

## Quantifying “apparent” impact and distinguishing impact from invasiveness in multispecies plant invasions

DEAN E. PEARSON,<sup>1,2,5</sup> YVETTE K. ORTEGA,<sup>1</sup> ÖZKAN EREN,<sup>3</sup> AND JOSÉ L. HIERRO<sup>4</sup>

<sup>1</sup>Rocky Mountain Research Station, USDA Forest Service, 800 East Beckwith Avenue, Missoula, Montana 59801 USA

<sup>2</sup>Division of Biological Sciences, University of Montana, Missoula, Montana 59812 USA

<sup>3</sup>Biyoloji Bölümü, Fen Edebiyat Fakültesi, Adnan Menderes Üniversitesi, 09100, Aydın, Turkey

<sup>4</sup>INCITAP (CONICET-UNLPam) and Facultad de Ciencias Exactas y Naturales, Universidad Nacional de La Pampa, Avenida Uruguay 151, 6300, Santa Rosa, Argentina

**Abstract.** The quantification of invader impacts remains a major hurdle to understanding and managing invasions. Here, we demonstrate a method for quantifying the community-level impact of multiple plant invaders by applying Parker et al.’s (1999) equation (impact = range  $\times$  local abundance  $\times$  per capita effect or per unit effect) using data from 620 survey plots from 31 grasslands across west-central Montana, USA. In testing for interactive effects of multiple invaders on native plant abundance (percent cover), we found no evidence for invasional meltdown or synergistic interactions for the 25 exotics tested. While much concern exists regarding impact thresholds, we also found little evidence for nonlinear relationships between invader abundance and impacts. These results suggest that management actions that reduce invader abundance should reduce invader impacts monotonically in this system. Eleven of 25 invaders had significant per unit impacts (negative local-scale relationships between invader and native cover). In decomposing the components of impact, we found that local invader abundance had a significant influence on the likelihood of impact, but range (number of plots occupied) did not. This analysis helped to differentiate measures of invasiveness (local abundance and range) from impact to distinguish high-impact invaders from invaders that exhibit negligible impacts, even when widespread. Distinguishing between high- and low-impact invaders should help refine trait-based prediction of problem species. Despite the unique information derived from evaluation of per unit effects of invaders, invasiveness scores based on range and local abundance produced similar rankings to impact scores that incorporated estimates of per unit effects. Hence, information on range and local abundance alone was sufficient to identify problematic plant invaders at the regional scale. In comparing empirical data on invader impacts to the state noxious weed list, we found that the noxious weed list captured 45% of the high-impact invaders but missed 55% and assigned the lowest risk category to the highest-impact invader. While such subjective weed lists help to guide invasive species management, empirical data are needed to develop more comprehensive rankings of ecological impacts. Using weed lists to classify invaders for testing invasion theory is not well supported.

**Keywords:** *Bromus tectorum*; *Centaurea stoebe*; invader impact; invasion thresholds; invasional meltdown; invasiveness; Montana, USA; noxious weed lists; weed impact rankings

### INTRODUCTION

The severe impacts that introduced species have in recipient systems have driven a massive effort to understand the causes and consequences of species introductions (Gurevitch et al. 2011). Quantifying invader impacts is essential to understanding biological

invasions and prioritizing invasive species for management (Parker et al. 1999, Byers et al. 2002, Pyšek et al. 2012, Barney et al. 2013), but in practice, empirical calculation of invader impacts at the community level has proven elusive. This gap in quantifying invader impacts also hinders our ability to test invasion theory, because studies attempting to identify the ecological and evolutionary factors underlying invader success are forced to use subjective, often politically derived weed pest lists as metrics for ranking invader success or impact (e.g., Mitchel and Power 2003, Ortega and

Manuscript received 5 December 2014; revised 25 March 2015; accepted 16 June 2015. Corresponding Editor: B. A. Newingham.

<sup>5</sup>E-mail: dpearson@fs.fed.us

Pearson 2005, Parker et al. 2006). If such indices are inaccurate, then the validity of this approach is in question.

In 1999, Parker et al. proposed a framework for quantifying the regional impacts of invaders based on the linear equation  $I = R \times A \times E$ , where  $I$  is invader impact (measured as a reduction in abundance or biomass of natives),  $R$  is the range or area occupied by the invader,  $A$  is the invader's mean local abundance (individuals, biomass, or equivalent per unit area), and  $E$  is the invader's per capita effect or per unit effect. This approach has received recent theoretical attention, but it has rarely been applied to estimate the impacts of plant invaders using empirical plot data as originally proposed due to significant logistical constraints (but see Thiele et al. 2010, Barney et al. 2013). First, obtaining the necessary plot data is challenging, as it requires a large number of plots, ideally well distributed over the range of the invader. Second, quantifying per capita effects of the invader that realistically reflect community-level impacts is somewhat untenable. Traditional approaches to calculating impact are based on classic competition studies where growth rates or other metrics are compared between species grown together and independently under greenhouse or common garden conditions (e.g., Goldberg and Werner 1983, Sun et al. 2013). However, this approach provides impact data for only a single species pair at a time, ignores effects of multiple species interactions, disregards environmental context, and fails to address the potential for invader abundance to influence per capita effects, i.e., nonlinearity between invader abundance and impacts (Goldberg and Werner 1983, Thiele et al. 2010, Barney et al. 2013). Recent approaches propose addressing several of these constraints by using field-based surveys that quantify differences in response metrics between invaded and uninvaded survey plots to generate an impact metric (Thiele et al. 2010, Barney et al. 2013). This approach lays important groundwork, but it does not address the additional ubiquitous problem that most invaded systems experience multiple invaders simultaneously that can interact in additive or synergistic ways (Simberloff and Von Holle 1999, Kuebbing et al. 2013), greatly complicating understandings of invader impacts.

Partitioning invader impacts into their constituent components is another key step to understanding invasions because it allows differentiation between strong invaders that have high impacts in recipient communities from weak invaders that may become widely established but exhibit little impact, and even behave similarly to native community members (Ortega and Pearson 2005). The term invasive has been qualitatively applied by researchers, policy makers, and managers to introduced species having high impact, and is commonly contrasted with terms like naturalized or colonizer to denote species categorically distinct from high-impact species (Richardson et al. 2000, Ricciardi

and Cohen 2007). Equating invasiveness with invader impact is problematic and has fueled semantic debates (Davis and Thompson 2000, Richardson et al. 2000, Daehler 2001, Barney et al. 2013). Invasiveness is not a qualitative term; it is a quantitative trait reflecting the ability of a species to spread over both local and broad scales (Richardson et al. 2000). Moreover, although invasiveness is related to invader impact, invasiveness does not necessarily equal impact (Ricciardi and Cohen 2007).

Parker et al.'s (1999) equation identifies the components of both invasiveness and impact. Specifically, a species' invasiveness can be quantified by its demographic success, i.e., its local population densities,  $A$ , and/or how widely that species establishes,  $R$ . The per capita effect term,  $E$ , is the metric that distinguishes the strength of one invader from another in terms of degree of impact per unit of invader abundance. Per capita effects, therefore, should allow for differentiating invaders that have high impacts from those that are simply successful invaders. Determining how the components of impact interact is essential for advancing prediction of invasion outcomes. For example, extensive efforts have been directed toward predicting invasion success from invader traits (Pyšek and Richardson 2007), but the failure to differentiate traits that contribute to invasiveness from those that drive impacts may be an important factor inhibiting progress in this line of research (Pyšek and Richardson 2007, Leffler et al. 2014). Being invasive and having impacts can be independent or correlated attributes.

The current lack of empirical data on invader impacts presents a major obstacle to advancing invasion theory. Studies attempting to evaluate the mechanisms driving invasion outcomes commonly employ noxious weed lists or other subjective weed pest lists to categorize invaders as high or low impact, problematic or not (e.g., Mitchel and Power 2003, Ortega and Pearson 2005, Parker et al. 2006, 2013). However, such lists are notoriously political documents because a species' listing is commonly linked to mandates for its control within the region generating the list (see, for example, the list maintained by the Center for Invasive Species Management, *available online*).<sup>6</sup> This can result in certain high-impact species going unlisted for political reasons while other species of high impact go unrecognized because their impacts are not yet widely known (Quinn et al. 2013). For example, cheatgrass (*Bromus tectorum*) is arguably one of the highest impact invaders in the western United States (Mack 1981, Knapp 1996, Humphrey and Schupp 2004). Yet this species is listed on only two of 11 state noxious weed lists in the western United States, and it is consistently categorized as a lower priority species (third tier) when it is listed, as by the Center for Invasive Species Management (see footnote 6). One reason for this is

<sup>6</sup><http://www.weedcenter.org/resources/state.html>

that cheatgrass has seasonal forage value for livestock (Thill et al. 1984), and introduced species that serve as livestock forage are commonly not included on noxious weed lists, as this would mandate control measures. While subjective lists play an important role in identifying and targeting certain invaders for management (Quinn et al. 2013), using such lists to identify high-impact invaders for evaluating invasion hypotheses may be problematic and should be critically evaluated.

Here we use survey data gathered from 620 1-m<sup>2</sup> vegetation plots across 31 grasslands in west-central Montana, USA to (1) demonstrate an approach for estimating invader impacts at the community level that addresses environmental context, tests for nonlinearity of invader impacts, controls for multiple invaders, and tests for interactions among invaders, (2) decompose the components of invader impact and evaluate the relationship between invasiveness and impact, and (3) examine how empirical data on invader impacts relate to the region's noxious weed list.

#### METHODS

We surveyed 31 grasslands in the intermountain valleys of west-central Montana over an area of 20 000 km<sup>2</sup> (elevation 800–1700 m above sea level). Native vegetation was dominated by perennial bunchgrasses, most often *Pseudoroegneria spicata* in combination with *Poa secunda*, *Festuca idahoensis*, or *F. caepstris* (Mueggler and Stewart 1980). Secondary bunchgrasses included *Koeleria macrantha* and *Stipa comata*. Common among diverse forb taxa were the perennials *Lupinus sericeus*, *Achillea millefolium*, and *Balsamorhiza sagittata*, and the annuals *Epilobium paniculatum*, *Microsteris gracilis*, and *Collomia linearis*.

We used ArcGIS (version 10.1; ESRI, Redlands, California, USA) to identify grasslands located on private, tribal, state, and federal lands within the study area. Sites were then visited and selected for sampling if they met the following criteria: they were proximal to roads, which serve as vectors for invaders (i.e., we selected portions of grasslands nearest to the roads, and we used no grasslands remote from roads); conformed to common grassland types as indicated by residual native perennial vegetation (Mueggler and Stewart 1980); had not been transformed by severe disturbances such as plowing, planting, extreme grazing, etc.; were a minimum of 1 ha in area; and we could obtain permission to access the property for sampling. Criteria did not include invasion characteristics, and selected sites represented a wide range of invasion levels (see *Results*). To ensure selected grasslands were scattered throughout the study area, we spaced selected sites >5 km apart and attempted to balance sampling effort among sub-regions.

Sampling of plant communities was conducted from late May to early July in 2011, 2012, and 2014. At

each site, we established a 100 × 100 m grid beginning at the point that was nearest to the road but beyond the immediate disturbance zone created by the road's construction or maintenance (typically >10 m from the road edge). At each site, we randomly selected  $n = 20$  1-m<sup>2</sup> grassland plots (shrub cover was <10%) located within the established grid, with a minimum of 10 m between plots. At each plot, we visually estimated percent cover for each native and exotic plant species within a frame marked to indicate 1% cover units. Cover <10% was estimated to the nearest 1%, and cover ≥10% was estimated to the nearest 5%. Species that occupied <1% of a plot were recorded as 0.5% cover. Observers were all trained by the principal investigator (DEP) and periodically co-estimated cover to ensure consistency. Species origin, life-form, and life-history strategy were assigned using Lackschewitz (1991) and Lesica (2012). We define the term native as species indigenous to the system, and we use the terms exotic and invader in reference to species that originate from outside the system but were introduced to the system. We use the terms invasive or invasiveness to refer to the degree of success that exotics attain within the system as measured by the size of the invaded range ( $R$ ) and/or the local abundance achieved ( $A$ ). Only herbaceous species were included in analyses as they comprised ≥99% of the total plant cover measured across sites (the remainder was native shrubs). Non-plant cover consisted primarily of bare ground (including litter and cryptogamic crust;  $\bar{x} = 54\% \pm 2\%$  across sites; mean  $\pm$  SE), with a small amount of rock ( $\bar{x} = 4\% \pm 1\%$ ).

To quantify the invasiveness of each exotic species we detected, we considered the first two terms in Parker et al. (1999)'s model:  $R$ , or invaded range, and  $A$ , mean invader abundance per unit area occupied. To estimate  $R$ , we tallied the number of 1-m<sup>2</sup> plots a species was found in (after Parker et al. 1999). The number of grassland sites a species occurred in was closely correlated with the number of plots ( $r^2 = 0.76$ ,  $P < 0.001$ ), but we chose the finer scale of occupancy given the typical patchiness of invasion within sites. For our measure of  $A$ , we calculated mean percent cover per plot in which the invader occurred. Percent cover per plot provides a proxy for plant abundance that helps to standardize for size differences among species (Thiele et al. 2010, Barney et al. 2013). The equivalent site-level measure, mean cover per plot and site, was less meaningful given that a species might occur in only a few plots at a particular site. As applied,  $R \times A$  represented total invader cover measured across all sampled grasslands in the study area, i.e., the equivalent score obtained by simply summing cover of the invader across all plots and sites. We refer to  $R \times A$  as the invasiveness score for each species, i.e., a measure of its invasion success across the local and landscape levels.

In order to evaluate how the population success of introduced plants relates to their impacts on native communities, we incorporated the  $E$  term in Parker's equation, which represents the per capita effect of the invader on natives. Because abundance was measured in terms of percent cover,  $E$  translates to the per unit effect of the invader (i.e., effect per unit cover). We estimated  $E$  for each invader and tested for significance of its impacts on natives using generalized linear mixed models (PROC GLIMMIX, SAS version 9.3; SAS Institute, Cary, North Carolina, USA). We ran a separate model for each exotic species deemed to have sufficient data to support the analysis; defined as invaders occurring in >5% of the plots (>32 of 620), all of which also occurred at >15% of the sites (>4 of 31). This cutoff represented a natural break in the data, below which detections were relatively sparse. Data from all plots were included in analysis of each species. The response variable was percent cover of native species per plot, derived by summing cover values across native species. Cover of the focal invader was treated as a fixed factor, as was cover of other exotics, summed across taxa per plot. As such, we allowed for additive effects of multiple invaders. We also added the interaction of focal invader cover and other invader cover to the base model to allow for synergistic effects among invaders, albeit at a rather crude scale (i.e., all other invaders lumped). In no case did this interaction term improve Akaike information criterion (AIC) scores (see *Results*), so we excluded it from final models for simplicity. Similarly, we tested for nonlinear relationships between native and focal invader cover by including a second-order polynomial term in the base model, suggested from inspection of scatterplots and consistent with other studies examining nonlinear invader impacts (Kedzie-Webb et al. 2001, Thiele et al. 2010). Because the more complex models were not well-supported, we excluded the polynomial term from final models (see *Results*). Hence, the parameter estimate (i.e., slope;  $E$ ) for the focal invader cover term represented the change in native cover associated with a one-unit increase in invader cover when controlling for cover of other exotics. We also ran a separate model to depict the overall relationship between cover of natives and exotics, testing for nonlinearity as described for individual invaders. Year and site were included in all models as random factors. To test for spatial autocorrelation among plots at each site (rather than assuming all plots at a site were equally correlated), we also included spherical spatial covariance terms in models, but they did not improve AIC scores and hence were not retained.

Gaussian models that fit a normal distribution to the response variable are often used to examine invader effects, but such models may not be the most appropriate (Thiele et al. 2010). In our case,

the dependent variable, native cover, was a composite measure typically derived from cover values of many species in a plot (range of 0–16 species). Hence, native cover could exceed 100% and as such, bound distributions such as the beta were not fully representative and complicated interpretation of coefficients. As an alternative, we tested for fit of the normal distribution by inspecting scatterplots of residuals against predicted values for all impact models. These explorations revealed no substantial deviation from assumptions of normality, linearity, or homoscedasticity (Tabachnick and Fidell 1989). Transformation (log, arcsin square root) of native cover to address minor positive skewness did not improve scatterplots, so we used the untransformed variable with the normal distribution in final models.

We used the significance of the focal invader cover term in each final model to indicate which invaders showed evidence of impacting native cover. For species with significant effects ( $P \leq 0.05$ ), the slope estimate,  $E$ , was always negative. Hence, we used the absolute value of the slope estimate to calculate impact as conceptualized by Parker et al. (1999). As applied, impact scores represented the total reduction in native cover associated with each exotic species across all sampled grasslands, i.e., the local invader effect summed across the landscape scale. For species lacking significant relationships with native cover, we set  $E$  to zero when calculating impact scores given that slope estimates did not differ statistically from zero. We used logistic regression to test whether the likelihood that an invader showed evidence of impact (yes vs. no) was related to invasiveness metrics ( $R$  and  $A$ ), life-history strategy, and/or life-form. To elucidate patterns of invader behavior, we examined correlations among components of impact ( $R$ ,  $A$ , and  $E$ ) using Spearman rank correlation coefficients (given nonnormality of variables). We also used a parallel analysis to compare the influence of these variables on invasiveness and impact scores. All cross-species analyses were limited to those 25 well-sampled exotics, as defined previously (see Appendix S1: Table S11 for details on all sampled species). We compared those invaders that showed evidence of significant impacts (all impacts in this study significant at  $P = 0.05$ ) on native plant cover in our system to the Montana noxious weed list to determine what proportion of these high-impact invaders were recognized by the list (Montana noxious weed list available online).<sup>7</sup>

## RESULTS

Sampled grasslands represented a range of invasion levels, with mean exotic cover per site ranging 1–60% ( $\bar{x} = 25\% \pm 3\%$ ; mean  $\pm$  SE), which represented 3–83%

<sup>7</sup><http://agr.mt.gov/agr/Programs/Weeds/PDF/2015WeedList.pdf>

of the mean total herbaceous cover per site ( $\bar{x} = 47\% \pm 4\%$ ). The number of exotic species per site varied 3–24 ( $\bar{x} = 13 \pm 1$  species), representing 9–57% of the total herbaceous species richness per site ( $\bar{x} = 40\% \pm 2\%$ ). Overall, we identified 48 exotic species and 141 natives, i.e., 25% of the herbaceous flora was introduced.

The number of plots occupied by each invader,  $R$  (range), was not significantly correlated ( $r^2 < 0.01$ ,  $P = 0.97$ ) with its mean cover per plot,  $A$  (local abundance), as invasion patterns differed substantially among the 25 exotic species analyzed (Fig. 1). Overall, variation in invasiveness scores,  $R \times A$ , was driven weakly by  $R$  ( $r^2 = 0.13$ ,  $P = 0.08$ ) and strongly by  $A$  ( $r^2 = 0.83$ ,  $P < 0.0001$ ). Of those 10 invaders occurring in the highest number of plots ( $>15\%$  of  $n = 620$ , high  $R$ ), four of these species also had relatively high mean cover ( $>3\%$ , high  $A$ ) and ranked high in terms of invasiveness scores (Table 1, Fig. 1). The annual grass, *B. tectorum*, topped the invasiveness chart with a score more than four times that of any other invader, as it occurred in the most plots (74% of  $n = 620$ ) and at the highest mean cover ( $\bar{x} = 14.9\%$ ). Other invaders with both high  $R$  and high  $A$  and hence high invasiveness scores were the perennial forbs *Centaurea stoebe* and *Potentilla recta* and the annual forb *Veronica verna*.

In contrast, six of 10 high  $R$  invaders had relatively low mean cover ( $<3\%$ ) and did not rank in the top 10 for invasiveness scores. These invaders with high  $R$  but low  $A$  were annuals or biennials and included forbs such as *Tragopogon dubius*, *Arenaria serpyllifolia*, and *Alyssum alyssoides*. Of those 15 invaders with relatively low  $R$  (occurring in  $<15\%$  of plots), seven species had high mean cover and ranked high in terms of invasiveness scores. These exotics with low  $R$  but high  $A$  were mostly perennials, including the forbs *Euphorbia esula* and *Linaria dalmatica* and the grasses *Poa pratensis* and *P. bulbosa*. In contrast, the eight invaders with both low  $R$  and low  $A$  were mostly short-lived species and ranked low in terms of invasiveness scores.

Of those 25 exotics analyzed, 11 species had significant negative relationships with native cover, i.e., slope estimate or per unit effect,  $E < 0$ , suggesting local-scale impacts on native taxa. Significant relationships between native and focal invader cover were linear, as models including nonlinear terms were not well-supported according to AIC scores ( $\Delta AIC = 3.6 \pm 0.8$ ; Appendix S2: Table S21). Relationships between native and focal invader cover also controlled for cover of other exotics present in plots, which varied negatively with native cover in all cases ( $P < 0.001$ ; Table 1). We found no evidence for synergistic relationships among invaders, as the interaction

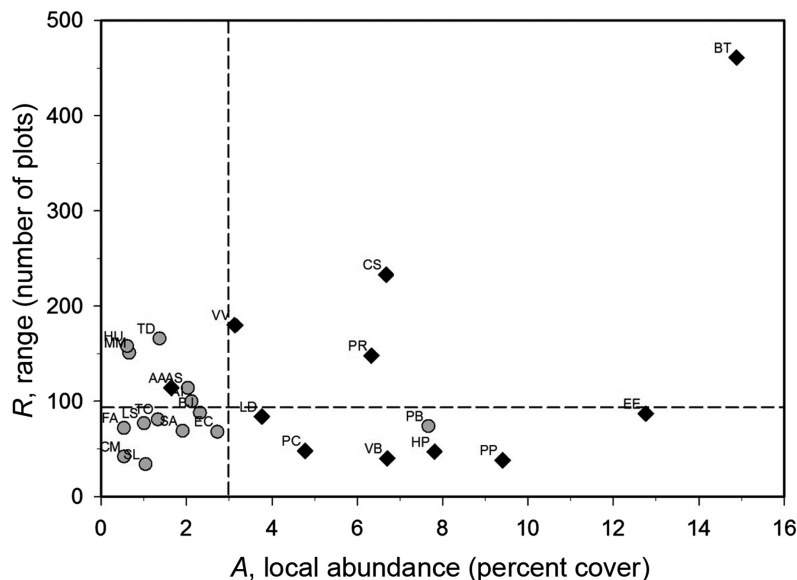


FIG. 1. The relationship between  $A$  (local abundance; mean percent cover in 1-m<sup>2</sup> plots) and  $R$  (range; the total number of plots occupied) for 25 exotic species in grasslands of west-central Montana, USA. Black diamonds represent species having significant impacts on native plant abundance within the system. Gray circles indicate species with no significant impacts on native plant abundance. Horizontal and vertical reference lines highlight natural breaks among subgroups signifying low and high levels of  $A$  and  $R$ , respectively (see Results). Species are *Alyssum alyssoides* (AA), *Agrostis interrupta* (AI), *Arenaria serpyllifolia* (AS), *Bromus japonicus* (BJ), *B. tectorum* (BT), *Camelina microcarpa* (CM), *Centaurea stoebe* (CS), *Erodium cicutarium* (EC), *Euphorbia esula* (EE), *Filago arvensis* (FA), *Hypericum perforatum* (HP), *Holosteum umbellatum* (HU), *Linaria dalmatica* (LD), *Lactuca serriola* (LS), *Myosotis micrantha* (MM), *Poa bulbosa* (PB), *P. compressa* (PC), *P. pratensis* (PP), *Potentilla recta* (PR), *Sisymbrium altissimum* (SA), *S. loeselii* (SL), *Tragopogon dubius* (TD), *Taraxacum officinale* (TO), *Verbascum blattaria* (VB), and *Veronica verna* (VV).

between focal invader cover and other invader cover did not improve AIC scores ( $\Delta\text{AIC} = 4.7 \pm 0.5$ ; Appendix S2: Table S1). Hence, invader effects appeared to be additive, with many species contributing to the overall negative relationship between native and exotic cover (Fig. 2). Across all 25 species analyzed, slope estimates for focal invader cover,  $E$ , did not vary significantly with the number of plots occupied,  $R$  ( $r^2 = 0.12$ ,  $P = 0.1$ ), but varied positively with increasing mean cover,  $A$  ( $r^2 = 0.18$ ,  $P = 0.03$ ). The likelihood that an invader showed evidence of impact (i.e.,  $E < 0$  at  $P \leq 0.05$ ) increased significantly with mean cover (logistic regression: odds ratio = 2.7,  $\chi^2 = 4.8$ ,  $P = 0.03$ ) but not with the number of plots occupied (odds ratio = 1.0,  $\chi^2 = 0.5$ ,  $P = 0.46$ ), life-history strategy (perennial vs. not; odds ratio = 7.1,  $\chi^2 = 1.0$ ,  $P = 0.33$ ), or life-form (forb vs. grass; odds ratio = 26.0,  $\chi^2 = 1.4$ ,  $P = 0.25$ ).

Driven in part by the positive association between the likelihood of invader impact and mean invader cover, impact scores,  $R \times A \times E$ , scaled closely with invasiveness scores,  $R \times A$ , with several notable exceptions (Table 1). The four high  $R$ –high  $A$  species topped impact scores as they had invasiveness scores, with the annual grass *B. tectorum* again ranking first. Of the seven remaining invaders with evidence of impacting natives, all but one was a low  $R$ –high  $A$  species with an invasiveness score in or near the top 10. Hence, 10 of 11 invaders with evidence of impact had high invasiveness scores and occurred at high  $A$ , i.e., high mean cover, but not necessarily at high  $R$ , i.e., in a large number of plots. The exception, *A. alyssoides*, was the one low  $A$  species to make the impact list; this widespread annual forb showed evidence of impact despite occurring at low mean cover and ranking 16th

TABLE 1. Components of exotic species invasiveness and impact based on surveys of  $n = 620$  1-m<sup>2</sup> plots in 31 grasslands across west-central Montana, USA.

| Species                                  | Type | Invasiveness |      |              | Impact |       |        |              | Other invaders |       |        |
|------------------------------------------|------|--------------|------|--------------|--------|-------|--------|--------------|----------------|-------|--------|
|                                          |      | $R$          | $A$  | Rank (score) | $E$    | $F$   | $P$    | Rank (score) | Slope          | $F$   | $P$    |
| <i>Bromus tectorum</i>                   | AG   | 461          | 14.9 | 1 (6861)     | −0.39  | 129.3 | <0.001 | 1 (2676)     | −0.50          | 147.9 | <0.001 |
| <i>Centaurea stoebe</i> <sup>†</sup>     | PF   | 233          | 6.7  | 2 (1555)     | −0.72  | 30.5  | <0.001 | 2 (1120)     | −0.43          | 252.1 | <0.001 |
| <i>Euphorbia esula</i> <sup>†</sup>      | PF   | 87           | 12.8 | 3 (1111)     | −0.53  | 37.5  | <0.001 | 3 (589)      | −0.43          | 229.1 | <0.001 |
| <i>Potentilla recta</i> <sup>†</sup>     | PF   | 148          | 6.3  | 4 (937)      | −0.50  | 19.1  | <0.001 | 4 (468)      | −0.43          | 242.5 | <0.001 |
| <i>Veronica verna</i>                    | AF   | 180          | 3.1  | 6 (564)      | −0.57  | 9.4   | 0.002  | 5 (322)      | −0.43          | 244.5 | <0.001 |
| <i>Linaria dalmatica</i> <sup>†</sup>    | PF   | 84           | 3.8  | 9 (316)      | −0.75  | 14.4  | <0.001 | 6 (237)      | −0.43          | 250.2 | <0.001 |
| <i>Poa pratensis</i>                     | PG   | 38           | 9.4  | 8 (358)      | −0.64  | 19.3  | <0.001 | 7 (229)      | −0.43          | 244.9 | <0.001 |
| <i>Alyssum alyssoides</i>                | AF   | 114          | 1.7  | 16 (188)     | −1.17  | 3.9   | 0.05   | 8 (220)      | −0.44          | 256.8 | <0.001 |
| <i>P. compressa</i>                      | PG   | 48           | 4.8  | 12 (229)     | −0.79  | 20.1  | <0.001 | 9 (181)      | −0.43          | 242.3 | <0.001 |
| <i>Hypericum perforatum</i> <sup>†</sup> | PF   | 47           | 7.8  | 7 (367)      | −0.44  | 8.3   | 0.004  | 10 (162)     | −0.44          | 253.3 | <0.001 |
| <i>Verbascum blattaria</i>               | BF   | 40           | 6.7  | 10 (268)     | −0.59  | 6.4   | 0.01   | 11 (158)     | −0.43          | 246.5 | <0.001 |
| <i>P. bulbosa</i>                        | PF   | 74           | 7.7  | 5 (568)      | −0.06  | 0.2   | 0.68   | (0)          | −0.45          | 267.7 | <0.001 |
| <i>Arenaria serpyllifolia</i>            | AF   | 114          | 2.0  | 11 (232)     | −0.16  | 0.3   | 0.61   | (0)          | −0.44          | 254.2 | <0.001 |
| <i>Tragopogon dubius</i>                 | BF   | 166          | 1.4  | 13 (228)     | −0.44  | 0.9   | 0.35   | (0)          | −0.44          | 256.1 | <0.001 |
| <i>Agrostis interrupta</i>               | AG   | 100          | 2.1  | 14 (212)     | 0.14   | 0.2   | 0.69   | (0)          | −0.44          | 260.1 | <0.001 |
| <i>B. japonicus</i>                      | AG   | 88           | 2.3  | 15 (204)     | −0.06  | 0.1   | 0.83   | (0)          | −0.44          | 258.2 | <0.001 |
| <i>Erodium cicutarium</i>                | AF   | 68           | 2.7  | 17 (186)     | −0.44  | 1.3   | 0.26   | (0)          | −0.44          | 248.4 | <0.001 |
| <i>Sisymbrium altissimum</i>             | ABF  | 69           | 1.9  | 18 (132)     | −0.74  | 2.8   | 0.10   | (0)          | −0.43          | 240.7 | <0.001 |
| <i>Taraxacum officinale</i>              | PF   | 81           | 2.3  | 19 (108)     | −0.91  | 1.3   | 0.26   | (0)          | −0.44          | 252.6 | <0.001 |
| <i>Myosotis micrantha</i>                | AF   | 151          | 0.7  | 20 (100)     | −2.20  | 2.0   | 0.16   | (0)          | −0.43          | 244.2 | <0.001 |
| <i>Holosteum umbellatum</i>              | AF   | 158          | 0.6  | 21 (97)      | 0.69   | 0.3   | 0.59   | (0)          | −0.44          | 255.1 | <0.001 |
| <i>Lactuca serriola</i>                  | ABF  | 77           | 1.0  | 22 (78)      | −1.09  | 0.9   | 0.35   | (0)          | −0.44          | 248.4 | <0.001 |
| <i>Filago arvensis</i>                   | AF   | 72           | 0.5  | 23 (39)      | −1.01  | 0.1   | 0.73   | (0)          | −0.44          | 255.6 | <0.001 |
| <i>S. loeselii</i>                       | ABF  | 34           | 1.0  | 24 (36)      | −1.69  | 1.2   | 0.28   | (0)          | −0.44          | 249.6 | <0.001 |
| <i>Camelina microcarpa</i>               | AF   | 42           | 0.5  | 25 (23)      | −7.12  | 2.0   | 0.16   | (0)          | −0.43          | 252.1 | <0.001 |

Notes: Invasiveness scores are the product of range ( $R$ ), number of plots occupied, local abundance ( $A$ ), and mean cover per plot (%). Impact scores incorporated  $E$ , the per unit effects of each invader on native species abundance, as estimated by the slope term in a mixed model regressing native cover against focal invader cover while controlling for other invader cover (see *Methods: Derivation of invasiveness and impact scores*). Species with impact scores of 0 correspondingly had no impact rank. Species are categorized according to life-form and growth form; annual (A), biennial (B), or perennial (P), and forb (F) or grass (G). The intercept term in models varied 37.2–37.8, representing cover (%) of native species in plots with no exotic species. For the focal invader term and other invader term, respectively,  $df = 1$  and 564–616 and  $df = 1$  and 603–616. *Veronica verna* included *V. arvensis*, a less common ecological equivalent that is difficult to distinguish, *Alyssum alyssoides* includes *A. desertorum*, a less common ecological equivalent that is difficult to distinguish.

<sup>†</sup>Listed as a noxious weed by the state of Montana.

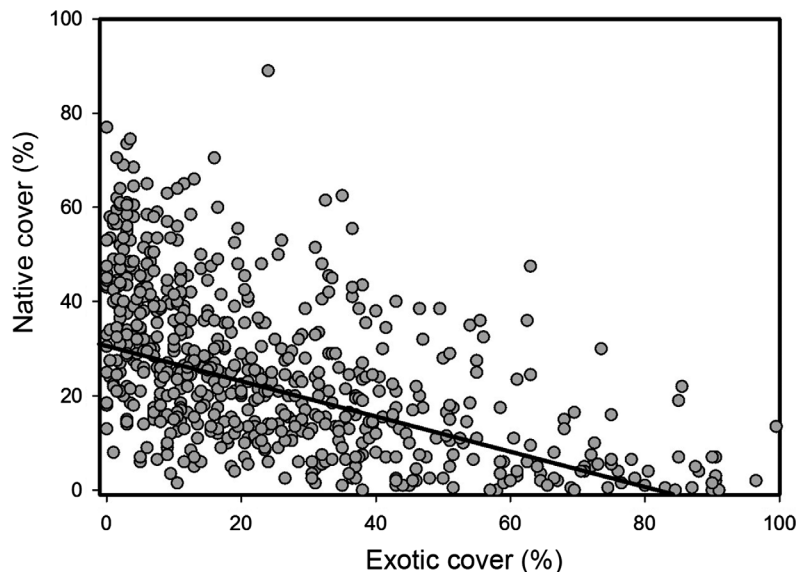


FIG. 2. The relationship between native and exotic cover based on data from  $n = 620$  1-m<sup>2</sup> plots in 31 grasslands across west-central Montana, analyzed via a mixed model (intercept = 37.3; slope or  $E = -0.44$ ,  $F_{1,609} = 256.8$ ,  $P < 0.001$ ). The model was not improved by addition of a second-order polynomial term representing nonlinear effects ( $\Delta\text{AIC} = 6.7$ ; see *Results*).

in terms of invasiveness. For the remaining 10 impact species, incorporation of estimated per unit effects into invasiveness scores shifted rankings little, as slope parameters,  $E$ , varied little compared to variation in mean cover,  $A$ , and especially the number of plots occupied,  $R$  (Table 1). Hence, across the group of 11 species with significant local-scale effects on native cover, impact scores were driven primarily by  $R$  ( $r^2 = 0.65$ ,  $P = 0.003$ ) rather than  $A$  ( $r^2 = 0.08$ ,  $P = 0.4$ ) or  $E$  ( $r^2 = 0.11$ ,  $P = 0.31$ ). In contrast, the 14 species with no evidence of local-scale effects had impact scores of 0 regardless of their invasiveness score. The list of “no impact” invaders included five of six high  $R$ –low  $A$  species identified previously, most of which had mid-range invasiveness scores due to their widespread occurrence. Also included on the no-impact list were eight species with both low  $R$  and low  $A$  and hence relatively low invasiveness scores. Remaining was the one no-impact species with high  $A$ , the perennial grass *P. bulbosa*, which ranked fifth in terms of invasiveness yet showed no evidence of impact.

Across the 25 species analyzed, invasiveness and impact metrics were correlated at a fairly high level ( $r^2 = 0.62$ ,  $P < 0.001$ ), reflecting the fact that the highest scoring impact species also had high invasiveness scores, while no-impact species tended to have low invasiveness scores (Table 1). However, we emphasize that a significant portion of the variation in impact scores was not accounted for by invasiveness scores, as (1) several invaders with no impact ranked in the middle of invasiveness scores given widespread occurrence coupled with low local abundance (high  $R$ –low

$A$ ), and (2) the invaders *A. alyssoides* (high  $R$ –low  $A$ ) and *P. bulbosa* (low  $R$ –high  $A$ ) defied patterns predicted by their invasiveness scores and specifically their local abundance, as detailed previously.

## DISCUSSION

The limited empirical data available on invader impacts has presented a major barrier to understanding and managing invasions for well over a decade (Pyšek et al. 2012, Barney et al. 2013). Here, we demonstrate a plot-based method (*sensu* Parker et al. 1999) for quantifying invader impacts at the community scale that addresses many of the major challenges inhibiting progress in this area, while also accounting for the ubiquitous problem of multispecies invasions. Our results provide the first empirically based impact rankings for multiple invaders developed at the community level and offer valuable insights regarding how the specific components of impact (range, local abundance, and per capita/unit effect) co-vary to influence measures of plant invasiveness vs. impact. We also demonstrate that for the 25 species we examined, invader impacts on abundance of native plants varied linearly with invader abundance at the local scale, and interactions among multiple invaders did not influence the magnitude of their impacts. Finally, in comparing our empirically based impact rankings with the noxious weed list for this region, we found that our plot-based metrics identified invaders having significant ecological impacts that were not recognized by the noxious weed list.

To understand and manage invasions, we must determine what factors separate strong invaders, those having significant impacts in native systems, from weak invaders, which have negligible impacts and even function like natives (Ortega and Pearson 2005). Our results demonstrate that while some strong invaders, including some of the worst invaders in our system (*B. tectorum*, *C. maculosa*, and *P. recta*), exhibited both high local abundance and widespread distributions as might be expected, other high-impact invaders, including several listed noxious weeds (Table 1), exhibited high local abundance with relatively moderate (*E. esula*, *L. dalmanica*) or even constrained distributions (*H. perforatum*, *P. pratensis*, and *V. blattaria*; Fig. 1). This pattern could suggest that these latter species are still increasing their ranges and hence their regional-scale impacts. Notably, some high-impact species with future range expansion potential are not currently recognized as problem species by the noxious weed list (e.g., *V. blattaria*, Table 1). Empirically derived impact estimates may represent equilibrium conditions for some invaders who have been in the system for extensive periods, but these estimates likely represent snapshots of active trajectories for many species. Future and potential long-term impacts could be evaluated for these species by combining estimates of local abundance and per capita/unit effects with estimates of projected ranges, i.e., replacing  $R$  with  $R_{t+1}$ , using habitat projection models (e.g., Rew et al. 2005). Combining current and future impact rankings would be extremely valuable for setting management targets.

We also show that some species may become very successful invaders achieving widespread distributions, but still have negligible impacts on natives if they are unable to attain high local abundance. Such low-impact invaders in our study included several ubiquitous species, most of which were short-lived forbs (Ortega and Pearson 2005). For example, the biennial forb *T. dubius* is widespread within our system and across North America (Clements et al. 1999), but we found no significant impacts of this species. Interestingly, recent research suggests that the local abundance of this species is greatly suppressed by native generalist consumers (Pearson et al. 2012). Our results suggest that the potential impact of this species and conversely the ecosystem services provided via its suppression by native consumers may be directly proportional to the reductions in abundance they bring about (due to linear impacts, see following paragraphs). *T. dubius*'s local abundance increases fivefold in the absence of consumers (Pearson et al. 2012). Such an increase would elevate the local abundance for this species to levels associated with significant impacts in this system (mean cover >3%; Table 1). This example demonstrates how empirically based impact calculations can provide a baseline for evaluating how changes in an invader's local abundance in response to changing conditions

(e.g., climate or biotic) may influence its future impacts on native species.

Decomposing the components of invader impacts demonstrated that the local abundance an introduced plant achieved was the primary factor associated with declines in native plant abundance in our system. Local abundance but not range was positively associated with the likelihood that an invader had significant impacts on native plant abundance. While expansion of any species' populations over space should allow local-scale impacts to accumulate, this only resulted in significant impacts for invaders that achieved mean local densities greater than ~3% cover (with the exception of *A. alyssoides*; Table 1, Fig. 1). Although our evaluation of per unit effects was key to determining which invaders had significant impacts, incorporation of per unit effect estimates, i.e.,  $E$ , into Parker's equation changed invader rankings little overall. We attribute this result to the nature of the local abundance metric we used. Percent cover essentially integrates plant size and density into a single metric of biomass per unit space (Thiele et al. 2010, Barney et al. 2013). In our system, the relationship between native and focal invader cover was similar across 11 high-impact exotics, i.e., these invaders had similar effects per unit biomass. This result is consistent with plant competition theory, which indicates that because plants compete for the same resources in a common stratum, competitive effects among plant species are similar once biomass is accounted for (Goldberg and Werner 1983, Schwinning and Weiner 1998). Given that competitive strength commonly correlates with plant size (Schwinning and Weiner 1998), the actual per capita effect of e.g., *B. tectorum*, which is a small annual grass, may have been much less than that of the larger perennial forb, *E. esula*. Yet both invaders occurred at comparably high mean cover, suggesting that the smaller species attained higher densities, which resulted in similar local-scale biomass and hence impacts relative to the larger species. In short, interspecific variation in actual per capita effects appeared to be subsumed by our local abundance metric, percent cover, which itself was predictive of impact. If this pattern is generalizable, percent cover alone could provide an integrative index of invader impacts for plants and other sessile organisms. This also suggests that species that attain high local abundance in the early stages of invasion are most likely to have large impacts over time. However, when counts of individual organisms are used to index abundance instead of percent cover or biomass, per capita effects are likely to be important for determining the relative strength of invader impacts.

If invader impacts change with invader abundance in a nonlinear manner, this can create threshold responses that greatly complicate the understanding and management of invasions (Yokomizo et al. 2009, Thiele et al. 2010, Barney et al. 2013). We know of only one study that empirically quantified the relationship between local invader abundance and impact in

the context of Parker et al. (1999). Thiele et al. (2010) found nonlinear effects of *Heracleum mantegazzianum* cover on native plant species richness resulting from negligible impacts at low invader cover and significant impacts at high cover. We tested for nonlinearity of invader impacts for 25 exotic plant species, providing one of the most comprehensive empirical assessments of this question to date. We found little evidence that the relationship between invader cover and native cover was nonlinear across the 25 species we examined. This finding suggests that management actions that reduce invader abundance should have monotonic reductions in invader impacts within this system, barring complicating side effects (Pearson and Ortega 2009). Notably, while Thiele et al. (2010) found nonlinear impacts of *H. mantegazzianum* on native species richness, they observed linear impacts of the invader on native plant cover in accordance with our findings. These differing outcomes likely stem from the fact that one response variable, plant abundance (cover, biomass, etc.), is additive, while the other, species richness, is not (Thiele et al. 2010). Hence, one might expect to find nonlinear effects of invader abundance on native species richness and not on native abundance. These findings raise an important question as to what response metric should be the focus of impact studies as they relate to invasive species management. While it is valuable to monitor native species richness responses to invasion, the effects of invaders on native species richness derive from invader impacts on native species' populations. As a result, abundance is a much more sensitive metric than richness or diversity (e.g., Ortega and Pearson 2005). Hence, we suggest that abundance is the fundamental metric to start from; other metrics may provide additional information, but they may be less sensitive for detecting changes.

An additional important consideration is that invasions may generate different impact relationships with native system components at different ecological scales. For example, it is feasible that *B. tectorum* might have nonlinear effects at the ecosystem scale that are not expressed at the local community scale. *B. tectorum* is known to impact native systems in arid regions of the western United States by creating extensive fine fuels that increase fire frequencies by an order of magnitude (Whisenant 1990), thereby shifting the system from one dominated by non-fire-adapted species to one that favors fire-adapted species and its own spread. This effect cannot take place until *B. tectorum* reaches a high enough density across the landscape to carry fire. Hence, it is very possible that *B. tectorum*'s impacts measured at the local scale are linear as we found, but if measured at the ecosystem scale, they may become strongly nonlinear, with thresholds occurring once *B. tectorum* achieves sufficient landscape coverage to create an ecosystem-level feedback. This scenario raises a general question about how certain processes may generate feedbacks at different ecological scales. Many introduced

plants produce higher litter levels than natives due to higher growth rates, a mechanism of impact (Ehrenfeld 2003, Farrer and Goldberg 2009) that may function linearly at the local neighborhood scale while having threshold effects at the ecosystem scale (D'Antonio and Vitousek 1992). Understanding how impact mechanisms function across ecological scales is a critical area for future research.

The concept of invasional meltdown was introduced to recognize the potential for multiple invaders to facilitate each other within recipient communities (Simberloff and Von Holle 1999). The phenomenon of multiple invaders is ubiquitous, with few invaded habitats likely experiencing a single invader (Kuebbing et al. 2013). We found a mean of 13 exotic plant species inhabiting grasslands of west-central Montana. Yet most research targets single invaders (Kuebbing et al. 2013). Some of the best examples of invasional meltdown involve multiple trophic levels via apparent competition, pollination, and other facilitating interactions (O'Dowd et al. 2003, Simberloff 2006, Relva et al. 2010), but to what extent do invaders within the stratum of primary producers interact to generate synergistic impacts? We explored this question for 25 invaders. Our approach was somewhat crude in that we isolated each target invader and treated the remaining invaders as a group rather than looking at all possible pairwise and multiple invader combinations. Additionally, our response variable was total native cover, combined across species. Hence, our approach might mask some interactive effects, particularly for uncommon invaders or natives, and results could differ for other response metrics such as soil nutrient pools, etc. Nonetheless, our approach should have captured major interactive effects on native cover. While we found evidence for additive effects of invaders, we did not find support for interactive effects indicative of synergistic processes or invasional meltdown. Invading species in our system may still interact to influence patterns of exotic abundance, but we did not find evidence that such interactions altered the total impact of exotics on natives. Certainly facilitative interactions occur among plant invaders, particularly for ecosystem engineers (Crooks 2002, Levine et al. 2003), but how invasional meltdown relates to cumulative impacts of invaders is not well understood.

The term invasive has been used extensively to infer high impact, but this usage has generated a semantic debate (Richardson et al. 2000, Ricciardi and Cohen 2007, Barney et al. 2013). We suggest that this usage is unjustified from a quantitative perspective and muddles understandings of the factors and traits that might differentiate high-impact invaders from invaders that are highly successful but have no measurable impact. Ricciardi and Cohen (2007) found little correlation between invasiveness and invader impact using subjective metrics for invader impacts. As we show here, species can achieve high success in establishing and

becoming widespread within a new range, i.e., be highly invasive, and still have no measurable impact on native species. While we found a reasonable correlation between species' invasiveness scores and their estimated impacts on native plant abundance, we attribute this to the fact that cover, our metric of local abundance, essentially subsumed per capita effects into a species' invasiveness score as discussed previously. Other factors such as ecological scale may also be important in differentiating invasiveness from invader impact (Ricciardi and Cohen 2007). Given that plant traits driving invasiveness may differ from those driving impact, we suggest that differentiating invasiveness from invader impact is a necessary first step in linking invader traits to invasion outcomes. For example, *T. dubius* has a windborne seed that effectively disperses over great distances (Clements et al. 1999), presumably contributing to its invasion success, but this same seed is also highly palatable to rodents, a trait linked to its limited local abundance (Pearson et al. 2012). In contrast, seeds of *C. stoebe* may be chemically defended from rodent foraging, a trait that appears to favor higher local abundance and hence impact in this species (Pearson et al. 2011). Focusing future studies toward distinguishing those traits associated with invasiveness from those linked to invader impacts could help to advance the prediction of high-impact invaders (Pyšek and Richardson 2007).

An important assumption underlying invader impact metrics generated from observational data is that differences in native response variables between invaded and uninvaded plots reflect invader impact (Thiele et al. 2010, Pyšek et al. 2012, Barney et al. 2013). While negative correlations between the abundance of invaders and natives may commonly result from competitive displacement of natives, such patterns can also be driven by extrinsic factors. For example, directional shifts in extrinsic factors associated with climate change or increased human-mediated disturbance may favor exotics over natives in situations where exotics are passengers, not drivers of observed changes (sensu MacDougall and Turkington 2005). In such scenarios, invasion may simply be a passive result of changing ecological conditions that favor the newcomers, but even as passengers, invaders may still exert substantial competitive impacts on natives, e.g., via founder effects (Seabloom et al. 2003, MacDougall and Turkington 2005). Regardless of the nature of native displacement, so long as the effect is not ephemeral, correlational metrics provide valuable indices of community change. Given that these mechanisms underlying community change are typically unknown, we suggest that the term apparent impact is more reflective of the correlational nature of so-called impact metrics derived from survey data. Ultimately, experimental manipulation is required to identify the mechanisms driving the observed changes, and this step is important for managing species once they are targeted.

In comparing our empirically derived estimates of invader impact with the noxious weed list for Montana, we found that the noxious weed list included 45% of the species we found to have significant apparent impacts in the system, but it missed 55% (of  $n = 11$ ). Notably, the species with the highest impact score, *B. tectorum*, is not listed as a noxious weed (although it is recognized as a lower-ranking species with potential impacts). These results can be attributed to the fact that some species are precluded from noxious weed lists for political reasons, while other species of high impact simply go unrecognized due to a lack of data documenting their impacts (Quinn et al. 2013). Conversely, of those 25 invaders we tested for impacts, 100% (of  $n = 5$ ) listed as noxious weeds showed evidence of impact. The noxious weed list for Montana also includes two species, *Cirsium arvense* and *Leucanthemum vulgare*, which occurred in <1% of the grassland plots we surveyed and hence could not be tested for impact (Appendix S1: Table S1). However, these species are clearly abundant in other habitats in our area (D. E. Pearson, *personal observation*), where they may have impacts. In short, invasion outcomes are community specific and our results are specific to the community type that we sampled. We suggest that while noxious and other weed lists can be very helpful starting guides for management, using such lists to categorize invaders for testing invasion hypotheses and driving invasion theory may be problematic. The methods recently developed for quantifying invader impacts (this study, Thiele et al. 2010, Barney et al. 2013) should be empirically applied as widely as possible to advance understandings of invader impacts and to better guide invasive species management.

#### ACKNOWLEDGMENTS

We thank B. Maxwell and two anonymous reviewers for helpful comments on this work. This research was made possible by the Bureau of Land Management, the Bitterroot and Lolo National Forests, the Montana Department of Natural Resources and Conservation, Montana Fish Wildlife and Parks, and the Salish and Kootenai Confederated Tribes providing access to conduct surveys. We are grateful to J. Birdsall, C. Casper, L. Glasgow, E. Masin, A. Pons, and J. Smith for their dedicated work in the field and to C. Brandt, P. Lesica, and P. Stickney for plant identification. Funding was provided by the Montana Noxious Weed Trust Fund to D. E. Pearson and Y. K. Ortega, and by the President's Early Career Award for Science and Engineering to D. E. Pearson.

#### LITERATURE CITED

- Barney, J. N., D. R. Tekiel, E. S. J. Dollete, and B. J. Tomasek. 2013. What is the real impact of invasive plant species? *Frontiers in Ecology and the Environment* 11:322–329.
- Byers, J. E., et al. 2002. Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* 16:630–640.

- Clements, D. R., M. K. Upadhyaya, and S. J. Bos. 1999. The biology of Canadian weeds. 110. *Tragopogon dubius* Scop., *Tragopogon pratensis* L., and *Tragopogon porrifolius* L. Canadian Journal of Plant Science 79:153–163.
- Crooks, J. A. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166.
- Daehler, C. C. 2001. Darwin's naturalization hypothesis revisited. *The American Naturalist* 158:324–330.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Davis, M. A., and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader: a proposed nomenclature scheme for invasions ecology. *Bulletin of the Ecological Society of America* 81:226–230.
- Ehrenfeld, J. G. 2003. Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–523.
- Farrer, E. C., and D. E. Goldberg. 2009. Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications* 19:398–412.
- Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *American Journal of Botany* 70:1098–1104.
- Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emerging insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14:407–418.
- Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422.
- Kedzie-Webb, S. A., R. L. Sheley, J. J. Borkowski, and J. S. Jacobs. 2001. Relationships between *Centaurea maculosa* and indigenous plant assemblages. *Western North American Naturalist* 61:43–49.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin Desert: history, persistence, and influences to human activities. *Global Environmental Change* 6:37–52.
- Kuebbing, S. E., M. A. Nuñez, and D. Simberloff. 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biological Conservation* 160:121–129.
- Lackschewitz, K. 1991. Vascular plants of west-central Montana. General technical report INT-277. USDA Forest Service, Ogden, Utah, USA.
- Leffler, A. J., E. D. Leonard, and J. J. James. 2014. Invasion is contingent on species assemblage and invasive species identity in experimental rehabilitation plots. *Rangeland Ecology and Management* 67:657–666.
- Lesica, P. 2012. Manual of Montana vascular plants. Brit Press, Fort Worth, Texas, USA.
- Levine, J. M., M. Vila, C. M. D'Antonio, J. S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society B* 270:775–781.
- MacDougall, A. S., and R. Turkington. 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology* 86:42–55.
- Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. *Agroecosystems* 7:145–165.
- Mitchel, C. E., and A. G. Power. 2003. Release of invasive plants from fungal pathogens. *Nature* 421:625–627.
- Mueggler, W. F. and W. L. Stewart. 1980. Grassland and shrubland habitat types of western Montana. General technical report INT-66. USDA Forest Service, Ogden, Utah, USA.
- O'Dowd, D. J., P. T. Green, and P. S. Lake. 2003. Invasional 'meltdown' on an oceanic island. *Ecology Letters* 6:812–817.
- Ortega, Y. K., and D. E. Pearson. 2005. Strong versus weak invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications* 15:651–661.
- Parker, I. M., et al. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1:3–19.
- Parker, J. D., D. E. Burkepile, and M. E. Hay. 2006. Opposing effects of native and exotic herbivores on plant invasions. *Science* 311:1459–1461.
- Parker, J. D., et al. 2013. Do invasive species perform better in their new ranges? *Ecology* 94:985–994.
- Pearson, D. E., and Y. K. Ortega. 2009. Managing invasive plants in natural areas: moving beyond weed control. Pages 1–21 in R. V. Kingely, editor. *Weeds: management, economic impacts and biology*. Nova Science Publishers, Hauppauge, New York, USA.
- Pearson, D. E., R. M. Callaway, and J. L. Maron. 2011. Biotic resistance via granivory: establishment by invasive, naturalized, and native asters reflects generalist preference. *Ecology* 92:1748–1757.
- Pearson, D. E., T. Potter, and J. L. Maron. 2012. Biotic resistance: exclusion of native rodent consumers releases populations of a weak invader. *Journal of Ecology* 100:1383–1390.
- Pyšek, P., and D. Richardson. 2007. Traits associated with invasiveness in alien plants: where do we stand? *Biological Invasions* 193:97–125.
- Pyšek, P., V. Jarosik, P. E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vila. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology* 18:1725–1737.
- Quinn, L. D., J. N. Barney, J. S. McCubbins, and A. B. Endres. 2013. Navigating the "noxious" and "invasive" regulatory landscape: suggestions for improved regulation. *BioScience* 63:124–131.
- Relva, M. A., M. A. Nuñez, and D. Simberloff. 2010. Introduced deer reduce native plant cover and facilitate invasion of non-native tree species: evidence for invasional meltdown. *Biological Invasions* 12:303–311.
- Rew, L. J., B. D. Maxwell, and R. Aspinall. 2005. Predicting the occurrence of nonindigenous species using environmental and remotely sensed data. *Weed Science* 53:236–241.
- Ricciardi, A., and J. Cohen. 2007. The invasiveness of an introduced species does not predict its impact. *Biological Invasions* 9:309–315.
- Richardson, D. M., P. Pyšek, M. Rejmanek, M. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization of invasive alien plants: concepts and definitions. *Diversity and Distributions* 6:93–107.
- Schwinning, S., and J. Weiner. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* 113:447–455.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences USA* 100:13384–13389.
- Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9:912–919.

- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21–32.
- Sun, Y., A. R. Collins, U. Schaffner, and H. Müller-Schärer. 2013. Dissecting impact of plant invaders: do invaders behave differently in the new range? *Ecology* 94:2124–2130.
- Tabachnick, B. G., and L. S. Fidell. 1989. Using multivariate statistics. HarperCollins, New York, New York, USA.
- Thiele, J., J. Kollmann, and B. Markussen. 2010. Impact assessment revisited: improving the theoretical basis for management of invasive alien species. *Biological Invasions* 12:2025–2035.
- Thill, D. C., K. G. Beck, and R. H. Callihan. 1984. The biology of downy brome (*Bromus tectorum*). *Weed Science* 32:7–12.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. General technical report INT-386. US Department of Agriculture, Forest Service, Intermountain Research Station, Fort Collins, Colorado, USA.
- Yokomizo, H., H. P. Possingham, M. B. Thomas, and Y. M. Buckley. 2009. Managing the impact of invasive species: the value of knowing the density-impact curve. *Ecological Applications* 19:376–386.

#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1890/14-2345.1/supinfo>