)	2.3 (1.5)	68
Desert shrub/Grassland	16	26 (1.7)	87 (3.7)	1.4 (0.26)	13 (3.7)	8.5 (2.2)	65
Pinyon–juniper	81	26 (0.83)	98 (0.74)	0.70 (0.09)	1.8 (0.7)	0.89 (0.32)	49
Desert shrub	29	22 (1.5)	90 (2.2)	1.8 (0.23)	9.8 (2.2)	6.2 (1.7)	63
Juniper	21	29 (1.7)	97 (1.3)	1.3 (0.17)	3.0 (1.3)	2.4 (0.99)	80
Juniper/sage	10	23 (2.0)	87 (4.9)	2.4 (0.67)	13 (4.9)	12 (4.3)	92
Pinyon–juniper/Sage	25	23 (1.2)	98 (0.7)	1.2 (0.21)	1.9 (0.7)	1.9 (0.71)	100
Sagebrush	32	20 (1.6)	89 (2.4)	1.7 (0.24)	11 (2.4)	6.0 (1.6)	55
Ponderosa pine/Manzanita	7	28 (2.1)	99 (0.8)	0.57 (0.2)	1.3 (0.8)	1.3 (0.85)	100
Blackbrush	24	21 (1.3)	93 (2.2)	1.3 (0.18)	6.8 (2.2)	6.1 (2.1)	90
Pinyon pine	4	26 (4.6)	93 (5.5)	1.3 (0.48)	7.1 (5.5)	7.1 (5.5)	100
Pinyon–juniper/Oak	16	32 (2.2)	99 (0.5)	1.1 (0.4)	1.1 (0.5)	0.76 (0.36)	69
Pinyon–juniper/Manzanita	6	36 (1.9)	100 (0.2)	0.33 (0.21)	0.29 (0.2)	0.29 (0.21)	100
Rabbitbrush	9	25 (1.5)	87 (6.2)	3.0 (0.62)	13 (6.2)	11 (6.3)	85
Aspen	6	33 (3.1)	88 (3.4)	4.7 (0.96)	12 (3.4)	10 (2.9)	83
Wet meadow	3	33 (5.4)	57 (11)	6.7 (0.88)	43 (11)	3.3 (2.1)	8
Perennial riparian	21	25 (2.2)	70 (5.1)	6.0 (0.4)	30 (5.1)	4.2 (1.8)	14
Spring	2	40 (4.0)	84 (14)	6.5 (14)	16 (14)	0.08 (0.08)	<1

Only data from the 1000-m^2 plots and 1-m^2 subplot were used in this study.

Presence of each species was noted in the 1000-m^2 plot (Stohlgren *et al.*, 1995). In the 1-m^2 subplots, absolute foliar cover of each species (%) and percentage cover of microbiotic crust by development stage were recorded. To determine development stage, we modified the National Park Service Soil Crusts Condition Assessment Index that details the stages of well-developed crusts (US Department of the Interior, 1995). With this index, the developmental stage of cryptobiotic crusts was recorded in eight classes from 1 (i.e. weakly developed) to 20 (i.e. fully developed; see Belnap, 1995, 1996). To simplify these classes for this study, cover values of weakly developed crusts were summed (i.e. classes 1, 2, 4, 6) and the cover values of fully developed crusts were summed (i.e. classes 10, 15, 20). A crust cover value of 0 indicated that no cryptobiotic crust was present.

Plants were sampled during peak phenology of most species; species not identified in the field were collected for later identification. Ancillary data recorded for each plot included elevation and UTM coordinates. In addition, five soil samples were taken from the corners and centre of each plot with a 2.5-cm diameter soil increment core to depths of 15 cm. These five soil samples were then pooled into one composite sample.

Three Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) summaries from a 3-year period (2001–03) of MODIS vegetation index product version 4 were provided for the study area. Although these dates do not completely overlap with those of the sampling, unpublished analysis examining dates of LandSat imagery has indicated that, unless it is an extreme weather year, the date of imagery and sampling do not need to match to still provide predictive capabilities. NDVI and EVI vegetation indices are calculated using the infrared, red and blue bands that contain information on vegetation as a measure of photosynthetic activity and biomass. The Fourier-fit method was used to summarize the data in three ways including average range in values per year derived from the amplitude, the date of peak value from the average data of peak vegetation (biomass) over the 3 years, and the average value over the 3 years. The range values indicate the variation in 'greenness' each year averaged over the 3 years and are a measure of the difference in vegetation seen between summer and winter months. The average date of peak indicates differences in the timing of peak vegetation, whereas the average values indicate differences in overall vegetation biomass.

Soil analyses

After conducting field sampling, soil samples were brought back to the laboratory and air dried for at least 48 h before analysis. Soil preparation involved sieving each sample using a standard no. 10 sieve (i.e. 2 mm pore size) and grinding a subset of each sieved sample. For texture analysis, a portion of each sieved sample was analysed using the standard hydrometer method to determine the percentage of sand, silt and clay content (Gee & Bauder, 1986). For chemical analyses, ground subsamples of soil were oven-dried at 55 °C for 24 h. Samples were analysed for percentage of total carbon and nitrogen using a LECO-1000 CHN analyser (Carter, 1993), and inorganic carbon from carbonates was determined using a volumetric method (Wagner *et al.*, 1998). Organic carbon was then calculated by subtracting the inorganic carbon

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from the total carbon value. Soil phosphorus was determined colourimetrically from a sodium bicarbonate extraction (Kou, 1996). Samples were analysed for the micronutrients potassium (K), magnesium (Mg), calcium (Ca) and sodium (Na) using inductively coupled plasma emission spectrometry.

Statistical analyses

All statistical analyses were conducted using SYSTAT (version 11.0, SSI Inc., Richmond, CA, USA), and $P < 0.05$ was used to determine significance in all tests. Missing auxiliary data for some of the plots and the removal of plots in highly disturbed vegetation types (i.e. chained, seeded, burned) reduced our sample size to 323 0.1-ha plots. All variables were assessed for normality and transformed using $\log_{10}(x+1)$ transformations when needed.

Average cover values were calculated for each plot by summing cover values for each 1-m^2 subplot and dividing by 10. Relative non-native cover and relative *B. tectorum* cover were calculated by dividing the average cover value of all non-natives and that of *B. tectorum* by the average total vegetation cover in each plot. Relative non-native cover excluding *B. tectorum* was calculated in a similar manner, excluding *B. tectorum* in all calculations. Summary statistics (i.e. mean, standard error) were then calculated for average relative non-native and *B. tectorum* cover by vegetation type. In addition, we calculated the percentage of relative non-native cover represented by *B. tectorum*.

Plots were then divided into mesic and xeric vegetation types to examine differences in vegetation parameters under dry and wet conditions (Table 1). Simple *t*-tests were performed to test for significant differences ($P < 0.05$) between relative non-native cover and relative *B. tectorum* cover in mesic and xeric vegetation types. Simple linear regressions were also plotted for relative non-native cover and relative *B. tectorum* cover on native richness and relative non-native cover and relative *B. tectorum* cover on non-native richness to quantify relationships between these parameters within and across vegetation types.

Regression tree analyses were used to determine predictors of relative non-native species and *B. tectorum* cover. All independent variables were tested for correlations, and highly cross-correlated variables were not included in the analysis ($r \pm 0.8$; Bonferroni tests). The regression tree for relative non-native species cover was developed using 14 independent variables (i.e. native and non-native species richness; elevation; percentage cover without cryptobiotic crusts, with weakly developed cryptobiotic crusts, and with well-developed cryptobiotic crusts; average native plant species cover; percentage of sand; NDVI average, range, and average date of peak; EVI average, range, and average date of peak; percentage of organic carbon and nitrogen; and phosphorus). The regression tree for relative *B. tectorum* cover was developed using these same 14 independent variables with the addition of average non-native plant species cover excluding *B. tectorum*. Proportion of reduction in error (PRE) values, similar to R^2 values in regression, were used to determine the amount of variation explained by the independent variables in each model (Hansen *et al.*, 1996).

RESULTS

All *t*-tests comparing mesic to xeric vegetation types were significant ($P < 0.05$). For relative non-native species cover, the *t*-test showed that the mesic vegetation types had significantly greater relative non-native species cover (24 ± 3.4%) than the xeric vegetation types (5.3 ± 0.6%). The mesic wet meadow vegetation type had the highest value of relative non-native species cover overall (43%), and the xeric pinyon–juniper/manzanita vegetation type had the lowest value (0.29%; Table 1). The mesic vegetation types also had significantly greater relative *B. tectorum* cover (6.3 ± 1.7%) than the xeric vegetation types (3.6 ± 0.4%). However, when looking at individual means within vegetation types, the mesic spring type had the lowest value of relative *B. tectorum* cover (0.08%), whereas the xeric juniper/sage type had the highest value (12%; Table 1).

These results were consistent with our first hypothesis that dominance would be greatest in species-rich vegetation types, so we examined this pattern further by calculating relative cover values by species within the mesic vegetation types. The wet meadow vegetation type had the third greatest number of native species while also having the greatest number of non-native species and greatest relative non-native cover value. Further analysis indicated that 7 of the 18 (39%) non-native species that were found in wet meadows had relative cover values above 1%. The perennial riparian vegetation type also had high native and non-native species richness and non-native dominance, but only 3 of 49 (6%) non-native species found within this vegetation type had relative cover values above 1%. Only 2 of 19 (11%) species in the rabbitbrush type, 5 of 22 (23%) in aspen, and only 1 of 16 (6%) in the spring vegetation type had a relative cover value above 1%. Similar patterns were seen for native species, with the wet meadow, perennial riparian, rabbitbrush, aspen and spring vegetation types having 15% (12 of 79), 7% (17 of 225), 13% (17 of 130), 22% (24 of 111) and 11% (7 of 64), respectively, of their total number of native species with relative cover values greater than 1%.

Bromus tectorum represented 100% of the relative non-native cover in four xeric vegetation types (i.e. pinyon–juniper/sage, ponderosa pine/manzanita, pinyon pine and pinyon–juniper/manzanita; Table 1). These vegetation types generally had low non-native species richness, and with the exception of the pinyon pine vegetation type, these vegetation types had relative non-native cover values below 2%. Half of the vegetation types had more than 70% of their relative non-native cover represented by *B. tectorum*. The juniper/sage, rabbitbrush and aspen vegetation types had high relative non-native cover values and more than 80% of their relative non-native cover was represented by *B. tectorum*.

The linear regressions of relative non-native cover and relative *B. tectorum* cover to native richness across vegetation types were not significant ($P > 0.05$; Fig. 1). However, the regression of relative non-native cover and relative *B. tectorum* cover to non-native richness across vegetation types were highly significant ($P < 0.05$) and positively correlated with R^2 values of 0.46 and 0.17, respectively (Fig. 1). Within vegetation types, linear regressions of relative

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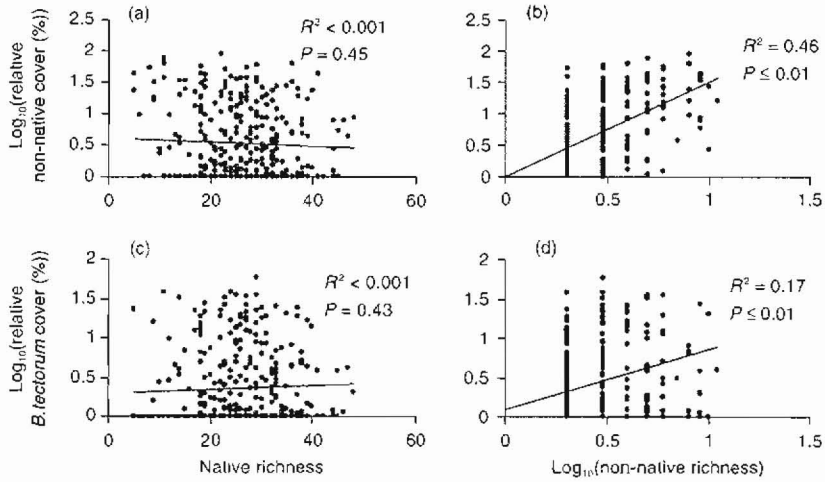

Figure 1 Linear regressions for relative non-native cover on native richness (a), relative non-native cover on non-native richness (b), relative *Bromus tectorum* cover on native richness (c), and relative *B. tectorum* cover on non-native richness (d) across vegetation types.

Table 2 Linear regression resnlts within vegetation types for relative non-native cover on native richness, relative non-native cover on non-native richness, relative *Bromus tectorum* (BRTE) cover on native richness and relative *B. tectorum* cover on non-native richness. A + or – indicates a positive or negative correlation between the two variables. An 'ns' indicates no significance. Regression analysis could not be performed on the spring vegetation type due to a small sample size ($n = 2$)

	Relative non-native cover and native richness			Relative non-native cover and non-native richness			Relative BRTE cover and native richness			Relative BRTE cover and non-native richness		
Vegetation type	+/–	R^2	P	+/–	R^2	P	+/–	R^2	P	+/–	R^2	P
Mountain shrub	+	0.00	ns	+	0.24	ns	–	0.00	ns	+	0.00	ns
Desert shrub/grassland	–	0.03	ns	+	0.36	0.01	+	0.00	ns	+	0.47	< 0.01
Pinyon–juniper	+	0.00	ns	+	0.23	< 0.01	+	0.00	ns	+	0.16	< 0.01
Desert shrub	–	0.00	ns	+	0.41	< 0.01	+	0.00	ns	+	0.12	0.04
Juniper	+	0.06	ns	+	0.10	ns	+	0.05	ns	+	0.03	ns
Juniper/Sage	–	0.12	ns	+	0.17	ns	–	0.13	ns	+	0.06	ns
Pinyon–juniper/Sage	+	0.03	ns	+	0.10	ns	+	0.02	ns	+	0.09	ns
Sagebrush	–	0.00	ns	+	0.27	< 0.01	+	0.02	ns	+	0.07	ns
Ponderosa pine/Manzanita	+	0.53	0.04	+	0.23	ns	+	0.53	0.04	+	0.15	ns
Blackbrush	–	0.00	ns	+	0.50	< 0.01	–	0.00	ns	+	0.52	< 0.01
Pinyon pine	+	0.99	< 0.01	+	0.42	ns	+	0.99	< 0.01	+	0.42	ns
Pinyon–juniper/Oak	+	0.18	ns	+	0.64	< 0.01	+	0.23	0.04	+	0.56	< 0.01
Pinyon–juniper/Manzanita	–	0.30	ns	+	0.77	0.01	–	0.30	ns	+	0.77	0.01
Rabbitbrush	+	0.38	0.04	–	0.00	ns	+	0.19	ns	–	0.05	ns
Aspen	–	0.00	ns	+	0.00	ns	–	0.08	ns	+	0.00	ns
Wet meadow	+	0.20	ns	+	0.18	ns	+	0.28	ns	+	0.26	ns
Perennial riparian	–	0.39	< 0.01	–	0.05	ns	+	0.00	ns	–	0.00	ns
Spring	.	.	.		.	.		.	.	.	.	.

non-native cover to native richness were only significant for four vegetation types (i.e. ponderosa pine/manzanita, pinyon pine, rabbitbrush and perennial riparian). The two variables were positively correlated except for the perennial riparian vegetation type (Table 2). Linear regressions of relative *B. tectorum* cover to native richness produced three significant relationships, all positive (i.e. ponderosa pine/manzanita, pinyon pine, pinyon–juniper/oak; Table 2). For the linear regressions of relative non-native cover to non-native richness, there were seven significant, positive relationships for seven vegetation types (i.e. desert shrub/grassland, pinyon–juniper, desert shrub, sagebrush, blackbrush, pinyon–juniper/oak, pinyon–juniper/manzanita; Table 2). For the regressions of *B. tectorum* to non-native richness, six positive significant relationships were seen between the two variables within these same vegetation types, excluding sagebrush (Table 2).

The regression tree for relative non-native cover identified non-native species richness and average absolute native cover as significant predictors, accounting for 49% of the variation (Fig. 2). The first split of the regression tree found that if non-native species richness within a plot was above 3.0 non-native species/plot, then relative non-native cover was almost six times

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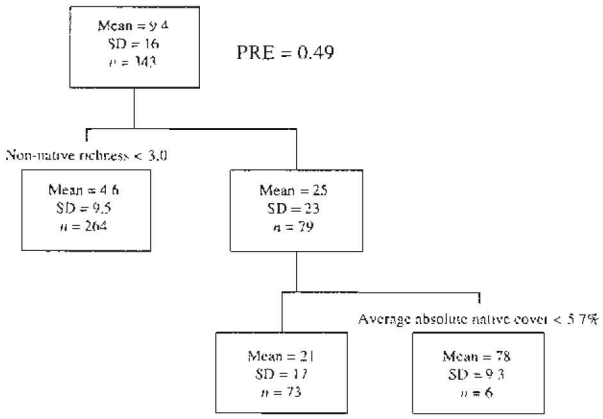

Figure 2 Regression tree for relative non-native cover (%) across vegetation types, including mean, standard deviation (SD), and sample size (n) for each break.

higher than areas with lower non-native species richness. The second split of the tree showed that when average absolute native cover fell below 5.7%, relative non-native cover values were over three times greater.

Regression tree analysis for relative *B. tectorum* cover identified five significant predictors, accounting for 39% of the variation in relative *B. tectorum* cover (Fig. 3). The first split of the regression tree found that phosphorus values above 5.1 p.p.m. increased relative *B. tectorum* cover threefold. Phosphorus values above 5.1 p.p.m., lower elevations (< 1426 m) and high native species richness (> 23) were significant variables in predicting high relative *B. tectorum* cover.

DISCUSSION

This data set provided us with a great opportunity to examine how both establishment and dominance can further our understanding of non-native species invasion patterns. We were able to greatly inferences on the patterns and predictors of establishment previously published (see Stohlgren *et al.*, 2005) to those of dominance examined here. An important caveat to note when examining our results (and the results of most field studies) is that these data are temporally constrained. Withont a detailed land use history, it is difficult to determine the stage of invasion these plots are in, or how establishment and dominance have been manipulated through time by disturbance or recruitment. However, the Monument has not been isolated from distnrbance and has a large non-native seed source, so it is unlikely that any of our results are a product of a short invasion history. In addition, by removing the few highly disturbed plots from the analyses, we were also able to examine patterns in the absence of severe, large-scale disturbances.

Patterns of establishment vs. dominance

Productivity is most correlated with water in arid environments (Barbour *et al.*, 1987), so our analysis of mesic vs. xeric vegetation types provided a way to examine patterns of dominance under different levels of productivity. Consistent with our first hypothesis, we found non-native species dominance was most likely to occur in highly productive, mesic environments. We previously found greater native and non-native species establishment in the most productive vegetation types that have greater moisture and soil fertility (Bashkin *et al.*, 2003; Chong *et al.*, 2005). It is likely that plentiful resources, numerous small-scale

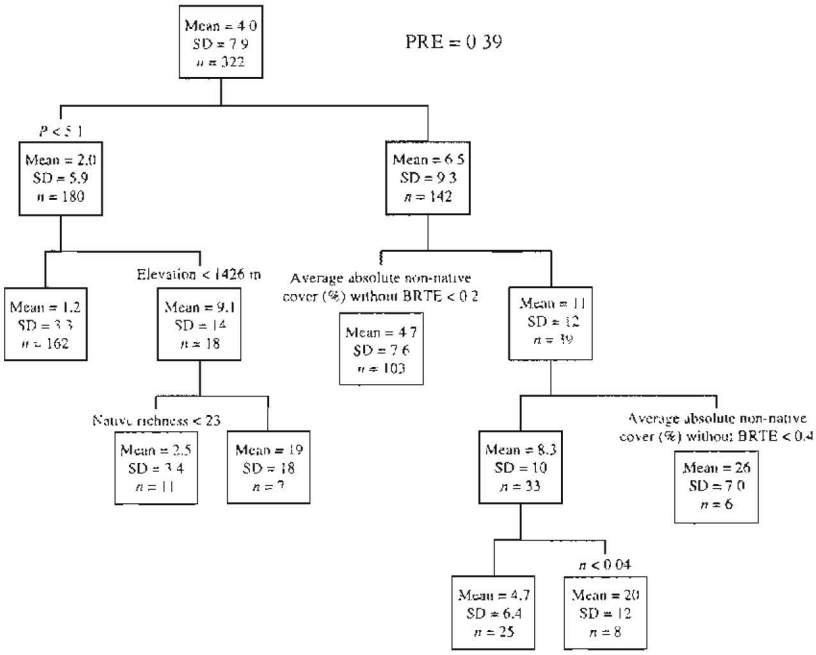

Figure 3 Regression tree for relative *Bromus tectorum* (BRTE)cover (%) across vegetation types, including mean, standard deviation (SD), and sample size (n) for each break.

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disturbances, and microhabitat heterogeneity promote coexistence rather than competitive displacement in these habitats.

In addition, these results may be because of the low species frequencies at neighbourhood scales (i.e. 1-m^2 scales). Several recent studies that examined patterns of species establishment across large spatial scales found that most plant species are locally rare and patchily distributed, a pattern similar to that of dominance seen here (Mistry *et al.*, 1999; Hubbell, 2001; Stohlgren, 2002). In the Monument specifically, 189 plant species occurred in only one or two plots and 62% of the flora can be considered locally rare (Stohlgren *et al.*, 2005). In this study, only a few species are able to utilize resources to such an extent that they occupy more than 1% of the total vegetation cover in any vegetation type. Few species are able to achieve dominance, while many species are able to coexist and contribute small amounts to total relative cover.

Similar to non-native species dominance, *B. tectorum* dominance was greatest in the mesic habitats. This finding was primarily driven by the percentage of relative non-native cover represented by *B. tectorum* in both the aspen and the rabbitbrush vegetation types (Table 1). In addition to the high availability of resources (Young *et al.*, 1987), the high relative cover of this species in these species-rich vegetation types may be the result of its life traits. *Bromus tectorum* may decrease native species richness through below-ground competition if its root system acquires water and nutrient resources earlier than other non-established perennials (Young & Evans, 1985; Davidson & Belnap, 1998). In the vegetation types studied, there may be enough moisture to minimize this potential competitive advantage of *B. tectorum*. Bilodeau (2001) found that *B. tectorum* dominance was dependent on the availability of moisture throughout the summer months. If enough moisture was available at this time, *B. tectorum* only decreased the biomass of native perennials, but it did not prevent their establishment.

As with any attempt to generalize an ecological complexity, exceptions to these patterns were found. When looking within vegetation types, we found non-native species dominance was low in areas of high species richness and vice versa. The pinyon–juniper/manzanita and pinyon–juniper/oak vegetation types had high native species, but had low non-native species richness and relative cover. It is likely that these large native perennial trees and shrubs are monopolizing light, water and nitrogen to reduce resource availability to potential non-native invaders, making it difficult for non-native plant species to establish and persist in these particular vegetation types (Stohlgren *et al.*, 1999). In contrast, the juniper/sagebrush and desert shrub vegetation types had low species richness values and high relative non-native cover values. A high percentage of *B. tectorum* contributed to this pattern, perhaps due to past fires or other factors (Young & Evans, 1973; Rosentreter & Jorgenson, 1986; Caldwell & Richards, 1989; Pierson & Wight, 1991). As *B. tectorum* gains dominance in these habitats, native species richness could be further reduced through competition or changes in the fire regime (Wright, 1985).

Exceptions to the overall general pattern of high dominance in areas of high species richness underscore the need for relative cover calculations to determine the extent of invasion. Although the mesic vegetation types had greater non-native dominance, this pattern had the potential to reverse when looking within vegetation types. We recommend the inclusion of some measure of dominance when determining invasion patterns and when taking a habitat or species approach due to these important exceptions at smaller scales.

Can plant species richness predict dominance?

Three fairly consistent findings suggest that plant species richness may predict dominance. First, as with earlier studies, we and others continue to find positive relationships between native and non-native species richness (Stohlgren *et al.*, 1998b, 1999, 2001; Lonsdale, 1999; Brown & Peet, 2003). Second, we continue to find positive relationships between non-native richness and absolute cover (Fig. 1; Stohlgren *et al.*, 1998b, 2001). Third, we consistently find positive relationships between resource availability (e.g. light, water, soil nutrients) and the cover of native and non-native species (Stohlgren *et al.*, 1998b, 1999, 2001). The patterns observed in this study partially supported our hypothesis that native and non-native species richness would be positively correlated with relative non-native species cover across vegetation types. Although non-native and *B. tectorum* dominance were positively correlated with non-native richness, there was no significant relationship between non-native and *B. tectorum* dominance and native species richness.

The patterns we are seeing here may be a product of the study area's stages of invasion succession. As non-native species establishment and biomass increase, native species richness or biomass could decline or may have already declined prior to any given survey. A study by Meiners *et al.* (2002) found a decline in non-native species richness and an increase in native species richness with increased canopy closure (> 20 year after old field abandonment) in an area that initially had non-native species representing > 50% of vegetation richness and cover. Many forested areas may have decreased the success of early successional, shade-intolerant species, which are common life history traits of non-native species in the study area. Therefore, we might find a positive correlation, no correlation, and possibly a negative correlation between native species richness and non-native dominance over time related to successional stage (Stohlgren, 2002). Monitoring relationships over time may provide additional insight into the patterns reported here since we may be witnessing the early stages of a much longer invasion process.

The many positive correlations among non-native species and *B. tectorum* dominance and native and non-native species richness are worrisome, especially given the mandate to protect native biodiversity. Increased *B. tectorum* dominance was associated with the establishment of non-native species, a pattern reflected across vegetation types that suggests a regional invasion. The perennial riparian vegetation type may be in a more advanced stage of invasion. It was the only one that showed a negative correlation between relative non-native cover and native richness. Invasion by highly competitive, non-native perennial trees such

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as *Tamarisk* sp. and *Elaeagnus angustifolia* may be reducing native species richness in this vegetation type.

Predictability of establishment vs. dominance

Unlike non-native species establishment, non-native species dominance could not be predicted by native species richness across vegetation types. However, adding biotic and abiotic variables explained almost half of the variation seen in non-native species dominance, and our regression tree analysis was used to try and determine these variables (Fig. 3). Additional field and remote sensing information may improve these predictions.

As hypothesized, different predictor variables were associated with non-native species establishment and dominance even though both of these invasion components were occurring in species-rich, mesic vegetation types. In our study area, and perhaps in other areas, establishment was more predictable than dominance. Robust plant growth and reproduction obviously takes place in a subset of establishment sites. Our results also explained 39% of the variation in *B. tectorum* dominance (Fig. 3). Although this is an improvement over the establishment model, other factors such as disturbance and seed sources may be important (De Gruchy *et al.*, 2005).

Management implications

Generalizing the ecological complexities associated with non-native species and their invasion patterns is a daunting task. Productive, species-rich vegetation types seem to be the most susceptible to non-native species establishment and dominance. This is an alert to many land managers seeking to focus their native species conservation and non-native species control efforts. Although no significant relationship currently exists between non-native and *B. tectorum* dominance and native species richness, these relationships may change following wildfires or as new non-native species establish that have the potential to alter the ecosystem they have invaded over time. Early detection and rapid response programs may be more cost-effected if targeted at areas of potential dominance. Likewise, control programs may be further targeted to infestations in highest quality potential dominance sites, and clusters of such sites because of seed source potential. This emphasizes the need for a long-term monitoring effort combined with remote sensing and spatial modelling (e.g. Chong *et al.*, 2001) to implement a proactive rather than a reactive control strategy.

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