Species' traits help predict small mammal responses to habitat homogenization by an invasive grass

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Abstract. Invasive plants can negatively affect native species, however, the strength, direction, and shape of responses may vary depending on the type of habitat alteration and the natural history of native species. To prioritize conservation of vulnerable species, it is therefore critical to effectively predict species' responses to invasive plants, which may be facilitated by a framework based on species' traits. We studied the population and community responses of small mammals and changes in habitat heterogeneity across a gradient of cheatgrass (*Bromus tectorum*) cover, a widespread invasive plant in North America. We live-trapped small mammals over two summers and assessed the effect of cheatgrass on native small mammal abundance, richness, and species-specific and trait-based occupancy, while accounting for detection probability and other key habitat elements. Abundance was only estimated for the most common species, deer mice (*Peromyscus maniculatus*). All species were pooled for the trait-based occupancy analysis to quantify the ability of small mammal traits (habitat association, mode of locomotion, and diet) to predict responses to cheatgrass invasion. Habitat heterogeneity decreased with cheatgrass cover. Deer mouse abundance increased marginally with cheatgrass. Species richness did not vary with cheatgrass, however, pocket mouse (*Perognathus* spp.) and harvest mouse (*Reithrodontomys* spp.) occupancy tended to decrease and increase, respectively, with cheatgrass cover, suggesting a shift in community composition. Cheatgrass had little effect on occupancy for deer mice, 13-lined ground squirrels (*Spermophilus tridecemlineatus*), and Ord's kangaroo rat (*Dipodomys ordii*). Species' responses to cheatgrass primarily corresponded with our a priori predictions based on species' traits. The probability of occupancy varied significantly with a species' habitat association but not with diet or mode of locomotion. When considered within the context of a rapid habitat change, such as caused by invasive plants, relevant species' traits may provide a useful framework for predicting species' responses to a variety of habitat disturbances. Understanding which species are likely to be most affected by exotic plant invasion will help facilitate more efficient, targeted management and conservation of native species and habitats.

Key words: community ecology; conservation; demography/life history; disturbance; grasses; mammals; North America; prairie/grasslands; rodents; species interactions.

Introduction

Plant community composition and structure are critical components of habitat and drivers of wildlife population and community patterns (Rotenberry 1985, Morrison et al. 2006). Disturbances such as fire or insect outbreaks can cause rapid and widespread changes in vegetation that may lead to shifts in wildlife populations and communities (Griffiths and Brook 2014, Saab et al. 2014). A pervasive and intensifying form of disturbance that can vastly alter wildlife habitat is nonnative species invasion (Crooks 2002, Simberloff et al. 2013). Invasive species threaten biodiversity worldwide and are considered the most significant conservation threat after habitat loss and fragmentation (Wilcove et al. 1998). Invasive plants, for example, can have direct and indirect effects on wildlife by replacing heterogeneous native plant communities with communities of highly simplified composition and structure (D'Antonio and Vitousek 1992, Vila et al. 2011). Habitat homogenization due to invasive plants and other drivers of habitat change can have a profound influence on local wildlife communities (Fuhlendorf et al. 2006, 2010, Vila et al. 2011). Understanding how species respond to habitat alteration by invasive plants, and which species or guilds are most vulnerable to such changes, is therefore critical.

Nonnative plants are commonly presupposed to have a negative impact on native animals and there is limited recognition of the potential for neutral or positive effects (Davis et al. 2011, however, see Vitule et al. 2012). There is increasing evidence, however, that responses to

invasive species depend on (1) the contrast between the composition and structure of the pre- and post-invaded plant community and (2) whether a native species' traits, such as natural history characteristics, predispose it to succeed or fail in the altered habitat (Crooks 2002, Martin and Murray 2011, Sih et al. 2011, Litt and Pearson 2013). These criteria may provide the foundation for a framework to improve prediction of native species' responses to invasive plants, and thus enable targeted conservation of species expected to be most vulnerable to particular habitat changes (Crooks 2002, Martin and Murray 2011). Few studies, however, have explicitly used species' traits in an a priori framework to predict animal responses to habitat alteration by nonnative plants (see Ehlers Smith et al. [2015] for an example in an agricultural system). Wildlife responses to invasive plants, moreover, may be non-linear, yet most studies have modeled the effect of invasive plants as binary rather than continuous, which can preclude the detection of nonlinear relationships such as thresholds (van Riper et al. 2008, Litt and Pearson 2013).

Habitat requirements, behavior, and morphology are likely important proximate factors influencing how native species respond to rapid environmental changes, such as from fire, grazing, or nonnative plant invasion (Crooks 2002, Fuhlendorf et al. 2006, Martin and Murray 2011, Sih et al. 2011). Responses to invasive plants have varied with habitat associations for many taxa, including small mammals (Litt and Steidl 2011), birds (Rogers and Chown 2014), insects (Steenkamp and Chown 1996), and amphibians (Mott et al. 2010). Microhabitats in nonnative pine plantations in Australia, for example, are cooler and moister than in native forests due to a planting pattern that creates a closed canopy (Mott et al. 2010). Community composition of reptiles shifted accordingly from open woodland species to closed-canopy species adapted to cooler microhabitats. Dietary requirements may also mediate animal responses to habitat change as the quality and relative abundance of food sources, such as native plant species and insects, may shift (Ortega et al. 2006, Litt and Steidl 2010, Pearson et al. 2011). Dense cover created by invasive plants can also impede movement for small mammals, birds, lizards, and likely insects (Steenkamp and Chown 1996, Litt and Steidl 2010, Rieder et al. 2010, Martin et al. 2015), which may inhibit foraging and predator avoidance. The extent to which movement is hindered can depend on body type and locomotion style, with larger hopping (saltatorial) vertebrates, for example, affected more than smaller running (cursorial) vertebrates (Rieder et al. 2010). Habitat alteration by disturbances such as invasive plants may thus favor particular types of native species over others (Crooks 2002).

Cheatgrass (*Bromus tectorum*) is a widespread invasive annual grass in North America that can drastically alter the structure and composition of wildlife habitat. Cheatgrass was introduced to North America predominately from Europe (Novak and Mack 2001), and has affected at least 40 000 km^2 of wildlife habitat in the Great Basin, USA alone (Bradley and Mustard 2005). Cheatgrass transforms habitats by replacing heterogeneous native plant communities with dense, homogeneous, grass cover (Knapp 1996). The continuous grass cover increases the frequency and extent of fires, which favors cheatgrass over native species, thereby creating a positive feedback loop (Balch et al. 2013). Cheatgrass may also benefit from increased CO_2 levels and altered precipitation patterns due to climate change, which could cause additional range expansions (Smith et al. 2000, Bradley 2009). Understanding and predicting the consequences of cheatgrass invasion for wildlife is therefore timely.

Small mammal abundance and diversity tend to decrease with increasing cheatgrass cover, however, responses often vary across species (e.g., Steenhof et al. 2006, Ostoja and Schupp 2009, Freeman et al. 2014). Understanding the consequences of invasive plants for small mammals is particularly important because small mammals regulate plant communities (Brown and Heske 1990, Bricker et al. 2010), improve soil quality (Fleming et al. 2014), and host zoonotic diseases (Ostfeld et al. 1996, Mills et al. 1999). Small mammals are also essential prey for many predators, including birds (Korpimaki and Norrdahl 1991), mammals (White et al. 1996), and reptiles (Madsen and Shine 2000).

Our objectives were threefold, to (1) quantify how cheatgrass altered habitat heterogeneity, (2) examine how small mammal abundance, species richness, and occupancy changed across a gradient of cheatgrass cover while accounting for other important habitat features, and (3) assess the efficacy of three focal traits—habitat association, diet preference, and locomotion style—to predict species' responses to cheatgrass cover (Table 1). We predicted that cheatgrass would be negatively associated with open habitat and saltatory species because the dense grass cover may impede movement (Rieder et al. 2010). Conversely, closed habitat and cursorial species may benefit from or be unaffected by the increased escape cover provided by cheatgrass (Rieder et al. 2010, Johnson and De León 2015). Green cheatgrass vegetation (in the spring) and cheatgrass seeds are viable food sources for small mammals (Richardson et al. 2013). Additionally, cheatgrass may indirectly provide food by increasing arthropod abundance (Ostoja et al. 2009, Litt et al. 2014). However, cheatgrass seeds are lower in nutritional quality and, due to persistent awns, likely require greater handling time to extract than many native seeds (Kelrick et al. 1986, Lucero et al. 2015; however, see Richardson et al. 2013). We thus predicted that cheatgrass would adversely affect granivorous small mammals whereas it would benefit or have no effect on omnivores. A trait-based approach could improve our mechanistic understanding of wildlife-invasive plant relationships, and provide a general framework for predicting wildlife responses to invasive plants and other forms of habitat change.

TABLE 1. Predicted and observed occupancy responses of small mammal species in Thunder Basin National Grassland, Wyoming, USA, 2013–2014, to cheatgrass based on focal traits and the literature.

Species	Habitat†	Diet‡	Locomotion§	Predicted	Observed
Deer mouse	generalist-closed	omnivore	cursorial	+, 0	0
13-lined ground squirrel	generalist-open	omnivore	cursorial	+, 0	0
Harvest mice	closed	omnivore	cursorial	+, 0	+
Northern grasshopper mouse	open	insectivore	cursorial	+, −, 0	¶
Pocket mice	open	granivore	saltatory	−	−
Ord's kangaroo rat	open	granivore	saltatory	−	0

Notes: Responses are positive (+), negative (−), and neutral (0). Habitat, diet, and locomotion traits were used in the occupancy analysis with all species pooled.

† Deer mice and 13-lined ground squirrels are generalists that tend toward closed and open habitats, respectively (Grant et al. 1977, Streubel and Fitzgerald 1978, Stapp et al. 2008). Harvest mice are associated with high cover, whereas grasshopper mice, pocket mice, and kangaroo rats are associated with intermediate to low cover (Grant et al. 1977, Lemen and Rosenzweig 1978, Genoways and Brown 1993, Jones et al. 2003).

‡ Deer mouse (Flake 1973, Stapp 1997), 13-lined ground squirrel (Flake 1973, Higgins and Stapp 1997), harvest mice (Webster and Jones 1982, Wilkins 1986), northern grasshopper mouse (McCarty 1978, Stapp 1997), pocket mice (Manning and Jones 1988, Genoways and Brown 1993, Best and Skupski 1994), and Ord's kangaroo rat (Flake 1973, Garrison and Best 1990).

§ Pocket mice hop quadrapedally and kangaroo rats hop quadrapedally and bipedally, whereas the other species are cursorial quadrapeds (Bartholomew and Caswell 1951, Bartholomew and Cary 1954, Rieder et al. 2010).

¶ Unable to estimate effect due to inadequate sample size.

FIELD METHODS

Study area

Field work was conducted in Thunder Basin National Grassland (TBNG), Wyoming, USA, which is a semi-arid grassland managed by the U.S. Forest Service (average annual precipitation 31.75 cm, range 14.22–49.53 cm; elevation range 1097–1585 m; Haufler et al. 2008, USFS 2011). Vegetation was primarily mixed-grass prairie. The dominant native herbaceous plants were western wheatgrass (*Elymus smithii*), blue grama (*Bouteloua gracilis*), and needle-and-thread (*Hesperostipa comata*). Cheatgrass was the dominant invasive plant followed by Japanese brome (*Bromus japonicus*), which was much less common. The shrub community was dominated by big sagebrush (*Artemisia tridentata*) or greasewood (*Sarcobatus vermiculatus*), with smaller amounts of silver sage (*Artemisia cana*), fringed sage (*Artemisia frigida*), black sage (*Artemisia nova*), and saltbush (*Atriplex* spp.; Haufler et al. 2008).

We selected 16 sites across a gradient of cheatgrass cover (Fig. 1) while minimizing variation in other landscape characteristics such as topography (median minimum distance between sites 872 m, range 207–8794 m). We compiled potential sites based on the U.S. Geological Survey ReGap land cover data (USGS 2011), local vegetation data from the Thunder Basin Grasslands Prairie Ecosystem Association (*unpublished report*), and recommendations from TBNG biologists. All sites excluded riparian areas, trees, and anthropogenic structures such as well pads, although some sites were adjacent to (≥5 m) such features. The final sites were selected based on visual assessments of site characteristics along transects, prioritizing a collection of sites that covered a broad range of cheatgrass cover.

Small mammal trapping

We used a robust trapping design (Williams et al. 2002) with four primary sampling periods (early to mid-summer and mid to late summer in 2013 and 2014) each consisting of four trap nights (secondary periods). In 2013, two sites (one low and one high cheatgrass cover) were added mid-summer and thus only trapped for three primary periods. We trapped the same 14 sites in 2013 and 2014 to assess temporal variation in the small mammal metrics and added two new sites in 2014 to increase sample size. There were four blocks that each contained four sites spanning a gradient of cheatgrass cover. We
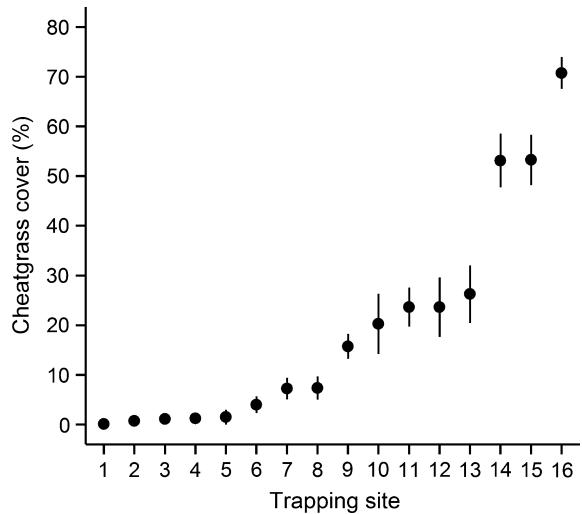

FIG. 1. Cheatgrass cover (mean ± SE) estimated with line–point-intercept surveys for each trapping site in Thunder Basin National Grassland, Wyoming, USA in 2013 and 2014.

simultaneously trapped all sites within a block to control for temporal autocorrelation due to factors such as weather; trapping at all blocks within a primary period was completed within 3–4 weeks.

We established a 135 × 165 m trapping grid at each site, consisting of 120 live traps separated by 15 m. Each site had the same number of traps, however, the trapping grid shape was slightly modified on four sites to stay within the primary habitats (trap spacing was unaltered). Trap type efficiency may vary by species, thus a broader suite of species can be targeted by using multiple trap types (O'Farrell et al. 1994). Each trapping grid therefore contained 80 Sherman (7.6 × 8.9 × 22.9 cm; H.B. Sherman Traps, Tallahassee, FL, USA) and 40 Havahart traps (7.6 × 7.6 × 25 cm; Woodstream, Lititz, PA, USA). Grids contained two Sherman traps followed by one Havahart trap in a repeating pattern, with one trap per station. Each trap was covered with a small plywood board to mitigate effects of adverse weather.

Traps were set in the afternoon and checked the following morning. We baited traps with a rolled oats-peanut butter mixture and provided polyester batting for bedding. We identified all individuals to species, where possible. Animals were marked with a PIT tag (passive integrated transponder; Biomark Boise, ID, USA) and released at the location of capture.

Predictors of population and community responses

Predictor variables were chosen a priori based on small mammal ecology (Table 2). We focused on factors likely to affect predation risk and food availability, which are major drivers of small mammal behavior and fitness (Longland and Price 1991, Falls et al. 2007).

Percent cover of vegetation was estimated in both years using line point intercept surveys (Bonham 2013) along eight 20-m transects distributed in a random, spatially balanced pattern on each site. Transects were separated by at least 20 m within a site. Shrub species were pooled in analyses because we assumed all species provided similar cover for small mammals. We identified cheatgrass and Japanese brome to species and classified native herbaceous plants as grass or forb.

Riparian areas can provide small mammals with refuges from predators and abundant food resources; consequently, riparian habitat may act as a population source for adjacent upland habitats (Hamilton et al. 2015). No site contained riparian habitat, however, multiple sites were adjacent to (≥5 m) riparian zones due to suitable trapping conditions in those areas. To account for a potential riparian effect, we created a 200-m buffer around each site based on home range sizes and dispersal distances of local small mammal species (French et al. 1968, Douglass et al. 2006). Polygons of riparian habitat were digitized at 1:1000 resolution using the National Hydrograph Dataset (USGS 2007) and NAIP imagery of Wyoming (NRCS-USDA 2012); we then calculated the percentage of the buffer that overlapped the

TABLE 2. Predictor names and descriptions for the habitat heterogeneity, deer mouse abundance, species richness, and species-specific occupancy analyses of small mammal species in Thunder Basin National Grassland, Wyoming, 2013–2014.

Predictor	Description
Habitat	
cheat†	cheatgrass cover (%) (yr)
shrub	shrub cover (%) (yr)
natv.g	native grass cover (%) (yr)
bare	bare ground cover (%) (yr)
rip	adjacent riparian habitat (%) (study)
cattle	cattle use index (count) (yr)
Abiotic	
moon	moon illumination (%) (pp)
ppt†	precipitation (mm) (yr and pp)
low.temp†	low temperature (°F) (yr and pp)
high.temp†	high temperature (°F) (pp)
Control	
null	constant (intercept-only)
site	trapping grid
yr	year (2014 = 1, 2013 = 0)
pp	primary period
effort	corrected number of trap nights (yr and pp)
prop.sherm	proportion of available traps that are shermans (yr)

Notes: The description column defines the predictor, units, and temporal resolution of data collection for each variable. Study, estimate does not vary over the time frame of the study (one estimate per site); yr, two estimates per site (one per year); pp, four estimates per site (one per primary period per year). The species' traits used in the occupancy analysis with all species pooled are listed in Table 1.

† Also included a quadratic version of the predictor in model sets.

riparian polygon for each site (ESRI 2012; data set and imagery *available online*).[4,5]

Grazing may indirectly influence small mammals by altering vegetation structure and composition (Bueno et al. 2012). To assess relative cattle use on each site, we counted cow dung piles on eight 20 × 1.5 m belt transects, which followed the same transects used for line point intercept surveys (mean site count 5, range 0.63–13). Finally, moonlight, temperature, and precipitation may affect small mammal detection by altering the costs of above ground activity (Orrock et al. 2004). Moonlight data were obtained from the U.S. Naval Observatory database (*available online*).[6] We obtained temperature and precipitation data from the Rochelle Hills Remote Automatic Weather Station (RAWS, http://raws.dri.edu/cgi-bin/rawMAIN.pl?wyWRCH) in TBNG (mean distance from sites 21 km; range 5–31 km). Because the weather data were not spatially paired with each site, we expected some inaccuracies in daily weather observations for a given site. For each block of four sites, moonlight, temperature, and precipitation data were therefore

[4] http://nhd.usgs.gov

[5] http://gdg.sc.egov.usda.gov

[6] http://aa.usno.navy.mil/data/docs/MoonFraction.php

averaged across the four trap nights within a primary period. Cloud cover data were not available for our sites.

ANALYTICAL METHODS

Habitat heterogeneity

To quantify how cheatgrass alters habitat, we generated a heterogeneity index for each site. We calculated the coefficient of variation separately for each cover type based on the line point intercept cover estimates. All of the coefficient of variation estimates were then averaged by site to generate an overall index of heterogeneity (e.g., Litt and Steidl 2011). The average coefficient of variation was the response in a linear mixed model (LMM) with cheatgrass cover (%), year, and a random intercept for site to account for repeated measurements ($n = 16$; Zuur et al. 2009, Bates et al. 2015).

Deer mouse abundance

We used Huggins robust design to estimate capture (p) and recapture (c) probability and abundance ($\hat{N}$) for deer mice only (effective $n = 2409$, which was estimated as the number of captures and recaptures) due to insufficient captures of other species (Williams et al. 2002). We model-averaged predicted abundance (Burnham and Anderson 2002, Cade 2015) from each model in the final model set to estimate abundance for every site–primary-period combination (the Huggins robust design model sets are presented in Ceradini and Chalfoun [2017]). For each site–year combination, we then averaged the two primary period abundance estimates to obtain average summer deer mouse abundance. The relationship between abundance and covariates, such as cheatgrass, cannot be determined using Huggins robust design because abundance is derived using p and c (Williams et al. 2002).

Deer mouse abundance was then modeled as a function of habitat predictors (Table 2) in a linear mixed model (LMM) with a random intercept for site ($n = 16$; e.g., Bailey et al. 2004; however, for a critique of this approach, see Link [1999]). Because the response variable was an estimate, we used a Monte Carlo simulation to assess if ignoring the variance of abundance biased the LMM estimates (Manly 1998). Additionally, assessing the influence of cheatgrass while accounting for other habitat features was important, yet, this led to moderately large models given our sample size (Babyak 2004). We therefore used leave-one-out cross-validation to calculate predicted R^2 of our best model (excluding random effects) to assess whether the model was overfit (Kutner et al. 2004).

Model fit was better for a LMM with a log-transformed response than a Poisson Generalized Linear Mixed Model (GLMM); moreover, our counts were relatively large with a small proportion of zeros (O'Hara and Kotze 2010). To log-transform two sites with zero deer mice in 2013, we added 1.0 to all $\hat{N}$ prior to transformation; true zeros thus became log-zeros. Back-transformed

predictions of abundance from the best model were adjusted using a correction term (Appendix S1).

For both LMM analyses (habitat heterogeneity and deer mouse abundance), we did not report P values, and assessed predictor significance based on t values and bootstrapped 95% confidence intervals (e.g., Doherty et al. 2015) because there is no consensus on how to calculate degrees of freedom for mixed models (Bolker et al. 2009). To assess goodness of fit, we visually inspected the residuals vs. fitted values for fanning (heterogeneity) and/or curvature, and assessed normality of both the residuals and random effects (Zuur et al. 2009). Finally, model performance was measured by the marginal (R_{m}^2) and conditional (R_{c}^2) coefficients of determination (Nakagawa and Schielzeth 2013, Barton 2015).

Species richness

We estimated richness using nonparametric estimators that correct observed richness by using the presence–absence patterns of species (Magurran and McGill 2011); however, estimates were unreliable likely due to insufficient sample sizes. We thus modeled observed species richness, which we consider a minimum count of species present. In a Poisson GLMM, a random intercept for site did not contribute to the model (SD ≈ 0, $R_{\mathrm{m}}^2 = R_{\mathrm{c}}^2$), so we modeled richness with a Poisson generalized linear model (GLM; $n = 16$). Goodness of fit was evaluated on the deviance residuals and an overdispersion estimate ($\hat{c}$; Zuur et al. 2009).

Occupancy

Occupancy analyses were conducted using the R package RMark (Laake 2013), which is an interface for MARK (White and Burnham 1999). Multi-season occupancy models did not converge for all species likely due to small sample sizes. We therefore used single-season occupancy models (MacKenzie et al. 2006) where each site represented a maximum of four samples, one for each primary period, and included year and primary period as predictors. The sample unit was site and the detection unit was trap night, resulting in a maximum of four occasions or surveys per site per primary period. We estimated the probability of detection (p) and occupancy (Ψ) for each species or genus separately (effective $n = 58$ per species) and for all species pooled and grouped by focal traits (effective $n = 348$; Table 1; MacKenzie et al. 2006). We used a multistage modeling approach to model detection and occupancy probability (Doherty et al. 2012). In stage one, occupancy was held constant as the global model while different detection models competed. In stage two, we used the top detection model from stage one while different occupancy models competed. If there was model selection uncertainty in stage one, competitive models moved forward to compete again in stage two. Goodness of fit was assessed on the global model in each model set

using the parametric bootstrap in program PRESENCE (MacKenzie and Bailey 2004, Hines 2006).

We assessed occupancy separately for each species except the olive-backed pocket mouse (*Perognathus fasciatus*) and silky pocket mouse (*Perognathus flavus*) were pooled, and the western harvest mouse (*Reithrodontomys megalotis*) and plains harvest mouse (*Reithrodontomys montanus*) were pooled, due to infrequent detections and challenges differentiating these congeners in the field. Models did not converge for the northern grasshopper mouse (*Onychomys leucogaster*), which was rarely detected; however, the northern grasshopper mouse was included in the species' traits analysis.

After quantifying species-specific responses, we tested our prediction that the effect of cheatgrass would vary with focal species' traits by including all species in one occupancy analysis and assessing an interaction between the trait and cheatgrass (Table 1). Species were divided into three coarse habitat associations: (1) closed species, which occur in areas with abundant cover, (2) open species, which occur in areas with sparse or patchy cover, or (3) generalist species, which occur in both closed and open habitats. Because of a priori uncertainty regarding the habitat associations of deer mice and 13-lined ground squirrels, we classified them in two ways (Table 1). Specifically, we included models where deer mice and 13-lined ground squirrels were classified as generalists and the habitat term thus had three levels (open, closed and generalist), and models where deer mice and 13-lined ground squirrels were classified as closed and open species, respectively. Diet was modeled with three levels (omnivore, granivore, and insectivore) and two levels (omnivore and granivore), depending on whether the northern grasshopper mouse was classified as an insectivore or omnivore. Locomotion was modeled as cursorial or saltatory.

Small-mammal–cheatgrass modeling

For all analyses, the number of predictors in a model and models in a set were adjusted depending on the ecology of the species and sample size (Babyak 2004). Cheatgrass cover (%) was included in most models because our questions centered on the implications of cheatgrass invasion for small mammals. However, cheatgrass was excluded from intercept, site, and year-only models, which represented null models, and models with bare ground, which was correlated with cheatgrass >|0.6|. All interactions represented a priori hypotheses and included main effects. Model selection was conducted with Akaike's information criterion corrected for small sample sizes (AIC_c), and ΔAIC_c and AIC_c weight were used to compare the relative support for each model (Burnham and Anderson 2002, Mazerolle 2015). We described the direction of important predictors in each of the best models when there was model selection uncertainty. Statistics reported are from the best model in each set unless otherwise noted.

Models that failed to converge or had uninformative parameters were removed at each modeling stage. We considered models to be uninformative if a nested model with one less parameter differed in deviance or log likelihood by ≤1 and was within 0~3.5 ΔAIC_c (Burnham and Anderson 2002, Arnold 2010, Murtaugh 2014). Models with uninformative parameters were presented in final model sets to facilitate interpretation; however, such models were excluded when calculating AIC_c weights. All analyses and plotting were done in program R (Wickham 2009, R Development Core Team 2015).

RESULTS

Vegetation heterogeneity, as indexed by the coefficient of variation, decreased with cheatgrass cover ($\beta = -0.04$ per 10% increase in cheatgrass, 95% CI = -0.08 to -0.01, $t = -2.38$; $R_m^2 = 0.23$, $R_c^2 = 0.39$; Fig. 2). Heterogeneity did not vary with year ($\beta = -0.08$, 95% CI = -0.22 to 0.07, $t = -1.07$), however, model fit was improved by a year term.

We captured 1140 individuals of six different small mammal species. No individual was captured on more than one site; we were therefore confident that sites represented primarily independent small mammal communities. Adjusted trapping effort (Beauvais and Buskirk 1999) was similar between years (11 855 and 12 359 trap nights in 2013 and 2014, respectively), however, 91% of captures were in 2014. The majority of captures were deer mice (84.65%), followed by 13-lined ground squirrels (6.84%), Ord's kangaroo rats (5.44%), western and plains harvest mice (1.84%), olive-backed and silky pocket mice (0.96%), and northern grasshopper mice (0.26%).
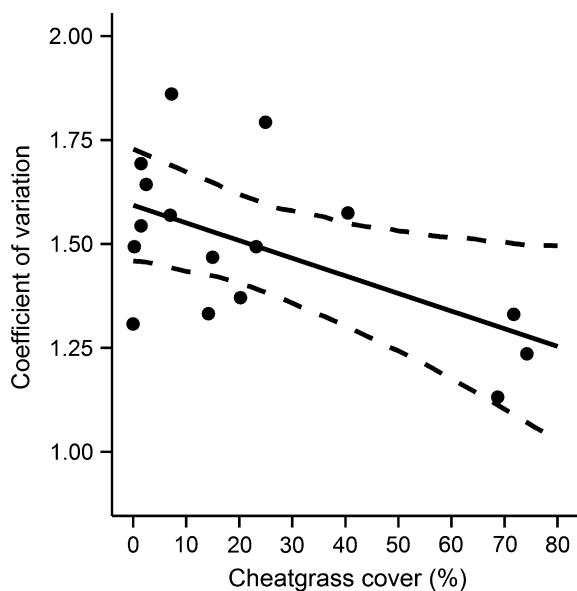

FIG. 2. Coefficient of variation of cover type estimates (mean; points) as a function of cheatgrass cover for each trapping site in the Thunder Basin National Grassland, Wyoming during 2014. Data from 2013 follow a similar pattern but are not shown. Solid and dotted lines are the predicted mean and 95% confidence intervals, respectively, from the linear mixed model.

Deer mouse abundance

Deer mouse abundance increased with cheatgrass cover, however, the effect was not consistent (exp $[\beta]$ = 1.08 per 10% increase in cheatgrass, 95% CI = 0.98–1.20, t = 1.54; Fig. 3; detection results in Appendix S2). There was a strong positive correlation between adjacent riparian habitat and deer mouse abundance (exp $[\beta]$ = 1.78 per 5% increase in riparian habitat, 95% CI = 1.40–2.26, t = 4.82; Fig. 3). The best deer mouse abundance model had overwhelming AIC_c support (Table 3; Appendix S3: Table S1). R^2 (0.89) and predicted R^2 (0.86) based on cross-validation were similar for the best model (excluding random effects), indicating that the model was not overfit. The effect of cheatgrass was positive when riparian habitat was excluded from the model (exp$[\beta]$ = 1.15 per 10% increase in cheatgrass, 95% CI = 1.00–1.33, t = 2.06), however, this model had <1% of AIC_c support (Table 3). Abundance in 2014 was 10.28 times greater (95% CI = 7.30–14.29, t = 14.19) than in 2013. The Monte Carlo simulation indicated that it was unnecessary to incorporate the variance of the abundance estimates into models.

Species richness

Species richness did not vary across the cheatgrass gradient (exp$[\beta]$ = 1.00, 95% CI = 0.91–1.10, z = 0.03). The best Poisson GLM had 100% of AIC_c weight and only included a year term (exp$[\beta]$ = 1.39, 95% CI = 0.88–2.23, z = 1.38; Appendix S3: Table S2).

Occupancy by species or genus

The relationship between cheatgrass and occupancy varied by species, predominantly corresponding with our a priori predictions (Table 1). All species-specific global models passed the parametric bootstrap goodness of fit test (α = 0.05, minimum P from all model sets = 0.31) and $\hat{c}$ was not adjusted. Cheatgrass and adjacent riparian habitat had a negative and positive effect, respectively, on pocket mouse occupancy in each of the best three models (cumulative AIC_c weight of 97%; Tables 4, 5, Fig. 4). By contrast, cheatgrass had a positive effect on harvest mouse occupancy (Table 4, Fig. 4). Pocket and harvest mice were also opposed in their response to moonlight, which had a negative and
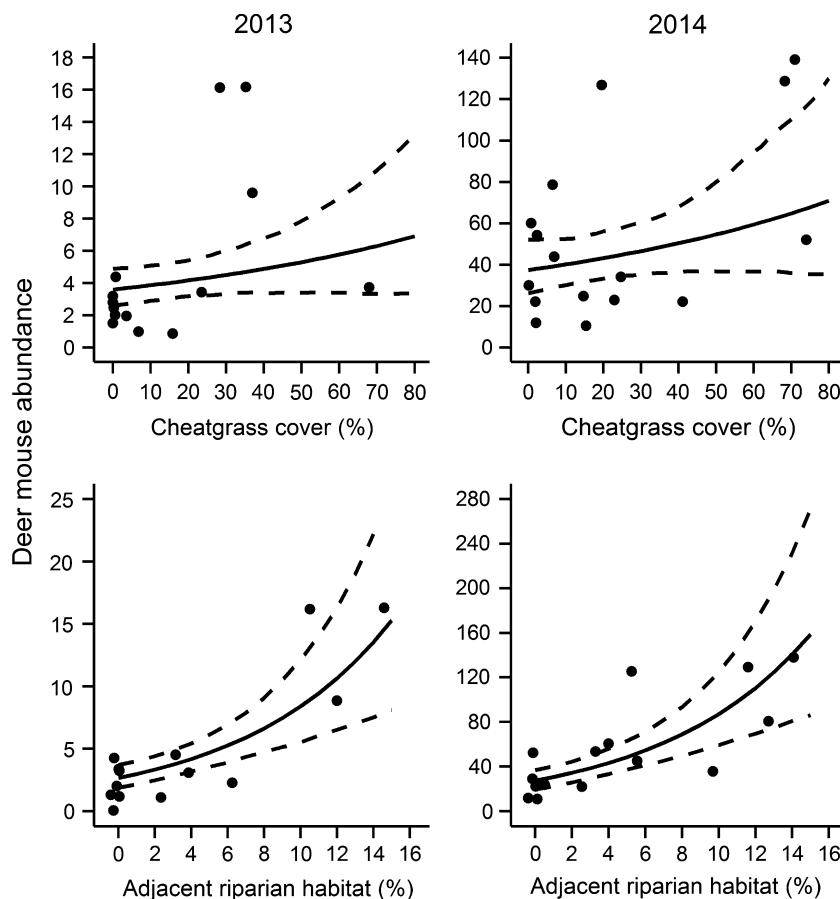

Fig. 3. Predicted deer mouse abundance in the Thunder Basin National Grassland, Wyoming from the best linear mixed model while holding the other covariate constant at its mean. Solid and dotted lines are the predicted mean and 95% confidence intervals, respectively. Points are model-averaged abundance estimates from the Huggins robust design models and are jittered to reduce over-plotting. The figures in the left and right columns are for 2013 and 2014, respectively.

TABLE 3. Subset of the linear mixed model set with deer mouse abundance ($\hat{N}$), estimated from the Huggins robust design analysis, as a function of habitat and control variables (complete model set is in Appendix S3: Table S1).

Model	K	ΔAIC_c†	w	LL	R^2_m	R^2_c
Cheat + rip + yr	6	0.00	1.00	−31.59	0.88	0.92
Cheat + rip × yr	7	1.87	NA	−30.81	0.88	0.92
Cheat × rip + yr	7	3.04	NA	−31.39	0.87	0.92
Cheat² + rip + yr	7	3.35	NA	−31.55	0.87	0.91
Global	10	12.30	0.00	−29.78	0.87	0.92
Cheat + yr	5	12.99	0.00	−39.67	0.72	0.92
Yr	4	14.37	0.00	−41.81	0.67	0.92

Notes: AIC$_c$, Akaike's information criterion corrected for small sample sizes; K, number of parameters; $\Delta AIC_c = AIC_{ci} - $ minimum AIC$_c$; w, AIC$_c$ model weight; LL, log-likelihood; R^2_m and R^2_c are marginal and conditional R^2, respectively. Data were collected in Thunder Basin National Grassland, Wyoming, 2013–2014. All models had a random intercept term for site. Models with NA under w meet the uninformative parameter criteria.
† Minimum AIC$_c$ = 78.84.

positive effect on pocket and harvest mouse detection, respectively (Table 5).

Cheatgrass did not affect 13-lined ground squirrel occupancy in any model (Tables 4, 5, Fig. 4), although, occupancy decreased with shrub cover. Deer mouse occupancy did not vary consistently with any predictors in the best three models (Tables 4, 5, Fig. 4). Finally, occupancy was constant in the best Ord's kangaroo rat model, which was intercept-only (predicted Ψ = 0.34, 95% CI = 0.21–0.51; Tables 4, 5, Fig. 4). The second-ranked Ord's kangaroo rat model was competitive and had a cheatgrass-riparian interaction, which was not significant (β = −0.10, 95% CI = −0.22 to 0.02, z = −1.66).

Occupancy by species' traits

Models representing the prediction that the effect of cheatgrass on occupancy varied with the simplified habitat association (closed × cheat) received 99% of AIC$_c$ weight (Table 6). The simplified habitat association classified deer mice and 13-lined ground squirrels as closed and open habitat species, respectively (Table 1). The best two models both contained a positive interaction between habitat association and cheatgrass (β = 0.87, 95% CI = 0.07–1.68, z = 2.12) and only differed by an insignificant year term (odds ratio [OR] = 1.75, 95% CI = 0.88–3.48, z = 1.60). The global species' traits model passed the parametric bootstrap goodness of fit test (P = 0.12) and $\hat{c}$ was not adjusted. The odds of occupancy for open habitat species decreased by 14.67% (95% CI = 0.00–26.88%, z = −2.01) for every 10% increase in cheatgrass cover (Fig. 5). The effect was weaker for closed habitat species, whose odds of occupancy increased by a factor of 2.04 (95% CI = 0.92–4.50, z = 1.77) for every 10% increase in cheatgrass cover (Fig. 5).

The best model representing the diet-cheatgrass prediction had <1% of AIC$_c$ weight (Table 6) and neither interaction was significant (β = 0.08, z = 0.27 and β = 0.16, z = 1.17, respectively). The best model representing the locomotion-cheatgrass prediction also had

<1% of AIC$_c$ weight (Table 6) and the interaction was not significant (β = 0.16, z = 1.23).

Discussion

Habitat alteration by invasive plants can have direct and indirect effects on fitness with consequences for wildlife populations and communities (Ortega et al. 2006, Pearson 2009, Vila et al. 2011). However, there is substantial evidence that invasive plants have varying effects on native species (Crooks 2002) and can shift native community composition (Litt and Steidl 2010, Mott et al. 2010, Freeman et al. 2014, Rogers and Chown 2014). Additionally, few studies have quantified the relative importance of relevant species' traits in determining responses to invaded habitats (e.g., Litt and Steidl 2011, Martin and Murray 2011). We documented a significant reduction in habitat heterogeneity with increasing cheatgrass cover and small mammal species' responses to cheatgrass varied predictably with focal species' traits, particularly habitat association.

Habitat homogenization

Heterogeneous habitats tend to support higher species diversity than less complex habitats (Macarthur and Macarthur 1961, Fuhlendorf et al. 2006, 2010). Invasive plants often homogenize habitats by simplifying plant community composition and structure, which frequently reduces plant and animal diversity (Vila et al. 2011). In our system, an index of habitat heterogeneity was negatively correlated with cheatgrass. We therefore expected the richness of small mammal species to decline (Ostoja and Schupp 2009, Freeman et al. 2014) or show a negative quadratic relationship (Litt and Steidl 2011) as cheatgrass simplified habitat composition and structure; however, richness did not change across the cheatgrass gradient. The composition of the small mammal community, conversely, shifted with cheatgrass dominance. As cheatgrass cover increased, pocket mouse (granivore associated with open habitats) occupancy primarily

TABLE 4. Subset of the occupancy model sets for each small mammal species or genus captured in Thunder Basin National Grassland, Wyoming, 2013–2014 (complete model sets are in Appendix S3: Tables S3–S7).

Model	K	ΔAIC$_c$	w	Deviance
Pocket mouse				
Ψ(cheat + rip + yr) p(moon)	6	0.00	0.65	77.57
Ψ(cheat + rip)	5	2.24	0.21	82.30
Ψ(cheat + rip + pp + yr)	8	3.62	0.11	75.90
Harvest mouse				
Ψ(cheat + cattle) p(moon)	5	0.00	0.80	87.65
Ψ(cheat + cattle + yr)	6	2.33	NA	87.49
Ψ(cheat)	4	4.87	0.07	94.92
Ψ(cheat + yr)	5	5.61	0.05	93.26
13-lined ground squirrel				
Ψ(cheat + natv.g + shrub) p(yr + high.temp)	7	0.00	0.62	157.29
Ψ(cheat + shrub)	6	1.68	0.27	161.56
Ψ(cheat + natv.g + shrub + yr)	8	2.68	NA	157.27
Ψ(cheat + shrub + yr)	7	3.51	NA	160.80
Ψ(global)	10	6.63	0.02	155.48
Deer mouse				
Ψ(cheat + cattle) p(yr + ppt.pp)	6	0.00	0.34	154.70
Ψ(cheat)	5	0.45	0.27	157.65
Ψ(cheat^2)	6	1.57	0.15	156.27
Ψ(cheat + natv.g)	6	2.01	NA	156.71
Ψ(cheat + rip)	6	2.18	NA	156.88
Ψ(cheat + shrub)	6	2.40	NA	157.10
Ψ(null)	4	3.10	0.07	162.69
Ψ(bare)	5	4.01	0.05	161.20
Ψ(cheat × rip)	7	4.26	0.04	156.37
Ord's kangaroo rat				
Ψ(null) p(yr)	3	0.00	0.48	112.12
Ψ(cheat × rip)	6	0.67	0.34	105.59
Ψ(bare)	4	1.88	NA	111.70
Ψ(cheat)	4	2.09	NA	111.90
Ψ(cheat^2)	5	2.59	0.13	110.00

Notes: K, number of parameters; ΔAIC$_c$ = AIC$_{ci}$ − minimum AIC$_c$; *w,* AIC$_c$ model weight. Occupancy (Ψ) and detection (*p*) probability were modeled as a function of habitat, abiotic, and control variables. For each species, models represent 90% confidence sets based on cumulative weight of Akaike's information criterion corrected for small sample sizes (AIC$_c$). Models with NA under *w* meet the uninformative parameter criteria. Detection probability (*p*) predictors are the same for all models within a species and thus are only listed for the first model in a set.

decreased while harvest mouse (omnivore associated with closed habitats) occupancy increased. This is particularly salient for Wyoming where multiple pocket mice species, including olive-backed and silky pocket mice, are species of conservation concern (Wyoming Game and Fish Department 2010). In a large-scale study, Litt and Steidl (2011) observed a similar shift in small mammal community composition with biomass of Lehmann lovegrass (*Eragrostis lehmanniana*), an invasive grass in the southwestern United States. As biomass of Lehmann lovegrass increased, granivorous and insectivorous small mammal species decreased in presence and abundance, while omnivorous and herbivorous species became more common (Litt and Steidl 2011).

The lack of change in species richness across the cheatgrass gradient was unexpected, as species diversity typically decreases with habitat homogenization (Macarthur and Macarthur 1961, Pickett et al. 1997, Fuhlendorf et al. 2006, 2010). However, this result can be understood within the context of our predictive framework; changes in habitat may favor certain species over others and cause predictable shifts in composition based on habitat requirements (Crooks 2002, Martin and Murray 2011, Sih et al. 2011). If certain native species benefit and others are inhibited by habitat alteration, there may be no net change in species richness. This effect may be particularly pronounced in systems with relatively low species richness, such as ours (*n* = 6), where two or more species may have opposing responses to a habitat alteration, resulting in no net change in richness. Our richness-composition result is therefore instructive because it provides a clear example of why

TABLE 5. Odds ratios (or exp[β]) for each predictor from the best occupancy model for each small mammal species or genus captured in Thunder Basin National Grassland, Wyoming, 2013–2014.

Predictor	OR	LCL	UCL	z
Pocket mouse				
Ψ(cheat)†	0.20	0.04	1.01	−1.95
Ψ(rip)‡	2.07	1.04	4.10	2.08
Ψ(yr)	14.77	0.65	334.47	1.69
p(moon)†	0.77	0.63	0.93	−2.73
Harvest mouse				
Ψ(cheat)†	5.06	0.97	26.42	1.92
Ψ(cattle)	1.68	0.94	3.01	1.74
p(moon)†	1.26	1.07	1.48	2.77
13-lined ground squirrel				
Ψ(cheat)†	1.10	0.71	1.69	0.43
Ψ(natv.g)†	2.16	0.83	5.63	1.58
Ψ(shrub)‡	0.81	0.68	0.96	−2.45
p(high.temp)	1.49	1.28	1.75	5.08
p(yr)	13.33	2.92	61.56	3.33
Deer mouse				
Ψ(cheat)†	1.53	0.65	3.61	0.97
Ψ(cattle)	1.61	0.69	3.74	1.11
p(ppt)	1.59	1.18	2.15	3.03
p(yr)	52.98	13.87	202.35	5.79
Ord's kangaroo rat				
p(yr)	48.91	11.13	212.72	5.17

Notes: Ψ, occupancy probability; *p*, detection probability; OR, odds ratio or exp(β); LCL and UCL, lower and upper 95% confidence limit of OR; *z* = β/standard error(β). Intercept estimates are not shown.
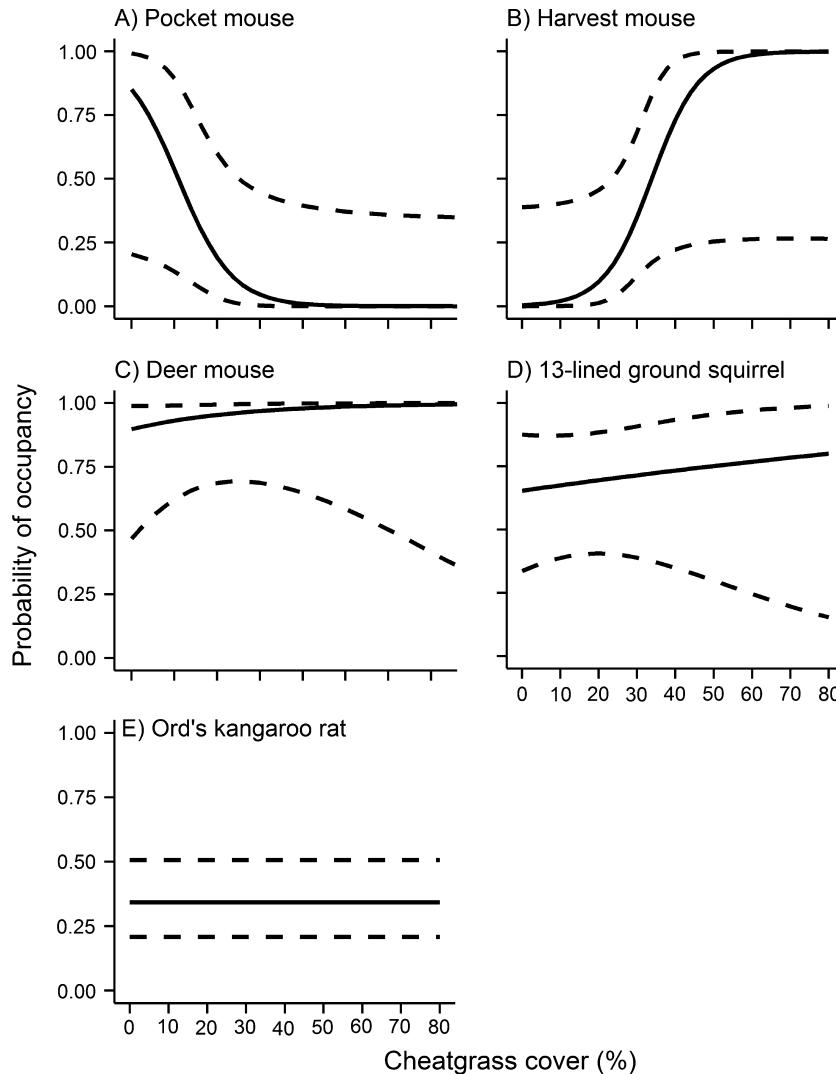
† Effect of a 10% increase.

‡ Effect of a 1% increase.

Fig. 4. Predicted probability of occupancy from the best model for each species or genus as a function of cheatgrass cover in the Thunder Basin National Grassland, Wyoming. Other covariates in the respective models are held constant at their mean. (A) The best pocket mouse model had an additive effect of year and the predictions shown are for 2014. (B–E) No other species' best model had a year effect. Solid and dotted lines are the mean and 95% confidence intervals, respectively.

species richness alone may not adequately capture wildlife community responses to habitat change.

Accounting for ecological context

The strength of the effects of habitat alteration by invasive plants may depend on co-occurring habitat elements. For example, in our study deer mouse abundance increased with cheatgrass when cheatgrass was considered in isolation. The effect of cheatgrass became marginal, however, after controlling for adjacent riparian habitat, which was the primary driver of deer mouse abundance. Invasive grasses have had generally inconsistent effects on deer mice (negative [Ostoja and Schupp 2009, Hall 2012], neutral [Litt and Steidl 2011, Freeman

et al. 2014], positive [MacCracken et al. 1985]), which may reflect interactions with other key habitat elements. Small mammal abundance is often greater in or near riparian habitats relative to uplands (Doyle 1990, Hamilton et al. 2015). To our knowledge, however, no study has assessed the effect of cheatgrass on wildlife while accounting for potential edge effects from dissimilar habitats, such as riparian zones, adjacent to sampling plots. This highlights the importance of considering ecological context when assessing wildlife–habitat relationships (e.g., Manson et al. 1999).

Disparities between studies in the response of wildlife to invasive plants may also be due to the historical context of invaded habitats. The effects of invasive species can be delayed (Crooks 2005), however, few studies are

TABLE 6. Complete model set for the species' traits occupancy analysis including all small mammal species captured in Thunder Basin National Grassland, Wyoming, 2013–2014.

Model	K	ΔAIC_c†	w	Deviance
Ψ(closed $\times$ cheat + yr)	9	0.00	0.55	823.24
Ψ(closed $\times$ cheat)	8	0.43	0.44	825.78
Ψ(closed $\times$ cheat + yr + pp)	10	1.90	NA	823.02
Ψ(closed + cheat)	7	8.38	0.01	835.82
Ψ(closed $\times$ cheat + generalist $\times$ cheat)	10	11.67	0.00	832.78
Ψ(insectivore + omnivore + cheat)	8	15.23	0.00	840.58
Ψ(insectivore $\times$ cheat + omnivore $\times$ cheat)	10	18.02	0.00	839.14
Ψ(closed + generalist + cheat)	8	18.47	0.00	843.82
Ψ(global)	26	31.45	0.00	816.85
Ψ(omnivore + cheat)	7	59.02	0.00	886.46
Ψ(cursorial + cheat)	7	59.02	0.00	886.46
Ψ(omnivore $\times$ cheat)	8	59.53	0.00	884.87
Ψ(cursorial $\times$ cheat)	8	59.53	0.00	884.87
Ψ(null)	5	63.18	0.00	894.77
Ψ(site + yr)	21	91.50	0.00	888.44

Notes: AIC_c, Akaike's information criterion corrected for small sample sizes; K, number of parameters; $\Delta AIC_c = AIC_{ci} -$ minimum AIC_c; w, AIC_c model weight. Models with NA under w meet the uninformative parameter criteria. For all models, detection probability $(p) =$ closed + generalist + yr. Occupancy (Ψ) and detection (p) probability were modeled as a function of species' traits, and habitat, abiotic, and control variables.

† Minimum $AIC_c = 841.77$.

able to assess the effect of time since invasion (Strayer et al. 2006). The negative effect of cheatgrass on particular small mammal species likely increases over time (Ostoja and Schupp 2009). We do not know when cheatgrass invaded our sites, and variation in invasion history among sites may account for the lack of a response by the Ord's kangaroo rat (granivore associated with open habitats); however, we could not test for this effect. Assessing the effect of time since invasion in future studies may provide insights on the rate of habitat degradation and species extirpation (Crooks 2005, Strayer et al. 2006, Ostoja and Schupp 2009). Moreover, variation in detection probabilities may confound comparisons within and between studies (Mackenzie et al. 2005). Ours is one of the few small mammal-invasive plant studies to estimate detection probability, which strengthens our conclusions (also see Litt and Steidl 2011).

The effects of invasive species may also vary in magnitude and direction depending on the response metric measured (Remes 2003, Pyšek et al. 2012). For the most common species, deer mice, we estimated occupancy and abundance, which both showed positive but insignificant trends with increasing cheatgrass cover. These independent lines of evidence both suggest that the deer mouse, a generalist small mammal, may tolerate habitat changes due to cheatgrass invasion. In the long-term, deer mice may

increase in relative abundance in invaded habitats if cheatgrass negatively affects other small mammal species (Hanser and Huntly 2006). *Peromyscus* species may be strong competitors and predators, and a shift in the relative abundance of small mammal species may have negative consequences for other trophic levels such as plants (Bricker et al. 2010, Dangremond et al. 2010) and nesting songbirds (Schmidt et al. 2001, Hethcoat and Chalfoun 2015).

Prediction using focal species' traits

We observed species-specific responses to cheatgrass invasion, which largely corresponded with our trait-based predictions. We quantified the relative importance of three focal traits to explain small mammal species' responses. We found that the effect of cheatgrass on occupancy varied with a species' habitat association but not with diet or mode of locomotion. As cheatgrass cover increased, the probability of occupancy decreased for species associated with open habitats while it primarily increased for closed habitat species. Open habitat species, such as heteromyids, require cover but are associated with sparse or patchy vegetation rather than dense continuous cover created by invasive grasses (Genoways and Brown 1993, Jones et al. 2003). Habitat modification by invasive grasses may adversely affect species that require open areas for dust bathing, foraging, and potentially detecting and avoiding predators (Kotler 1984, Genoways and Brown 1993).
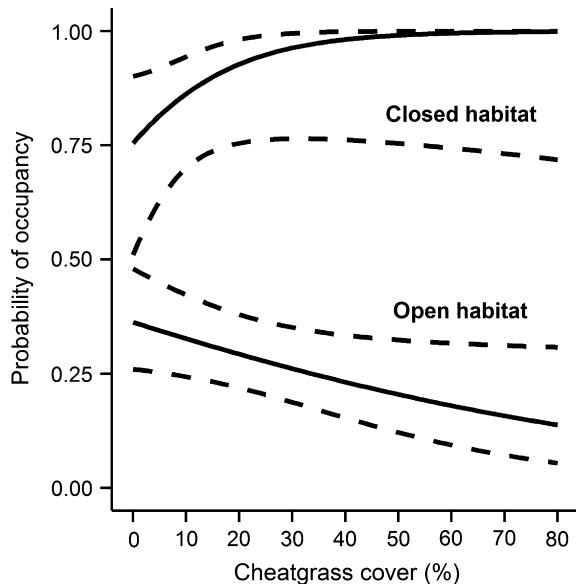

FIG. 5. Predicted probability of occupancy in the Thunder Basin National Grassland, Wyoming for pooled small mammal species as a function of an interaction between a species' habitat association and cheatgrass cover. Solid and dotted lines are the mean and 95% confidence intervals, respectively, from the best occupancy model. The best model contained an additive effect of year, which was not significant, and estimates shown are for 2014.

We did not have support for the locomotion prediction; however, mode of locomotion may help explain the effect of habitat association. Small vertebrates, for example, may experience a tradeoff between dense grass cover reducing predation risk (Johnson and De León 2015) and impeding movement (Rieder et al. 2010). The costs are likely greater for open habitat species that are typically saltatory and cannot move through dense vegetation as efficiently as cursorial, closed habitat species (Rieder et al. 2010). Additionally, the lack of support for the locomotion and diet predictions may be partly due to our relatively low species richness ($n = 6$) limiting our ability to detect an effect.

When selecting species' traits to use for prediction it is critical to consider the ecology of and the primary selective pressures on the native species within the context of the rapid habitat change, such as nonnative species invasion (Sih et al. 2011). Predicting the responses of highly adaptable, generalist species such as deer mice to habitat changes is challenging. For example, deer mice have been shown to respond positively (MacCracken et al. 1985), negatively (Ostoja and Schupp 2009, Hall 2012), and neutrally (Litt and Steidl 2011) to cheatgrass invasion. A trait-based framework may thus be more effective at predicting the responses of more specialized species. Although this is a limitation of a functional traits approach, a primary advantage of this approach is to efficiently prioritize the management and conservation of species expected to be most vulnerable to habitat changes. Highly plastic species are more likely to successfully adapt to rapid changes and thus, for example, less likely to be vulnerable to local extinction (Sih et al. 2011).

Habitat conversion by invasive species will continue as the distribution of many exotics expands due to positive feedbacks and anthropogenic disturbances (Mack and Antonio 1998, Smith et al. 2000). In addition, nonnative species are continually introduced and a fraction of them are likely to become new invaders (van Kleunen et al. 2015). Given the global scope of current and potential impacts of invasive species, and limited resources for research and conservation efforts, it is critical to effectively predict their influence on native species. Our research demonstrates how native species' traits, such as natural history characteristics, can be used to improve prediction of wildlife responses to habitat alteration by invasive plants. Trait-based prediction may streamline research and conservation efforts by identifying species likely to be most vulnerable to invasives without requiring a separate study for each native species, which is often not feasible. Ideally, this trait-based predictive framework should continue to be evaluated in other systems and with additional metrics, particularly indicators of fitness (van Horn 1983). For rare species, however, quantifying metrics such as survival is often infeasible due to small sample sizes, and the probability of occupancy is a rigorous alternative population vital rate (Mackenzie et al. 2005). We encourage the use of native species' traits to improve prediction of the effects of habitat changes due to invasive species and other habitat disturbances, and to help guide future research and conservation efforts.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1535/full

Data Availability

Data can be accessed through the University of Wyoming Research Data Repository https://doi.org/10.15786/M2MS34