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ORIGINAL PAPER

# Darwin's naturalization hypothesis up-close: Intermountain grassland invaders differ morphologically and phenologically from native community dominants

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**Abstract** Darwin's naturalization hypothesis predicts that successful invaders will tend to differ taxonomically from native species in recipient communities because less related species exhibit lower niche overlap and experience reduced biotic resistance. This hypothesis has garnered substantial support at coarse scales. However, at finer scales, the influence of traits and niche use on invasibility and invader impacts is poorly understood. Within grasslands of western Montana, USA, we compared morphological and phenological traits for five top exotic invasive forbs and five dominant native forbs using multivariate techniques to examine niche separation between exotics and natives. Exotic forbs differed from native forbs in multivariate space. Phenologically, native forbs synchronized vegetative growth with bolting and flowering early in spring. In contrast, exotics initiated vegetative growth concurrent with natives but bolted and flowered later. Morphologically, vegetative growth of exotics was three times shorter and narrower, but flowering stem growth was 35% taller and 65% wider than the natives. Collectively, these patterns suggest different strategies of resource uptake and allocation. Additionally, following wildfire, survival was four times higher for exotics compared to natives, and three times more of the surviving exotics flowered. The exotics we examined appeared to be exploiting an empty community-level niche. The resulting pattern of trait differences between exotics and natives suggests a predictable pattern of invasion and a predictable trajectory of community change. Our results illustrate how quantifying trait differences between invading exotics and natives at the within-community scale can improve understandings of community invasibility and invader impacts.

**Keywords** Biotic resistance · Fire · Invasion · Life history strategy · Morphology · Niche · Phenology

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## Introduction

The notion of an "ideal weed" (Baker 1965) spawned much research in invasion biology directed at determining whether certain sets of plant traits could be used to predict a plant's invasiveness (Pysek et al. 1995; Williamson and Fitter 1996; Pysek 1998). Not surprisingly, predicting invasiveness based on a plant's traits alone has met with limited success (Mack 1996; Pysek and Richardson 2007). Although some species may act as superinvaders independent of

the communities they invade, most of what we currently know about invasion ecology suggests that invasion is a community phenomenon, and developing general predictive understandings requires knowledge of the invaders' attributes in a community context (Shea and Chesson 2002; Richardson and Pysek 2006). In fact, Darwin recognized early on that invader traits were best understood in the context of the recipient community. Darwin's naturalization hypothesis (Darwin 1859) states that exotic species that are more taxonomically distinct from the recipient community are most likely to become established because they will be less similar in form and function to native species and so experience less competition.

Tests of Darwin's naturalization hypothesis have generated mixed results. While many studies have shown that naturalized species differed taxonomically from the natives, thereby supporting the naturalization hypothesis (Mack 1996; Ricciardi and Atkinson 2004; Strauss et al. 2006; Jiang et al. 2010; Ordonez et al. 2010; Tecco et al. 2010), others have shown that naturalized species either did not differ from null expectations or were more related to natives than expected (Daehler 2001; Lambdon and Hulme 2006; Ricciardi and Mottiar 2006; Diez et al. 2009; Tecco et al. 2010). These conflicting results can largely be explained by a paradox in the naturalization hypothesis originally recognized by Darwin—at broad spatial scales, naturalized species should be taxonomically similar to the natives because they must be adapted to the same environment, while at fine scales, a lower degree of similarity should promote naturalization via reduced biotic resistance. Thus, Darwin's original prediction—that successful invaders should be distinct from natives—is most applicable at fine scales. Recent studies have shown that spatial scale can influence patterns of similarity between exotics and natives in a manner consistent with Darwin's stated paradox (Diez et al. 2008; Proches et al. 2008; Thuiller et al. 2010). This work has helped to refine Darwin's naturalization hypothesis, allowing it to be more effectively applied for understanding and predicting biological invasions.

An important next step in this line of research is examining how species traits relate to invasion at finer within-community scales. Most multi-species studies examining how traits influence invasion compare entire floras over large spatial scales. Moreover, they generally use relatedness or phylogenies as surrogates for actual plant traits or use coarse qualitative life history traits (e.g., annual vs. perennial growth habit) or generic measures for quantitative traits (e.g., height or flowering time) rather than actually measuring traits of individual plants within communities (e.g., Williamson and Fitter 1996; Sutherland 2004; Pysek and Richardson 2007; Ordonez et al. 2010; but see Tecco et al. 2010). Recent phylogenetic studies examining traits of exotics and natives at the within-community scale have illustrated some very interesting patterns (e.g., Cadotte et al. 2010). However, using relatedness as a proxy for niche overlap may have limitations (Daehler 2001; Diez et al. 2008; Thuiller et al. 2010), particularly at finer within-community scales and when examining causal mechanisms for such patterns. The use of relatedness to measure niche overlap dates back to Darwin and is based on the idea that more related species will exhibit more similar form and function and therefore greater niche similarity and competition (Peterson et al. 1999). However, this is not always the case (see Thuiller et al. 2010). For example, Cahill et al. (2008) found that phylogenetic distance did not predict competition strength for 142 plant species. Moreover, some traits can vary so broadly across populations that they can differ as much or more within species as between species (Albert et al. 2010; Messier et al. 2010). Direct measures of trait values on individual plants may provide a more sensitive metric for quantifying how traits relate to invasion within specific communities. Directly measuring traits also favors the use of multivariate techniques to describe and evaluate niche overlap at the within-community scale, where the relationship between niche space and competition is most relevant.

An additional aspect of Darwin's naturalization hypothesis that has not been considered is how it relates to invader impacts. If the naturalization hypothesis is false, then invasive species will generally be similar in form and function to the species they replace. In this situation, we might expect invaders to reduce native species diversity due to higher niche overlap and competitive exclusion (e.g., MacDougall et al. 2009), but community function is likely to change little as new species replace rather than alter the functional roles of native species (Duffy 2002). However, if the naturalization hypothesis is true, as suggested by recently accumulating studies and reconciliation of Darwin's paradox (Ricciardi and Atkinson 2004; Strauss et al. 2006; Jiang et al. 2010), then community function

should change as functionally unique species come to dominate the community. In this case, low niche overlap between invaders and natives might be predicted to result in low direct impact on native species richness due to reduced competition (MacDougall et al. 2009). However, native species diversity could still be impacted when invader-induced shifts in community function alter ecosystem processes like fire regimes, nutrient cycling, microbial communities, etc. (e.g., D'Antonio and Vitousek 1992). Understanding to what degree invaders differ from natives is integral to predicting changes in species richness, community structure, and ecosystem services following invasion (e.g., Moles et al. 2008).

Intermountain grasslands of western North America are being rapidly overtaken by a host of exotic weeds, particularly exotic forbs (Sheley et al. 1998; DiTomaso 2000). Our general observations in this system suggest that the dominant invading forbs exhibit common attributes of size, architecture, and phenology that differ from the dominant native forbs they are replacing. We hypothesized that these apparent differences in plant traits might favor successful invasion into this system and that differences between traits of exotics and natives might indicate shifts in community function. Hence, we measured a range of morphological and phenological traits for five dominant invasive forbs and five dominant native forbs over a large area of western Montana for 2 years to (1) quantify whether invader traits actually differed between the exotics and the natives and (2) evaluate the implications of these results for community invasibility and invader impacts.

## Materials and methods

### Site description

We conducted research in the Intermountain grasslands of western Montana. Within this region, average annual precipitation is approximately 33 cm per year. May and June each receive approximately 5 cm of precipitation and comprise the wet season. Intermountain grasslands are characterized by the dominance of relatively few species of tussock-forming bunchgrasses intermingled with forbs that commonly comprise 80-90% of the species richness (Pokorny et al. 2004; Ortega and Pearson 2005). Some species of native forbs can be large, and total forb biomass can exceed grass biomass at the peak of the growing season in some areas (Pokorny et al. 2004; Ortega and Pearson 2005). With the exception of cheatgrass (*Bromus tectorum*), the dominant invaders in these systems are exotic forbs (Ortega and Pearson 2005), which appear to produce less vegetative biomass, larger, more persistent flowering stems, and flower later relative to most native forbs. The unique characteristics of these exotic forbs appear to be changing the form and function of the vegetative community (e.g., Pearson 2009). To formally evaluate these potential differences in plant traits and better understand their potential ramifications, we focused our study on the dominant exotic and native forbs in the system.

### Study design

We selected five study sites indicative of low-elevation bluebunch wheatgrass (*Pseudoroegneria spicata*) and rough fescue (*Festuca scabrella*) Intermountain grasslands habitats. These sites were scattered across the Flathead, Missoula, and Blackfoot valleys and have been described in prior studies (Pearson 2009). We compared five of the most commonly occurring and locally abundant native forbs on our sites; silky lupine (*Lupinus sericeus*: Fabaceae), common yarrow (*Achillea millefolium*: Asteraceae), Wyeth biscuitroot (*Lomatium ambiguum*: Apiaceae), arrowleaf balsamroot (*Balsamorhiza sagittata*: Asteraceae), and western stoneseed (*Lithospermum ruderale*: Boraginaceae); and five prominent exotic forbs, which were the most widespread strong invaders across the sites; spotted knapweed (*Centaurea stoebe* previously *C. maculosa*: Asteraceae), leafy spurge (*Euphorbia esula*: Euphorbiaceae), tall tumblemustard (*Sisymbrium altissimum*: Brassicaceae), sulphur cinquefoil (*Potentilla recta*: Rosaceae), and Dalmatian toadflax (*Linaria dalmatica*: Scrophulariaceae). All species are perennial in this system except *S. altissimum*, which is annual to biennial. Four of these five invaders (the exception is *S. altissimum*) are recognized as among the top invasive forbs across western North American rangelands (DiTomaso 2000).

At each site, we randomly selected individuals of each species along 10 parallel 100 × 1 m belt transects spaced 10 m apart and running perpendicular to the slope. We marked 2 individuals per species along each transect for a total of 20 marked plants per

species per study site. Plants were selected by walking transects and marking the first two individuals of each species encountered while enforcing a 10-m minimum spacing between marked conspecifics. Plants were marked using uniquely numbered aluminum tags anchored with a hair pin near the base. A bread tie was attached to the base of the tallest stem once plants flowered to demarcate it for measurements. At each visit, we measured the following morphological variables for each plant: height to the top of the vegetative portion of the plant (excluding the flowering stem), maximum width of the vegetative portion of the plant, height of the tallest flowering stem, width of the tallest flowering stem, and the total number of flowering stems that remained erect. By remeasuring these traits several times over the growing season, we were also able to quantify growth and flowering phenologies for each species. This set of traits was explicitly targeted because field observations suggested that the dominant exotics differed from the natives along these trait axes, so they might prove informative regarding both community invasibility and invader impacts. Traits such as plant size and flowering phenology have commonly been shown to differ in course-scale tests of the naturalization hypothesis, while traits such as lateral spread and timing of vegetative growth relative to bolting and flowering have rarely been examined (e.g., Pysek and Richardson 2007). Sampling was initiated in June 2007, when the earliest species were finishing bolting and beginning to flower. Sampling was repeated every 1–2 weeks in July, August, and October, and ceased when snow precluded further measurements. In April 2008, we recounted remaining flowering stems from 2007 to examine their persistence. Beginning with new growth in May of 2008 and continuing through September, we repeated the above measurements every 1–2 weeks. New plants were selected early in 2008 to replace those that died (particularly the annual-biennial *S. altissimum*) or could not be relocated (about 30% of 2007 plants). In 2008, we did not conduct measurements at one of five sites for logistical reasons. We lost a second site to sheep grazing in May 2008 and a third site to wildfire in July 2008 (on Mount Sentinel in the Missoula valley). However, we were able to use the latter site to evaluate survival and flowering of marked plants following the fire.

In April 2009, we measured overall flower stem densities to assess the cumulative effect of differences in stem production per plant, stem persistence, and plant densities between invaded and native communities. We counted the total number of exotic and native forb stems from the previous growing season within each of 16 0.5 $m^2$ quadrats haphazardly distributed within invaded and uninvaded patches at three of the study sites (one each in the Flathead, Blackfoot, and Missoula valleys; we omitted the burned and grazed sites).

## Data analysis methods

Main analyses included only plants that produced flowering stems during the sampling year and study sites having complete sampling histories (2007: $n = 5$; 2008: $n = 2$). In 2008, a majority of *A. millefolium* and *P. recta* plants were grazed by sheep, so these species were dropped from analyses for this year. Otherwise, measurements of plants taken prior to grazing events were included in analyses where possible (exceptions noted below).

We used principal components analysis (PROC PRINCOMP; SAS Institute 2009) to examine multivariate differences in morphology and phenology between exotic and native forbs for each year separately. Plants with evidence of grazing (2007: $n = 43$ of 427; 2008: $n = 15$ of 96) were excluded from this analysis. Eight variables were included in the PCA: maximum values of morphological measures; dates when the maximum stem height, width, and number of stems were recorded (measured as number of days since initiating sampling on April 1); and proportion of flowering stems persisting from spring through the end of the sampling period (2007: number of stems counted April 2008/maximum number of stems counted 2007; 2008: number of stems counted September 2008/maximum number of stems counted 2008). Dates for maxima of vegetative measures could not be included in the analysis because a few species lacked basal vegetation. Values for the first two principal components were compared between native and exotic plants using a general linear model (PROC GLM; SAS Institute 2009), and means and associated standard errors were output to determine centroids and 95% confidence intervals.

We used mixed effects linear models (PROC MIXED; SAS Institute 2009) to test for differences in individual morphological measures between exotic and native plants. Plants showing evidence of grazing

(see above) were excluded from this analysis. For each variable, we compared the maximum measure obtained per plant in each year, including site as a random effect and species as a fixed effect to control for differences in sample sizes among taxa. We used the same model to compare persistence of flowering stems per plant in each year (see definitions above). We also used mixed effects linear models to compare phenology of exotic and native plants over the growing season. Response variables were monthly measures of basic plant morphology from 2008, and the model included origin (exotic vs. native), month, and month × origin, with the latter testing for variation in phenological patterns between groups. The mid-month sample for each plant was treated as a repeated measure, and species was included as a fixed effect to control for differences in sample sizes among taxa. We also used a mixed effects linear model to compare overall stem densities between invaded and uninvaded patches, treating site as a random effect and origin as a fixed effect. Results from mixed models were reported as least squares means with associated standard errors (SAS Institute 2009) to account for any imbalances in sample size by site, species, or month.

To check for large deviations from assumptions of normality, linearity, and homoscedasticity, we inspected scatterplots of residuals for all dependent variables analyzed with linear models. These models should be robust to minor violations of assumptions given large sample sizes (error degrees of freedom >20; Tabachnick and Fidell 1989). Transforming variables for the PCA to improve normality did not change results, so non-transformed variables were used (Tabachnick and Fidell 1989).

To examine the response of exotic and native forbs to wildfire, we compared the proportion of marked plants that survived the July 2008 fire on Mount Sentinel (as determined by post-fire growth) using a $\chi^2$ homogeneity test (PROC FREQ; SAS Institute 2009). For surviving plants, we compared the proportion of plants that flowered in the same season using Fisher's Exact Test for low cell counts.

## Results

Individual plants representing the five dominant species of exotic and native forbs showed significant separation in principal components space as determined by combined morphological and phenological variables. The first and second principal components (PCs) together accounted for 48% of the variation in both years (Fig. 1). The resultant centroids for native and exotic groupings significantly differed in both 2007 (PC1: $F_{1,326} = 160.5$, $P < 0.001$; PC2: $F_{1,326} = 8.1$, $P = 0.005$) and 2008 (PC1: $F_{1,76} = 36.0$, $P < 0.001$; PC2: $F_{1,76} = 17.6$, $P < 0.001$). In both years, native plants had relatively high mean scores for PC1, which was correlated with wider and taller vegetative growth and lower flowering stem persistence. In contrast, exotic plants had relatively high mean scores for PC2, which was correlated with taller and wider flowering stems, later stem production (and hence flowering), and higher stem persistence. Thus, native forbs tended to invest more into vegetative growth and less into flowering stem size, and flowered earlier in the season, while exotic forbs tended to do the opposite.

Examination of individual plant attributes concurred with PCA results and illustrated the details of these differences (Fig. 2). In both years, vegetative growth of exotic forbs was substantially narrower (2007: $F_{1,352} = 350.8$, $P < 0.001$; 2008: $F_{1,60} = 220.4$, $P < 0.001$) and shorter (2007: $F_{1,347} = 257.5$, $P < 0.001$; 2008: $F_{1,70} = 137.6$, $P < 0.001$) than that of native forbs. In contrast, exotic forbs produced flowering stems in both years that were wider (2007: $F_{1,351} = 22.9$, $P < 0.001$; 2008: $F_{1,42} = 10.2$, $P = 0.003$) and taller (2007: $F_{1,351} = 138.0$, $P < 0.001$; 2008: $F_{1,38} = 6.9$ ($P = 0.012$) than those of natives. On average, native forbs produced more flowering stems than exotics (Fig. 3a) in 2007 ($F_{1,348} = 37.4$, $P < 0.001$) and 2008 ($F_{1,70} = 5.0$, $P = 0.03$). However, stem persistence from spring 2007 to spring 2008 ($F_{1,270} = 50.8$, $P < 0.001$; Fig. 3b) and from spring to fall 2008 ($F_{1,70} = 17.5$, $P < 0.001$) was substantially higher for exotics than natives. Because exotic forbs have relatively high stem survival and attain densities far exceeding those of native species due to the monocultures they form, overall stem densities were 47 times higher in invaded versus uninvaded grassland plots in spring 2009 ($F_{1,92} = 355.3$, $P < 0.001$; Fig. 3c).

Phenologies also differed between the exotic and native forbs we examined. Mean vegetation width and height (Fig. 4a, b) peaked fairly discretely for exotics in June 2008, falling about 50% in July and disappearing by September, whereas for natives, these

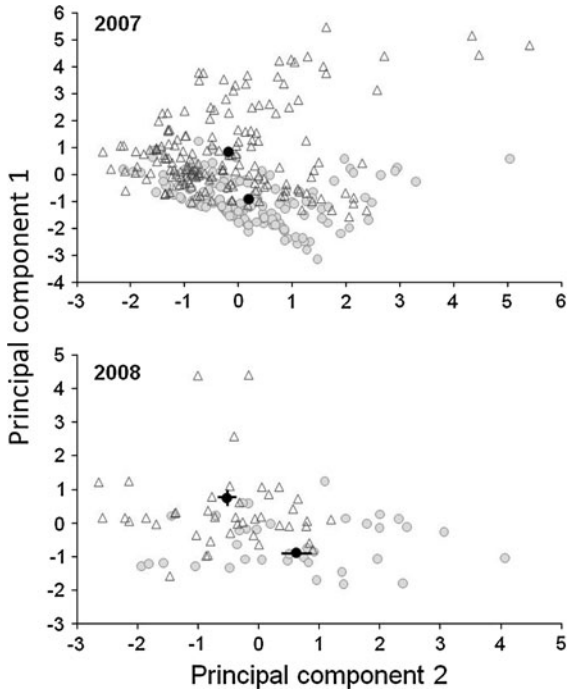



**Fig. 1** Results of principal component analysis of morphological and phenological variables for prominent exotic invasive and native forbs in Intermountain grasslands of western Montana, 2007 and 2008. In both years, PC1 was correlated with wider and taller vegetative growth and low persistence of flowering stems, and PC2 was correlated with taller and wider flowering stems, later stem production and flowering, and higher stem persistence. *Open triangles* and *shaded circles* indicate native and exotic species, respectively. *Filled black circles* and associated *bars* indicate the means ± SE for the group centroids. *Error bars* not visible are smaller than the centroids. Statistics are given in the text

measures peaked in June but then remained relatively high through July before falling to low numbers by September (plant origin × month for width and height, respectively: $F_{4,280} = 9.4$, $P < 0.001$ and $F_{4,286} = 7.4$, $P < 0.001$). Exotic forbs showed an initial delay in development of flowering stems before reaching a strong peak in mean stem width and height in July, whereas native forbs reached peak mean stem width and height by June, with relatively little variation in these measures among months (Fig. 4c, d; plant origin × month: $F_{4,241} = 12.1$, $P < 0.001$ and $F_{4,235} = 9.5$, $P < 0.001$ for width and height, respectively). Numbers of stems per plant showed similar patterns (Fig. 4e), with exotics experiencing a marked increase in stem production from May and June to their peak in July, and natives showing little monthly variation in mean stem densities following their rapid peak in June (origin × month: $F_{4,305} = 6.4$, $P < 0.001$).

The wildfire that burned many marked plants in July 2008 provided valuable information on how dominant exotic and native forbs respond to fire, albeit at one site. Exotic plant survival into August and September 2008 following the burn was 82% (27 of 33 plants) compared with only 24% (10 of 41 plants) for the native forbs ($\chi^2 = 24.1$, $P < 0.001$). Moreover, surviving plants represented all five exotic species, while only two native species had survivors (90% of these were *A. millefolium* and 10% *L. ruderale*). Of the total surviving plants, 33% of exotics flowered (these were all *E. esula* and *L. dalmatica*) compared to 10% of natives (only one individual of *L. ruderale*). This last difference is not significant (Fisher's exact test, $P = 0.23$), but this may be related to the reduced sample size ($n = 37$ total survivors, with only 10 of these flowering).

## Discussion

Darwin's naturalization hypothesis has been extensively applied at course scales of global and regional floras to understand invasion. However, this hypothesis is inherently a community-based hypothesis that postulates that invasion will best be understood by examining invader traits in the context of the specific local community being invaded (Thuiller et al. 2010; Jiang et al. 2010). In this study, we directly measured morphological and phenological traits of five prominent invasive forbs and five dominant native forbs within Intermountain grassland communities to examine niche separation between exotics and natives. We found that exotics differed from natives in multivariate niche space due to differences in both morphology and phenology that suggest exotics may use distinct resource allocation strategies. Examination of these differences offers interesting insights regarding community invasibility and potential invader impacts in this system.

### Trait differences

Morphologically, vegetative growth of exotic forbs was three times shorter and narrower than the natives, but exotics generated flowering stems that were 35%

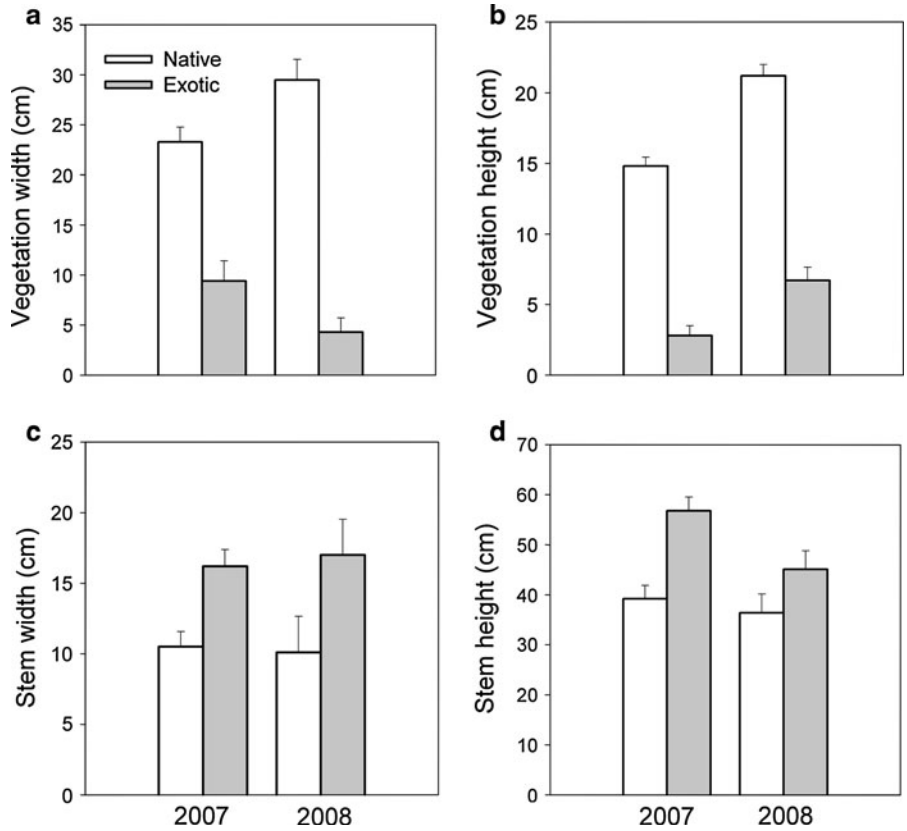
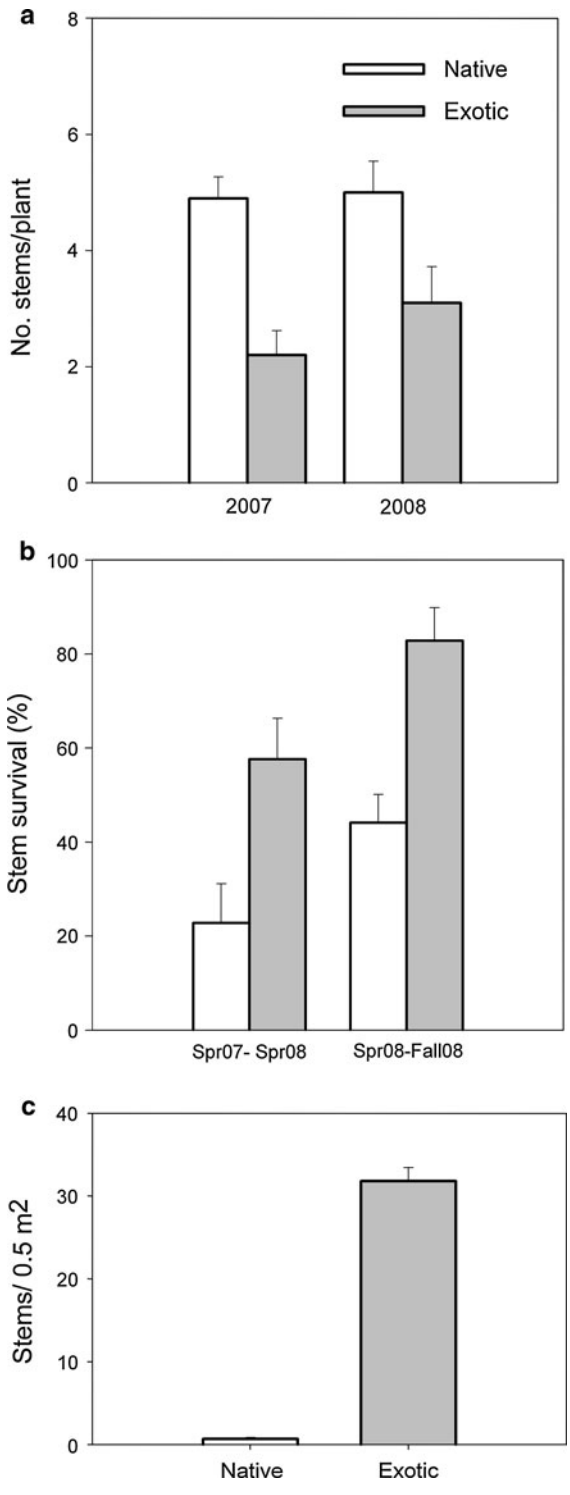



**Fig. 2** Comparison of **a** vegetation width, **b** vegetation height, **c** stem width, and **d** stem height for prominent exotic invasive and native forbs in Intermountain grasslands of western Montana, 2007 and 2008. *Bars* represent means + SE. Statistics are given in the text

taller and 65% wider. These results are corroborated by a recent study that used PCA to compare four morphological traits (plant height, lateral spread, shoot to root ratio, and specific leaf area) for three exotic forbs common to our study (*C. stoebe*, *L. dalmatica*, and *P. recta*) and ten native Intermountain grassland species (including *A. millefolium*), based on measurements taken under common garden and greenhouse conditions (Maron and Marler 2008). Our finding that exotics were taller than natives is also consistent with many course-scale studies of plant traits (Pysek et al. 1995; Crawley et al. 1996; Williamson and Fitter 1996; see review in Pysek and Richardson 2007; but see Ordonez et al. 2010), but course-scale studies rarely measure lateral spread. Although the native forbs averaged two times more stems per plant in our system, exotic forbs achieved higher absolute stem densities because they form monocultures and reach higher conspecific plant densities. The dead flowering stems of exotics also remained standing far longer than dead stems of the natives. This combination of higher absolute stem densities and greater persistence of dead stems resulted in 47 times higher stem densities in invaded grassland patches by the next spring. Since the vegetative biomass of both native and exotic forbs senesces soon after seed dissemination, the observed difference in stem densities represents a profound shift in the overall architecture of Intermountain grassland communities for most of the year.

Phenological differences were linked to morphological traits in ways that suggest the exotic forbs in our study may exhibit different overall life history strategies from the natives. Exotics showed a distinct temporal separation between vegetative growth, flower stem production, and flowering. Vegetative growth of exotics peaked in June, but began to senesce concurrent with initiation of bolting such that when flower stalks reached peak growth in July, the vegetative portions of the plants were already substantially reduced. Thus, exotics discretely reallocated resources from vegetative growth to flowering stem production over the growing season. This was not the case for the natives, which peaked simultaneously in vegetative and flower stem growth in June and July. In fact, most natives began bolting simultaneously with the




◀ **Fig. 3** Comparison of **a** number of flowering stems produced per plant and **b** % survival of stems, for prominent exotic invasive and native forbs in Intermountain grasslands of western Montana, 2007–2008. Panel **c** shows stem density per 0.5 $m^2$ for adjacent invaded and uninvaded patches in 2009. *Bars* represent means ± SE. Statistics are given in the text

emergence of vegetative growth in the spring or very soon after. In absolute terms, exotics peaked earlier than natives in vegetative growth (June vs. June–July) but reached peak flowering after natives (July vs. June). Flowering phenology has commonly been shown to differ between exotics and natives, with exotics flowering longer, earlier, or later than natives (Crawley et al. 1996; Lake and Leishman 2004; Cadotte et al. 2006; see review in Pysek and Richardson 2007). Exotics that flower earlier or later than the natives may be filling different empty niches in different communities. Although our exotics flowered later than the dominant natives we examined, flowering by less prominent natives in this system occurs during and after the peaks for the dominant exotics. Hence, the exotics did not appear to be "trying harder" than the natives by flowering longer (with the exception of *E. esula*, which exhibits an extended flowering period) or flowering at extreme early or late periods (sensu Crawley et al. 1996). Overall, they seemed to exploit a window during the growing season that was relatively underexploited by the natives. Other studies have not examined how vegetative phenology relates to flowering phenology.

## Implications for invasibility

Collectively, our results provide interesting insights into the process of invasion in this system. Although we evaluated only 10 species, the native forbs are community dominants that comprise about 50% of total plant cover and 70% of forb cover in uninvaded communities, and the exotics are among the top invaders dominating these systems (Ortega and Pearson 2005). Thus, these ten species account for a majority of the biomass in these communities. The picture that emerges in multivariate-trait space is one of the exotics filling a community-level niche that is distinct from the dominant natives. Niche differences relative to resource availability are extremely important in determining plant competition and community invasibility (e.g., Kennedy et al. 2002; Fargione et al. 2003; Wolkovitch and Cleland 2011). Our results suggest that the success of the dominant exotics relative to the dominant natives in this system may be attributable to different resource allocation strategies

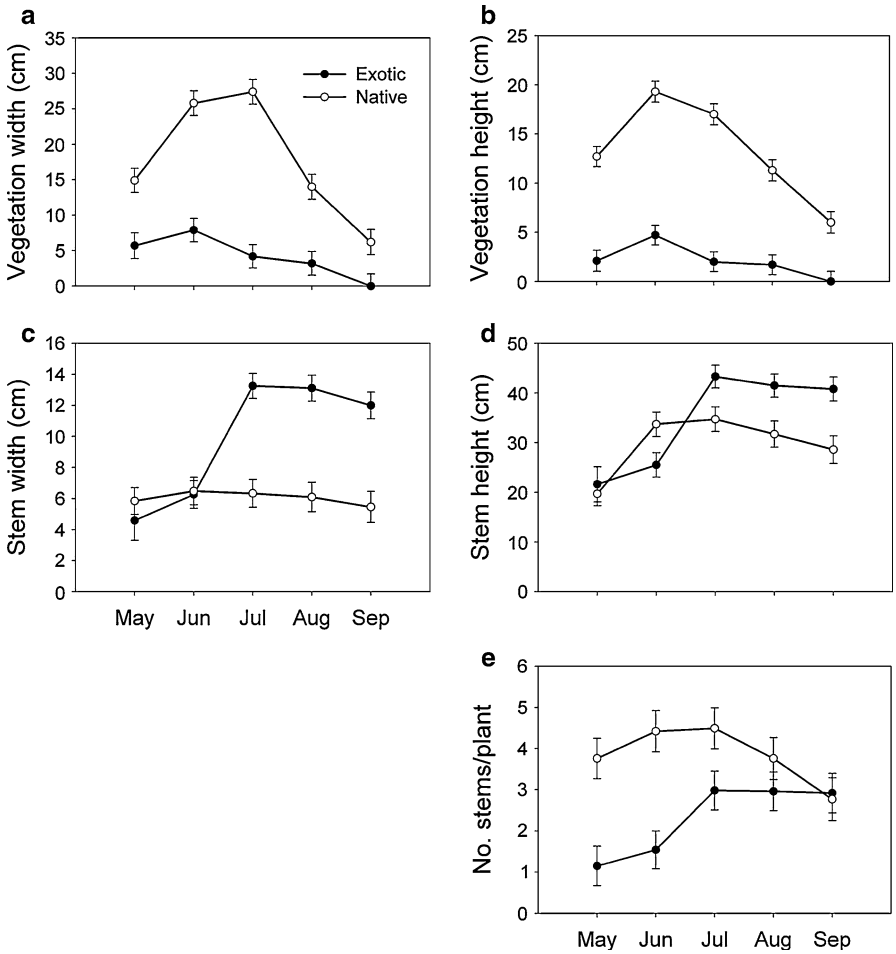



**Fig. 4** Monthly measures for **a** vegetation width, **b** vegetation height, **c** stem width, **d** stem height, and **e** number of flowering stems per plant for prominent exotic invasive and native forbs in Intermountain grasslands of western Montana in 2008. *Bars* represent means ± SE. Statistics are given in the text

as they relate to growth, reproduction, and temporal availability of resources. Relative to the natives, the exotics emphasized growth of flowering stems over vegetative growth, and appeared to shift resource allocation from vegetative growth in early spring to flower stem growth and flower production later in the season. Of the phenologically based hypotheses postulated to explain invader success (Wolkovitch and Cleland 2011), our results are most consistent with the empty niche hypothesis given that the exotics use a resource space that is discrete from, but not earlier than, the dominant natives (thereby precluding the priority effects and niche breadth hypotheses; though we cannot exclude a plasticity-climate change hypothesis). Follow-up studies that directly compare biomass allocation among vegetative, flowering, and belowground growth relative to resource uptake and the timing of resource inputs may provide greater insights into the specific mechanisms for invasion in these grasslands.

An important question, then, is why would exotics benefit from this resource space and why have natives not already exploited it? The convergence in strategies among the exotics relative to the natives is particularly interesting given that each of the exotics we examined represents a distinct plant family. Thus, phylogenic relatedness cannot explain the collective success of these exotics. For natives, one might argue selective pressures within the system drove their convergence in traits across taxa (the native taxa represent four families and five genera), but for exotics, the most parsimonious hypothesis would seem to be that there is currently an "empty niche" at the community level, and introduced plants with traits that fit this resource space are simply more successful. But why would there be an empty niche in this community? It is well

recognized that islands can be more invasible due to obvious empty niches such as lack of predators or specific plant functional groups that result from founder effects (Simberloff 1995). However, mainland systems may also experience empty niches if natives are evolutionarily constrained from filling certain niches (Futuyma 2010; Wiens et al. 2010), or if those environmental conditions that selected for the original community have since changed to favor strategies the natives have not yet evolved to fill (Moles et al. 2008)—in essence the ghost of "environments" past (sensu Connell 1980). This idea parallels current hypotheses postulating that exotics may benefit over natives from contemporary climate change (e.g., Wolkovitch and Cleland 2011). Invasion biology has convincingly established that communities are rarely species saturated (e.g., Levine 2000). One plausible explanation for this that is rarely considered is that abiotic conditions are not static and contemporary communities may not always reflect complete or optimal exploitation of current conditions (Moles et al. 2008). If this is the case and enough exotics are introduced into the system, by chance some are likely to be better adapted than the natives. A rigorous test of the hypothesis that environmental-community mismatches render communities susceptible to invasions would require careful analysis of the paleontological record. However, even without fully understanding the cause for an empty niche, the implication is that there may be a specific set of plant attributes that can predict invasion success in such situations (Moles et al. 2008). To shed light on the elusive Holy Grail of the "ideal weed", traits associated with successful invaders may not predict invader success across all systems, but they may predict the success of prospective invaders within a specific recipient community.

## Implications for invader impacts

Our results also provide important information regarding the consequences of invasion. If dominant invaders differ from the native community as predicted by Darwin's naturalization hypothesis, then we should expect community function to change, perhaps in predictable ways. Our results suggest a strong pattern of change in Intermountain grassland communities in response to invasion that should influence the form and function of these communities. Even the more subtle changes we have documented in plant architecture can profoundly affect other species and interactions. For example, the increase in the abundance and size of flowering stems following invasion in this system has dramatically increased native spider densities and doubled their per capita prey capture rates, with significant ramifications for their invertebrate prey and cascading indirect effects in the system (Pearson 2009, 2010). There are also important, though less clear, implications for ecosystem services and processes. Changes in timing of flowering could affect pollinator communities and their associations (Traveset and Richardson 2006). Differences in timing of plant tissue growth likely translate to differences in timing, and potentially rates, of nutrient and water uptake between native and invaded systems, which could affect nutrient cycling (Ehrenfeld 2003). Recent studies suggest that exotic communities differ from native communities in terms of biomass and overyielding (Ehrenfeld 2003; Maron and Marler 2008; Wilsey et al. 2009). The greater emphasis by exotic forbs on flower stem versus vegetative growth suggests a shift at the community level in the overall types and/or quantities of biomass being produced. Moreover, the substantial difference in persistence between exotic and native flower stems suggests that decomposition rates may differ greatly between these taxa. Such changes can influence not only nutrient cycling but also fire frequency and intensity (D'Antonio and Vitousek 1992).

Shifts in plant traits can affect how plant communities respond to and interact with disturbance processes (e.g., D'Antonio and Vitousek 1992; Funk et al. 2008). The wildfire that burned many marked plants at one site proved informative regarding the response of dominant native and exotic forbs to the primary source of disturbance in this system. Survival of exotic forbs was 82% versus 24% for natives, and 33% of the exotics that survived still flowered in the same year versus only 10% of surviving natives. This fire was of low intensity because it occurred slightly earlier than the normal onset of fire season in this region (early July vs. August), but it was similar in intensity and timing to controlled spring burns used for restoration (Zouhar et al. 2008). Studies examining the effects of prescribed burning in this region similarly found that adult *L. dalmatica* and *P. recta* are not killed by low-intensity fire and that recruitment for these species increases following such treatments (Lesica and

Martin 2003; Jacobs and Sheley 2003). The results from this fire are unique in that we followed marked individual plants before and after the fire. No other studies have directly compared the responses of native and exotic forbs to prescribed burning, and the response of exotics to natural wildfire has rarely been documented in these systems (Zouhar et al. 2008). The later phenologies of exotic forbs and also the temporal separation between vegetative growth and flowering phases may have reduced sensitivity of the exotics to fire under the conditions we observed.

Dissimilarity between invaders and natives might also predict low direct impacts on native species richness due to low niche overlap and therefore reduced competition (MacDougall et al. 2009). We found low niche overlap between the dominant exotics and natives, yet prior work in this system indicates that these exotics strongly reduce native species richness; including the natives we studied here (Ortega and Pearson 2005). So what is the mechanism for these impacts? Given the evidence we found indicating that these invaders are shifting community function, it is quite possible that natives could be affected via indirect interactions resulting from changes in nutrient inputs, timing of nutrient inputs, pollinator communities, etc. instead of direct competitive interactions. Experimental work is necessary to explicitly test the influence of direct resource competition versus the indirect effects of functional changes in the community on native species richness. Such studies could offer important insights not only into the specific mechanisms for invader impacts, but also the degree to which such impacts can be predicted based on examination of exotic and native trait differences.

## Darwin's naturalization hypothesis up-close

Studies that have rejected Darwin's naturalization hypothesis have tended to treat all invaders alike (Daehler 2001; Duncan and Williams 2002; Lambdon and Hulme 2006; Ricciardi and Mottiar 2006; Diez et al. 2009; Tecco et al. 2010). Meanwhile, studies that have examined the naturalization hypothesis while differentiating between weak and strong invaders (sensu Ortega and Pearson 2005) have consistently shown that strong invaders, those that come to dominate invaded communities, tend to fit the naturalization hypothesis (they differ from the natives) while weak invaders do not (Lockwood et al. 2001; Ricciardi and Atkinson 2004; Strauss et al. 2006). Given that most exotics are weak invaders (Williamson and Fitter 1996), examining floras without making this distinction can confound conclusions about the process of invasion, especially for those invaders we are most concerned about. We found that traits of strong invaders differed from those of dominant natives at the within community scale—consistent with Darwin's naturalization hypothesis. However, we focused on strong invaders because they are of greatest conservation concern, so we could not assess how traits of weak invaders related to those of natives or strong invaders within this system. Nonetheless, accumulating evidence suggests that future studies at both coarse and fine scales should consider invader status for understanding both invasion and invader impacts (Ortega and Pearson 2005; Strauss et al. 2006; Kleunen et al. 2010).

Our study did not explicitly test Darwin's naturalization hypothesis because we did not compare the entire biota of natives and exotics in this system. Nonetheless, it illustrates how Darwin's ideas regarding invader traits and their relationship to the recipient community might help predict not only invader success but also invader impacts at the within-community scale. The differences we observed between the traits of highly successful invaders and dominant natives suggest that the invaders were exploiting underutilized resource space. Hence, these traits highlight the potential susceptibility of the community to certain types of exotics, and may thereby serve to predict future invaders. The trait differences observed between the invading exotics and dominant natives also suggest directional shifts in community function related to changes in plant architecture, types of plant biomass being produced, timing of flowering, decomposition rates, and resource uptake timing that are likely to profoundly affect other organisms and ecosystem processes and services. Applying Darwin's ideas regarding naturalization at the local scale by directly quantifying traits of exotic relative to native plants within specific communities may help elucidate the mechanisms underlying invasion and predict invader impacts. However, more studies of this type are needed across different communities to determine the generality of these concepts.

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