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Source: Invasive Plant Science and Management, 8(3) : 292-306

Published By: Weed Science Society of America

URL: https://doi.org/10.1614/IPSM-D-14-00076.1

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Invasive Plant Science and Management 2015 8:292–306

Meta-Analysis of Exotic Forages as Invasive Plants in Complex Multi-Functioning Landscapes

John Derek Scasta, David M. Engle, Samuel D. Fuhlendorf, Daren D. Redfearn, and Terrance G. Bidwell*

Introducing exotic forages in the attempt to enhance livestock and wildlife forage has been practiced widely for over a century. These forage species are selected for traits conferring persistence under stress, potentially yielding invaders that transform native plant communities. Using standardized systematic review guidelines and meta-analytical techniques we quantified effects of exotic forage invasion on change of native plant community structure, and compared the magnitude and direction of change across exotic forage species, plant functional groups, and structure of plant communities. Our study of 13 exotic forage species in North America (six C_4 grasses, three C_3 grasses, and four legumes) yielded 35 papers with quantitative data from 64 case studies. Nine of the 13 species met our inclusion criteria for meta-analysis. The overall effect of exotic forage invasion on native plant communities was negative ($\bar{\bar{E}}$ −0.74; 95% confidence interval [CI]: −0.29 to −0.25). The effect size was most negative for two C_4 grasses, Lehmann lovegrass and Old World bluestems. A negative effect was also expressed by C_3 and C_4 grass functional groups, and these effects were stronger than for legumes. Effect size differed among measures of plant community structure, with the greatest negative effect on native plant biomass and the least negative effect on species evenness. Weighted fail-safe numbers indicated publication bias was not an issue. Exotic forage species are important for agricultural production but may threaten complex multi-functioning landscapes and should be considered as a subset of potentially invasive exotic species. Characteristics making exotic forages different from other exotic plants hinge on pathways of selection and dispersion: selection is based on persistence mechanisms similar to characteristics of invasive plants; dispersion by humans is intentional across expansive geographic regions. Exotic forages present a complex socio-ecological problem exacerbated by disconnected scientific disciplines, competing interests between policy and science, and organized efforts to increase food production.

Nomenclature: Lehmann lovegrass, *Eragrostis lehmanniana* (Nees); Old World bluestems, (plains) *Bothriochloa ischaemum* var. *ischaemum* (L.) Keng. and (yellow) *Bothriochloa ischaemum* var. *songarica* (Rupr. ex Fisch. & C.A. Mey.) Celarier & Harlan

Key words: Alien species, biotic invasions, ecology of invasive plants, exotic plants, grassland, rangeland.

The introduction of exotic forages has been purposeful, widespread, driven by economic factors, and often perceived as beneficial (Arriaga et al. 2004; Barnes et al. 2007; Wilkins and Humphreys 2003). The intent of exotic forage introduction has been to enhance agricultural production for domestic livestock (McCoy et al. 1992; Nixon 1949) and winter foraging for game and non-game wildlife populations (Hehman and Fulbright 1997). Combined, these intentions have broadly dispersed exotic forage seed sources across North America and differ fundamentally from introductions of most other invasive plants.

Human-accelerated selection of species or traits for stress tolerance is a driving component of exotic forage dispersion. Forage plants experience many types of stress including defoliation by grazing animals or mowing, moisture deficit, nutrient limitation, and pest damage (Barnes et al. 2007). The basis of human selection has been agronomic traits that mitigate the negative effects of stress for long-term persistence (including ease of establishment,

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DOI: 10.1614/IPSM-D-14-00076.1

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Management Implications

The breeding, selection, and introduction of exotic forages have led to changes in native terrestrial plant communities in North America. Although not all exotic forages have become invasive, many have become problematic and shown aggressive expansion into areas beyond the initial plantings. Potential changes to the native plant community include reduced species richness, evenness, and diversity, and lower total cover and biomass. These exotic forage species are successful invaders because they are selected for traits conferring persistence under stress such as grazing, repeated haying, and environmental stress. Many of the desirable traits selected for in forage species are similar to traits common in invasive plants such as ease of establishment, high seed production with extensive longevity, vigorous vegetative reproduction, rapid growth rate, competitive resource use, and resistance to removal and predators (insects and disease). Managers should carefully consider invasion potential to guide species selection when exotic forage is proposed in a hay or permanent pasture scenario. Managers may also consider using native seed mixes, especially for restoration of natural areas, but native seed costs are currently prohibitive and exotic seed is typically cheaper. This cost discrepancy continues to constrain reseeding natural areas or planting of Conservation Reserve Program fields with seed mixes to optimize wildlife use. We also suggest that managers monitor areas of exotic forage presence and begin measuring expansion over time into other areas. Our results also suggest that managers consider limiting the establishment of wildlife food plots with exotic forage species that may invade beyond the planted areas. Finally, dialogue between managers and other stakeholders is needed to discuss innovative solutions for exotic forage invasion situations or potential situations.

adequate seed production, seedling vigor, vegetative reproduction, rapid growth rate and high yield, competition for resources, resistance to defoliation, and insect and disease resistance) (Wilkins and Humphreys 2003). Forage plants and invasive plants may not be intuitively similar, but the characteristics that make a species an ideal forage plant are strikingly similar to characteristics that define invasive plants (Baker 1974; Barnes et al. 2007; Sutherland 2004) (Table 1). Although profiling successful invading plants and associated traits has been considered simplistic, difficult, or both, the similarities between invasive plants and exotic forages in the context of our study cannot be ignored (Pyšek and Richardson 2007).

Intentional introductions of exotic forages across broad geographic regions have produced persistent stands of exotic forages as well as widespread invasion of native grassland (Arriaga et al. 2004; Henderson and Naeth 2005; Nixon 1949). Although the ecological impacts of exotic plant invasions are typically negative (specifically, the decline of resident species' abundance and diversity), the impacts are not uniform or unidirectional (Vilà et al. 2011). Furthermore, impacts of invasive plants are broad, difficult to quantify and empirically test, and often characterized by anecdotal observation rather than quantitative analyses (Barney et al. 2013). This suggests that broad conclusions about the invasiveness of exotic forages should consider different types of community-level impacts, rely on quantitative data, and consider studies across broad temporal and spatial scales.

Table 1. Characteristics of ideal forage plants compared to characteristics of common invasive plant species.

The ideal forage plant[a]	The common invasive plant[b]
Easy to establish	Germinates in many environments
Adequate seed production, seedling vigor	Extensive seed production with good seed longevity
Vegetative reproduction	Vigorous vegetative reproduction
Rapid growth rate and high yield	Rapid growth (vegetative phase to flowering)
Competes for resources	Competes interspecifically (structure, allelopathy)
Resistant to herbivory or removal	Armed or toxic to escape herbivory
Insect and disease resistant	Free from native predators

[a] Adapted from Barnes et al. 2007.

[b] Adapted from Baker 1974; Sutherland 2004.

Given the agronomic basis of selection and breeding of exotic forage species (described as human-directed evolution [Barnes et al. 2007]), and the scale of intentional introductions across the landscape, we asked to what extent these exotic forage species affect plant communities. Our objectives were to (1) apply standardized systematic review guidelines and meta-analytical techniques to 13 exotic forage species widely distributed in North America, (2) quantify the effect of exotic forage invasion on change of native plant community structure, and (3) compare the magnitude and direction of change across exotic forage species, plant functional groups, and structure of the plant communities.

MATERIALS AND METHODS

Systematic Review and Literature Search. We drafted our review protocol using systematic review guidelines (Centre for Evidence-Based Conservation 2013). Online databases including Google Scholar, Ingenta, JSTOR, and Web of Science were used to search the literature using scientific and common names individually, and then in combination with the following terms: invasion, prairie, rangeland, richness, and diversity. We first limited our search to 13 perennial and exotic forage plants widely distributed in North America that fit specific search criteria (Tables 2 and 3). The selection of the initial 13 species was based on the current forage textbook (Barnes et al. 2007) and the

Table 2. Origin, plant functional group, extent of invasion in United States, and mechanisms of persistence for 13 exotic forage species intentionally introduced into North America.

Species nomenclature[a]	Origin	Year of U.S. introduction	Functional group	Named cultivars	U.S. extent	Potential persistence mechanisms
Crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.]	Asia	~ 1900	C_3 grass	Many	25 states	Effective belowground competitor; drought–tolerant; high seedling vigor
Old World bluestems, (plains) *Bothriochloa ischaemum* var. *ischaemum* (L.) Keng. and (yellow) *Bothriochloa ischaemum* var. *songarica* (Rupr. ex Fisch. & C.A. Mey.) Celarier & Harlan	Eurasia	1917	C_4 grass	'Plains'	17 states	Rapid maturation; effective belowground competitor; drought-tolerant
Smooth brome (*Bromus inermis* Leyss.)	Eurasia	1880	C_3 grass	Many	48 states	Rapid N cycling (low C:N ratio); rapid decomposition rates; rhizomatous
Bermudagrass [*Cynodon dactylon* (L.) Pers.]	Africa	1751	C_4 grass	Many	41 states	Rhizomatous/stoloniferous; deeply rooted; adapted to a range of soils
Kleberg's bluestem; [*Dichanthium annulatum* (Forssk.) Stapf]	Eurasia	1917	C_4 grass	'KR'	3 states	Rapid maturation; effective belowground competitor; drought-tolerant
Lehmann lovegrass [*Eragrostis lehmanniana* (Nees)]	Africa	1937	C_4 grass	Unknown	6 states	Drought-tolerant; efficient winter moisture use; stoloniferous
Sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don]	Asia	1896	Legume	'AU Grazer'	32 states	Rhizobium symbiosis; polyphenols and condensed tannins; prolific seed production
Alfalfa (*Medicago sativa* L.)	Asia	~ 1850	Legume	Many	50 states	Rhizobium symbiosis; deeply rooted; tolerant of herbivory/haying
Sweetclover [*Melilotus* spp.]	Europe	~ 1700	Legume	Many	50 states	Rhizobium symbiosis; rapid growth; high seedling vigor
Buffelgrass [*Pennisetum ciliare* (L.) Link]	Africa/Asia	1949	C_4 grass	'T-4464'	10 states	Structurally competitive; rapid seedling growth; deeply rooted and drought-tolerant
Tall fescue [*Schedonorus arundinaceus* (Schreb.) Dumort.]	Europe	~ 1800	C_3 grass	'KY 31'	48 states	Endophyte symbiosis/mutualism; drought-tolerant; tolerant of herbivory/haying
Johnsongrass [*Sorghum halepense* (L.) Pers.]	Mediterranean	~ 1830	C_4 grass	Unknown	49 states	Rhizomatous; high seedling vigor; stress-tolerant
White clover (*Trifolium repens* L.)	Europe	~ 1700	Legume	Many	50 states	Rhizobium symbiosis; stoloniferous; prolific seed production

[a] Nomenclature and extent based on WSSA 2015.

Table 3. Criteria for inclusion of studies in the systematic review and meta-analysis.

Inclusion category	Specific criteria
Subjects	Prairie, rangeland, and pasture studies that are observational (invaded versus uninvaded areas) or experimental that manipulate invasions by inducing or removing the invasive species. Common names, Latin names and synonyms for 13 exotic forage plants. Studies that only consider sites that have been modified with intensive agronomic practices were not considered.
Temporal range	Searched 1970 to July 2013
Spatial range	North America
Treatments	Large or small plot comparisons with either manipulated or naturally occurring invasion. Studies that measure the addition or removal of a target species and its impact on the plant community. If studies considered highly manipulated planted monocultures (i.e., plowed, sprayed, planted) as invaded areas or were confounded by other invasive species they were not included.
Outcomes	Study measured abundance, species richness, species composition, species diversity (H′), and biomass or cover as influenced by the abundance of a targeted species or its mechanism of persistence (if measureable such as endophyte for tall fescue).

experience of the authors regarding the most widely planted species in central North America. Then we conducted a “blind search,” with the term “exotic forage” in place of a species name, to identify any species or studies that we may have not considered. Spatially we limited our search to North American countries: Mexico, the United States, and Canada. If studies considered highly manipulated planted monocultures (i.e., plowed, sprayed, planted) as invaded areas or were confounded by other invasive species they were not included. If a paper met the initial inclusion criteria, the full text was examined for (1) quantitative data of abundance, species richness, species composition, species diversity, native plant cover or biomass, (2) measures of variance and sample size, and (3) effects attributed to the exotic forage species and not driven by other disturbances (short-term effects of herbicides, soil disturbance, mechanical manipulations of woody plants).

Meta-Analysis. Quantitative data were associated with a control (i.e., a noninvaded site or a site where the invasive species was removed) and a treatment (i.e., the invaded site). First, we calculated the effect size (E) and variance for each case within each unique invasion study using only a single variable. Then we calculated the overall effect $\left(\bar{\bar{E}}\right)$ (with all data combined across all species), grouped by species, grouped by plant functional groups (C_4 grass, C_3 grass, and legume), and grouped by measurements of plant community structure (species richness, evenness, diversity [Shannon’s H′]), and cover or biomass) as determined by within and between heterogeneity using a categorical fixed effects meta-analytic model (see below). The natural log of the response ratio, which measures relative difference, was used as the effect size or the measure of central tendency and all analyses were conducted in MetaWin 2.0 (Equation 1; Rosenberg et al. 1999). The following equation characterized effect size:

$$\text{Effect size } \bar{\bar{E}} = \ln R = \ln\left(\frac{\bar{\mathrm{x}}^{\mathrm{i}}}{\bar{\mathrm{x}}^{\mathrm{ni}}}\right) \qquad [1]$$

where $\bar{\mathrm{x}}^{\mathrm{i}}$ is the mean of the invaded site and $\bar{\mathrm{x}}^{\mathrm{ni}}$ is the mean of the noninvaded site, and means are for each of the categories (i.e., all data, by species, by plant functional groups or by measurements of plant community structure). To estimate the range of values and potential unknown values we calculated 95% confidence intervals (CI).

Variance of each effect size was weighted by the sample size (Equation 2; Rosenberg et al. 1999):

$$\text{Variance in R} = \left(\frac{\left(\sigma^{\mathrm{i}}\right)^2}{n^{\mathrm{i}}\left(\bar{\mathrm{x}}^{\mathrm{i}}\right)^2} + \frac{\left(\sigma^{\mathrm{ni}}\right)^2}{n^{\mathrm{ni}}\left(\bar{\mathrm{x}}^{\mathrm{ni}}\right)^2}\right) \qquad [2]$$

where σ^{i} is the standard deviation of the invaded site and σ^{ni} is the standard deviation of the noninvaded site, n^{i} is the sample size of the invaded site and n^{ni} is the sample size of the noninvaded site, and means are based on the categorical definitions described in Equation 1.

To assess variability of effect sizes we used Q statistics as a measure of heterogeneity (Hedges and Olkin 1985). Total heterogeneity (Q_{T}) was calculated as an indication of effect size homogeneity (tested against a chi-square distribution) and as an indicator of additional structure in the data (Equation 3; Rosenberg et al. 1999):

$$Q_{\mathrm{T}} = \sum_{i=1}^{n} w_i\left(E_i - \bar{\bar{E}}\right)^2 \qquad [3]$$

where n is the total number of studies, w_i is the weight for the i^{th} study (as the reciprocal of the sampling variance or $1/v_i$), E_i is the effect size for the i^{th} study, and $\bar{\bar{E}}$ is the overall effect size. To account for sources of variation and the potential differences among the effect sizes for particular categories of studies, we similarly calculated heterogeneity

Table 4. Studies with quantitative data suitable for meta-analysis. A total of 35 papers had quantitative data suitable for incorporation into the review. More than one measure of change may have been studied in a single paper (for example, the effect of a particular species on species richness and diversity) and we considered each a separate case study. Thus, the 35 papers offered a total of 64 case studies for meta-analysis.

Functional group/*species*	Location	Cases	Time	Type[a]	Metrics	Reference
C_4 grasses						
Bothriochloa ischaemum	Texas	2	2001	Obs	R, D	Gabbard and Fowler 2007
Bothriochloa ischaemum	Kansas	1	2001	Obs	C	Hickman et al. 2006
Bothriochloa ischaemum	Oklahoma	3	2007–2008	Obs	R, D, E	Robertson et al. 2012
Bothriochloa ischaemum	Texas	1	2006	Obs	C	Ruffner 2012
Eragrostis lehmanniana	Arizona	1	1972–2000	Obs	C	Angell and McClaran 2001
Eragrostis lehmanniana	Arizona	2	1984–1990	Obs	C	Bock and Bock 1992
Eragrostis lehmanniana	Arizona	1	1954–1968	Obs	B	Cable 1971
Eragrostis lehmanniana	Arizona	1	2003–2004	Exp	R	Crimmins and McPherson 2008
Eragrostis lehmanniana	Arizona, New Mexico	1	NA	Obs	C	Hupy et al. 2004
Pennisetum ciliare	Arizona	3	2011	Obs	C, R, D	Abella et al. 2012
Pennisetum ciliare	Texas	6	2001–2002	Obs	C, R	Flanders et al. 2006
Pennisetum ciliare	Mexico	2	2006–2007	Obs	R	Franklin and Molina-Freaner 2010
Pennisetum ciliare	Arizona	1	2008	Obs	R	McDonald and McPherson 2011
Pennisetum ciliare	Arizona	2	2008–2009	Obs	R, D	Olsson et al. 2012
Pennisetum ciliare	Texas	4	2005–2006	Obs	R, D	Sands et al. 2009
Sorghum halepense	Texas	3	2005–2007	Obs	R, D, E	Rout et al. 2013
C_3 grasses						
Agropyron cristatum	Canada	1	2001	Obs	D	Henderson and Naeth 2005
Bromus inermis	South Dakota	3	2005–2006	Exp	C, R	Bahm et al. 2011
Bromus inermis	Canada	4	2007	Obs	D, R, E, C	Fink and Wilson 2011
Bromus inermis	Wyoming	2	2006–2007	Obs	C	Ruehmann et al. 2011
Bromus inermis	Canada	1	1986	Exp	C	Wilson 1989
Bromus inermis	Canada	1	1987	Obs	C	Wilson and Belcher 1989
Schedonorus arundinaceus	Kentucky	2	2002–2003	Exp	C, R	Barnes 2007
Schedonorus arundinaceus	Indiana	3	1994–1998	Exp	R, D, E	Clay and Holah 1999
B. inermis, S. arundinaceus	Kansas	1	2004	Obs	R	Jog et al. 2006
Schedonorus arundinaceus	Indiana	1	2005	Exp	D	Mattingly et al. 2010
Schedonorus arundinaceus	Indiana	1	2002–2007	Exp	R	Rudgers et al. 2010
Schedonorus arundinaceus	Oklahoma	1	1999–2001	Exp	R	Tunnell et al. 2004
Schedonorus arundinaceus	Kentucky	1	1996–1997	Exp	R	Washburn et al. 2000
Legumes						
Lespedeza cuneata	Kansas	1	2001–2003	Obs	R	Blocksome 2006
Lespedeza cuneata	Illinois	2	1998–1999	Exp	R	Brandon et al. 2004
Lespedeza cuneata	Tennessee	1	2002–2003	Exp	B	Garten et al. 2008
Lespedeza cuneata	Oklahoma	1	1995–2000	Exp	B	Koger et al. 2002
Lespedeza cuneata	Tennessee	2	1995–2000	Obs	D, E	Price and Weltzin 2003
Melilotus spp.	Colorado	1	1998	Obs	R	Wolf et al. 2003

[a] Abbreviations: Obs, observational; Exp, experimental; B, biomass; C, cover; R, richness; D, diversity (Shannon's H′); E, evenness.

within categorical groups (Q_W) (Rosenberg et al. 1999). Q_T and Q_W are a weighted sum of squares similar to the total sum of squares in analysis of variance. Square-root pooled variance and mean study variance were compared as a ratio to assess between-study variance vs. within-study variance as an indication of additional data structure (Rosenberg et al. 1999). When the number of available studies are low, and when multiple cases per study exist, a single study could be overrepresented in the calculation of the overall effect size. We addressed this problem by first calculating the effect size for each individual case study and reporting those individually, and then using heterogeneity values to determine the differences of particular effect sizes for a particular case study or categories of studies so the

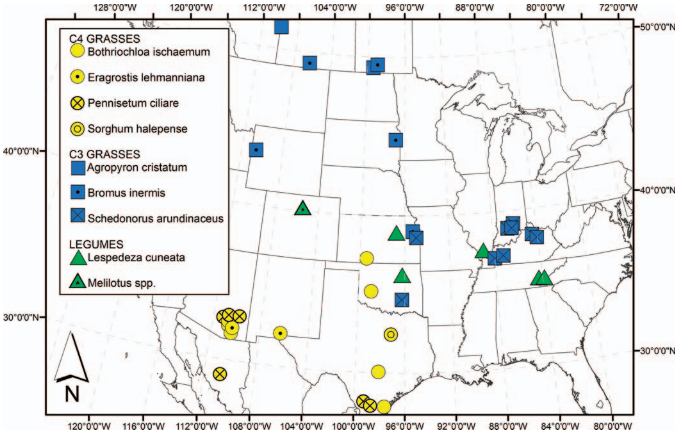

Figure 1. Distribution map of study locations of exotic forage invasions in North America used in the meta-analysis.

question of how much a unique case study is influencing the results can be determined.

To assess publication bias we employed two methods. First, we calculated unweighted and weighted fail-safe numbers that indicate the number of nonsignificant unpublished studies needed to result in a nonsignificant effect compared to the number of available studies ($5n + 10$) (Rosenberg 2005; Rosenthal 1979). Secondly, we assessed rank-order correlations between effect and variance to determine potential bias to publish studies with large effect sizes (Rosenberg 2013; Rosenberg et al. 1999; Rothstein 2006). Rank-order correlation is analogous to appraising funnel plot symmetry and is particularly powerful for studies of our sample size or larger (Begg and Mazumdar 1994).

RESULTS AND DISCUSSION

A total of 35 papers had quantitative data suitable for incorporation into the review. More than one measure of change may have been studied in a single paper (for example, the effect of a particular species on species richness and diversity) and we considered each a separate case study. Thus, the 35 papers offered a total of 64 case studies for meta-analysis (Table 4). Suitable studies fell within 25° and 50° N parallels and the 84° and 112° W meridians with C_3 invasions occurring primarily in the northern half of the continent, C_4 invasions in the southern half of the continent, and legumes across the central portions of the continent (Figure 1). Of the 64 case studies, 26 (41%) assessed species richness, 17 (27%) assessed native plant cover, 13 (20%) assessed diversity (Shannon's H′), 5 (8%) assessed evenness, and 3 (5%) assessed native plant biomass (Table 4). Study length ranged from 1 to 29 yr (mean ± SE = 3 ± 1 yr) and 80% of studies were 2 yr or less (Table 4). Thirty-one studies (90%) had been published since 2000 (mean = 2005). Suitable studies with quantitative data for meta-analysis were found for crested wheatgrass [*Agropyron cristatum* (L.) Gaertn.], Old World bluestems [jointly 'plains' *Bothriochloa ischaemum* var. *ischaemum* (L.) Keng. and 'yellow' *Bothriochloa ischaemum* var. *songarica* (Rupr. ex Fisch. & C.A. Mey.) Celarier & Harlan], smooth brome (*Bromus inermis* Leyss.), Lehmann lovegrass, [*Eragrostis lehmanniana* (Nees)], sericea lespedeza [*Lespedeza cuneata* (Dum. Cours.) G. Don], sweetclover [*Melilotus* spp.], buffelgrass [*Pennisetum ciliare* (L.) Link], tall fescue [*Schedonorus arundinaceus* (Schreb.) Dumort.], and johnsongrass [*Sorghum halepense* (L.) Pers.] but not for Bermudagrass [*Cynodon dactylon* (L.) Pers.], Kleberg's bluestem; [*Dichanthium annulatum* (Forssk.) Stapf], alfalfa (*Medicago sativa* L.), and white clover (*Trifolium repens* L.). We consider the lack of studies for *C. dactylon*, *D. annulatum*, *M. sativa*, and *T. repens* to be a significant result because these four species have anecdotally been considered invasive in rangelands, yet empirical data are not available to evaluate that claim.

The overall effect of exotic forage invasion across all metrics and species was negative ($\bar{\bar{E}} = -0.27$; 95% CI: -0.29 to -0.25; $P \leq 0.05$). The majority of studies reported a negative effect (54 studies or 85%). Two studies had a neutral effect (3%), and eight had a positive effect (13%) (Table 5). Square-root pooled variance (between study) was 0.37 and mean study variance (within study) was 0.10, yielding a ratio of 3.71, indicating a categorical meta-analysis has merit in determining the source of within-study variance (Table 6). The effect size was most negative for two of the C_4 grasses, *E. lehmanniana* ($\bar{\bar{E}} = -0.93$; 95% CI: -1.14 to -0.72) and Old World bluestems ($\bar{\bar{E}} = -0.39$; 95% CI: -0.47 to -0.30) (Table 6). For plant functional group, the effect size was negative for C_3 grasses ($\bar{\bar{E}} = -0.28$; 95% CI: -0.31 to -0.25) and similarly negative for C_4 grasses ($\bar{\bar{E}} = -0.28$; 95% CI: -0.31 to -0.24) (Table 6). Legumes had the least negative effect of the plant functional groups ($\bar{\bar{E}} = -0.17$; 95% CI: -0.27 to -0.07) (Table 6). Plant biomass and canopy cover were the most negatively affected plant community structure variables ($\bar{\bar{E}} = -0.65$ and -0.37, respectively). Diversity, evenness, and richness had similar negative effect sizes ($\bar{\bar{E}} = -0.21$ to -0.26) but confidence intervals were widest for evenness and narrowest for richness (Table 6).

Effect size ($\bar{E}$) across all studies ranged from -5.48 to 3.41. Total heterogeneity was high and significant ($Q_T = 1{,}045$, df = 63, $P < 0.001$), causing us to reject the null hypothesis that all effect sizes are equal (homogeneity among group categories) and indicating that underlying structure to the data justifies a categorical meta-analysis. The additional structure to the data reflects differences among species, differences among measures of plant community structure, and differences among plant func-

Table 5. Effect size and variance of all cases for each unique invasion study used to calculate overall effect and subsequent categorical meta-analyses.

Species code[a]–metric[b]	Reference	Effect size	Variance
Agropyron cristatum-D	Henderson and Naeth 2005	−0.20	0.01
Bothriochloa ischaemum-C (F)	Hickman et al. 2006	−0.59	0.04
Bothriochloa ischaemum-C (G)	Ruffner 2012	−5.48	1.02
Bothriochloa ischaemum-D	Robertson et al. 2012	−0.23	0.01
Bothriochloa ischaemum-D	Gabbard and Fowler 2007	−0.89	0.01
Bothriochloa ischaemum-E	Robertson et al. 2012	−0.21	0.01
Bothriochloa ischaemum-R	Robertson et al. 2012	−0.07	0.01
Bothriochloa ischaemum-R	Gabbard and Fowler 2007	−0.43	< 0.01
Bromus inermis-C	Wilson and Belcher 1989	−1.43	0.06
Bromus inermis-C(F)	Bahm et al. 2011	−0.32	0.03
Bromus inermis-C(G)	Ruehmann et al. 2011	−4.89	0.25
Bromus inermis-C(G)	Bahm et al. 2011	−0.91	0.03
Bromus inermis-C(G)	Wilson 1989	−1.56	0.02
Bromus inermis-C(W)	Ruehmann et al. 2011	0.29	< 0.01
Bromus inermis-C(W)	Fink and Wilson 2011	3.41	1.25
Bromus inermis-D	Fink and Wilson 2011	−0.84	0.10
Bromus inermis-E	Fink and Wilson 2011	−0.60	0.55
Bromus inermis-R	Fink and Wilson 2011	0.30	0.03
Bromus inermis-R	Bahm et al. 2011	−0.15	0.01
Eragrostis lehmanniana-B(G)	Cable 1971	−0.29	0.06
Eragrostis lehmanniana-C(F)	Bock and Bock 1992	−0.84	0.02
Eragrostis lehmanniana-C(G)	Angell McClaran 2001	−1.27	0.02
Eragrostis lehmanniana-C(G)	Hupy et al. 2004	−0.57	0.23
Eragrostis lehmanniana-C(G)	Bock and Bock 1992	−2.07	0.07
Eragrostis lehmanniana-R	Crimmins and McPherson 2008	−0.24	0.04
Lespedeza cuneata-B	Garten et al. 2008	−1.05	0.04
Lespedeza cuneata-B(G)	Koger et al. 2002	−0.56	0.03
Lespedeza cuneata-D	Price and Weltzin 2003	−0.12	< 0.01
Lespedeza cuneata-E	Price and Weltzin 2003	−0.19	0.12
Lespedeza cuneata-R	Brandon et al. 2004	−2.40	0.48
Lespedeza cuneata-R	Brandon et al. 2004	−1.30	0.58
Lespedeza cuneata-R	Blocksome 2006	−0.72	0.16
Melilotus spp.-R	Wolf et al. 2003	0.10	0.01
Pennisetum ciliare-C	Abella et al. 2012	−0.56	0.06
Pennisetum ciliare-C(F)	Flanders et al. 2006	−0.24	0.02
Pennisetum ciliare-C(G)	Flanders et al. 2006	−1.50	0.04
Pennisetum ciliare-C(W)	Flanders et al. 2006	0.04	0.01
Pennisetum ciliare-D	Olsson et al. 2012	−0.89	0.01
Pennisetum ciliare-D	Abella et al. 2012	0.00	< 0.01
Pennisetum ciliare-D(F)	Sands et al. 2009	−0.86	0.06
Pennisetum ciliare-D(G)	Sands et al. 2009	−1.84	0.23
Pennisetum ciliare-R	Olsson et al. 2012	−0.67	0.01
Pennisetum ciliare-R	McDonald and McPherson 2011	−0.52	0.04
Pennisetum ciliare-R	Franklin and Molina-Freaner 2010	−0.81	0.05
Pennisetum ciliare-R	Abella et al. 2012	0.00	0.01
Pennisetum ciliare-R(F)	Sands et al. 2009	−0.99	0.08
Pennisetum ciliare-R(F)	Flanders et al. 2006	−0.13	< 0.01
Pennisetum ciliare-R(G)	Sands et al. 2009	−1.22	0.10
Pennisetum ciliare-R(G)	Flanders et al. 2006	−0.21	0.01
Pennisetum ciliare-R(W)	Franklin and Molina-Freaner 2010	−0.49	0.08

Table 5. Continued.

Species code[a]–metric[b]	Reference	Effect size	Variance
Pennisetum ciliare-R(W)	Flanders et al. 2006	0.22	0.01
Schedonorus arundinaceus-D	Mattingly et al. 2010	−0.18	< 0.01
Schedonorus arundinaceus-D	Barnes 2007	−0.71	0.01
Schedonorus arundinaceus-D	Clay and Holah 1999	−0.83	0.01
Schedonorus arundinaceus-E	Clay and Holah 1999	−0.53	0.01
Schedonorus arundinaceus-R	Barnes 2007	0.07	0.01
Schedonorus arundinaceus-R	Rudgers et al. 2010	−0.11	< 0.01
Schedonorus arundinaceus-R	Tunnell et al. 2004	−0.24	< 0.01
Schedonorus arundinaceus-R	Jog et al. 2006	−0.84	0.04
Schedonorus arundinaceus-R	Clay and Holah 1999	−0.55	< 0.01
Schedonorus arundinaceus-R	Washburn et al. 2000	−0.40	0.09
Sorghum halepense-D	Rout et al. 2013	−0.07	0.01
Sorghum halepense-E	Rout et al. 2013	0.44	0.02
Sorghum halepense-R	Rout et al. 2013	−0.66	0.01

[a] Plant species nomenclature based on WSSA 2015.

[b] Abbreviations: B, biomass, C, cover, R, richness, D, diversity (Shannon's H′), E, evenness; parenthetical letters denote measurement of a specific plant functional group (G, graminoids, F, forbs, and W, woody plants).

tional group. Heterogeneity within categorical groups (Q_W) (within species, plant community structure, and plant functional group) ranged from 6 to 536 and was always significant ($P \leq 0.05$) (Table 6). Source of heterogeneity (Q_w) was always higher within groups than between groups and always significant ($P \leq 0.05$). For example, Q_w was 9 times greater by species, 51 times greater by plant community structure, and 174 times greater by plant functional group. These significant Q_W values indicate additional data structure within categorical groups. We attribute this heterogeneity of effect sizes within categorical groups to the variation in the number and types of studies available for each species. Other sources of heterogeneity potentially include site differences between studies and the variability of study timing at various points along an invasion gradient.

The unweighted fail-safe number (16,987) and the weighted fail-safe number (13,613) exceed the calculated (5n + 10) minimum number of 340 studies by > 40×. These fail-safe numbers, relative to the number of observed studies, support the robustness of our data and the reliability of the expression of the true effect (Rosenberg et al. 1999). The rank correlation between the effect and the variance, however, were significant for the both Kendall's tau ($tau = -0.235$, $Z = -2.746$, $P = 0.006$) and the Spearman rank-order ($Rs = -0.357$, $P = 0.004$). Significant correlation here indicates a bias to publish studies with larger effect sizes (in our study negative) over smaller effect sizes (Begg and Magumdar 1994). Given that the studies we used compared invaded and noninvaded sites and not a gradient of invasion, this bias is not surprising. It does, however, reflect that the invaded sites used in all studies were highly invaded and very different from areas that were not invaded and that the gradient of invasion by exotic forages has been neglected. Because the time since invasion is often unknown, we suggest that researchers adopt three strategies in designing future research: (1) rather than placing observational studies in invaded/uninvaded sites, quantify invaded sites by a gradient that begins at zero and goes to the highest value possible, (2) design more experimental studies across the invasion gradient to better understand the rate and net effects of nonnative forage species, and (3) record abiotic and biotic disturbance variables and include these in the analysis.

The invasion of exotic forage species generally, but not always, reduced richness, diversity, evenness, cover, or biomass of the native plant community. The reduction of species richness varied in magnitude such as *L. cuneata* studies that reported effect sizes from $E = -2.40$ (Brandon et al. 2004) to $E = -0.72$ (Blocksome 2006) (Table 5). Species richness reductions were similar regardless if sites had had low ($E = -0.67$, 19 species in uninvaded sites; Olsson et al. 2012), moderate ($E = -0.81$; 24 species in uninvaded sites; Franklin and Molina-Freaner 2010), or high species richness potential ($E = -0.84$, 74 species in uninvaded sites; Jog et al. 2006) (Table 5). Species diversity and evenness followed similar trends to the reductions of species richness with *S. arundinaceus* and *B. inermis* studies (diversity $E = -0.84$ and evenness $E = -0.60$ [Fink and Wilson 2011]; diversity $E = -0.83$ and evenness $E = -0.53$ [Clay and Holah 1999]) (Table 5). However, the direction of the effect on these plant community metrics was not consistent within an

Table 6. Summary data of mean effect size and categorical meta-analyses by plant species, plant community structure variables, plant functional group, and overall effect.[a]

Category	n	Q	Prob (χ^2)	Effect size	95% CI	
					Lower	Upper
Cumulative		Q_T				
	64	1,048	< 0.001	−0.27	−0.29	−0.25
Species		Q_W				
Agropyron cristatum	1	na	na	−0.20	na	na
Bothriochloa ischaemum	7	79	< 0.001	−0.39	−0.47	−0.30
Bromus inermis	11	315	< 0.001	−0.15	−0.24	−0.06
Cynodon dactylon	No studies					
Dichanthium annulatum	No studies					
Eragrostis lehmanniana	6	43	< 0.001	−0.93	−1.14	−0.72
Lespedeza cuneata	7	37	< 0.001	−0.22	−0.33	−0.12
Medicago sativa	No studies					
Melilotus spp.	1	na	na	0.10	na	na
Pennisetum ciliare	18	205	< 0.001	−0.19	−0.24	−0.14
Schedonorus arundinaceus	10	209	< 0.001	−0.30	−0.34	−0.26
Sorghum halepense	3	42	< 0.001	−0.14	−0.43	−0.15
Trifolium repens	No studies					
Community structure						
Diversity	13	212	< 0.001	−0.26	−0.31	−0.22
Evenness	5	37	< 0.001	−0.21	−0.35	−0.06
Richness	26	290	< 0.001	−0.26	−0.29	−0.23
Biomass	3	6	0.04	−0.65	−1.16	−0.14
Cover	17	482	< 0.001	−0.37	−0.45	−0.29
Functional group						
C_3 grass	21	536	< 0.001	−0.28	−0.31	−0.25
C_4 grass	35	463	< 0.001	−0.28	−0.31	−0.24
Legume	8	44	< 0.001	−0.17	−0.27	−0.07

[a] Heterogeneity is measured with the Q statistic, a weighted sum of squares for all cumulative samples (Q_T) or within categories of samples (Q_W) tested against a chi-square distribution, (Prob (χ^2). Mean effect size is reported as the natural log response ratio between noninvaded and invaded sites (± 95% confidence intervals [CI]). Mean study variance and the ratio compared to within study variance are presented as an indication of additional data structure and the need for categorical meta-analysis.

individual study. For example, Rout et al. (2013) reported reduced species richness ($E = -0.66$) and reduced diversity ($E = -0.07$), but increased evenness ($E = 0.44$) associated with *S. halepense* invasion. Using canopy cover measurements provides additional insight into how specific plant functional groups may be affected by exotic forage invasion. In Flanders et al. (2006), the reduction in canopy cover by *P. ciliare* invasion was greatest for native grass ($E = -1.5$), followed by a less negative reduction of forbs ($E = -0.24$), and a positive effect for woody plants ($E = 0.04$) (Table 5). A similar grass : forb pattern emerged for *Bromus inermis* ($E = -0.91$ and $E = -0.32$, respectively), Old World bluestem invasion ($E = -5.48$ and $E = -0.59$, respectively), and *E. lehmanniana* ($E = -1.27$ and $E = -0.84$, respectively (Angell and McClaran 2001; Bahm et al. 2011; Bock and Bock 1992; Hickman et al. 2006; Ruffner 2012). The positive association of woody plant cover was also evident for sagebrush (*Artemisia* spp.) ($E = 0.29$) and snowberry (*Symphoricarpos occidentalis* Hook.) ($E = 3.41$) cover relative to *B. inermis* invasion (Fink and Wilson 2011; Ruehmann et al. 2011) (Table 5). Biomass of the native plant community tended to be lower in invaded areas, although only three studies reported this metric (Cable 1971; Garten et al. 2008; Koger et al. 2002).

Not all species studied had suitable data for meta-analyses. This result is important because the anecdotal labeling of a species as "invasive" could limit its use for agriculture with no supporting empirical data or because the label "invasive" is not ubiquitous for all exotic forage species. For example, the lack of suitable studies for *D. annulatum* was not surprising as it has been restricted to southern regions of Texas but the lack of suitable studies for *M. sativa* is important because this species has been extensively cultivated, broadly planted, has beneficial nutrient fixation qualities, is a source of high-quality forage, and is not invasive. However, the lack of suitable studies for both *T. repens* and *C. dactylon* was unexpected given their broad distribution, dates of introduction more than 2.5 centuries earlier, and the fact that *C. dactylon* is considered one of the most invasive plants globally (Holm et al. 1977). Competitively, both species are considered midsuccessional plants with prostrate growth forms and sensitivity to shading, making them both poor resource competitors against taller plants. This limitation restricts *C. datylon* even when water and nitrogen are not limited (Guglielmini and Satorre 2002). Finally, of the papers that met the initial inclusion criteria, 258 were disqualified due to lack of adequate data metrics, confounding treatment effects, a comparison of taxa other than vascular plants (birds, insects, etc.), or because they were geospatial papers focused on detection.

Ecological Effects. Exotic forage invasion not only transforms native plant communities but may also cause cascading ecological effects across spatial scales, ecological processes, and trophic levels (Barney et al. 2013; D'Antonio and Vitousek 1992; Vilà et al. 2011). First, *S. arundinaceus* invasion changed the natural variability of vegetation structure to a more homogenous and uniform structure (McGranahan et al. 2012b). Secondly, historical disturbance patterns such as the fire regime may be constrained or accelerated by either increasing fire frequency or intensity (in the example of *P. ciliare* [Abella et al. 2012; Arriaga et al. 2004; Franklin and Molina-Freaner 2010; McDonald and McPherson 2011; Olsson et al. 2012; Stevens and Falk 2009]) or decreasing fire spread (in the example of *S. arundinaceus* [Mattingly et al. 2010; McGranahan et al. 2012a]). Lastly, soil/water processes and soil microbial communities are also at risk. In arid and semiarid regions water infiltration is reduced and evaporation is increased as *E. lehmanniana* invades (Crimmins and McPherson 2008; Moran et al. 2009). In more mesic conditions, soil microbial communities have been changed by *L. cuneata* and Old World bluestem (Brandon et al. 2004; Cable 1971; Clay and Holah 1999; Wilson et al. 2012; Yannarell et al. 2011).

Although not evaluated in our meta-analysis, a review of the literature suggests exotic forage invasion also degrades wildlife habitat and populations, specifically birds, small mammals, and invertebrates. First, grassland bird habitat and abundance has been negatively correlated with the invasion of exotic forage, specifically *S. arundinaceus, P. ciliare, E. lehmanniana,* and Old World bluestems (Flanders et al. 2006; Hickman et al. 2006; Pillsbury et al. 2011; Washburn et al. 2000). Evidence also suggests that grasshopper sparrow nest survival may be reduced by *S. arundinaceus* and *B. inermis* invasion (Hovick et al. 2012). Secondly, small mammal abundance is also at risk as exotic forages invade and levels of antiherbivory compounds are increasingly present on the landscape. For example, small mammal richness was not impacted but small mammal abundance was reduced by the infection rate of the symbiotic fungal endophyte of *S. arundinaceus* (Coley et al. 1995). Native invertebrates are also subject to negative impacts associated with this fungal endophyte as it can alter granivorous ant foraging behavior (Knoch et al. 1993). Furthermore, ant community composition has also been altered by *P. ciliare* invasion (Bestelmeyer and Schooley 1999).

Human-Mediated Invasion. Invasion of exotic forages is driven by human selection, introduction, and dispersion (D'Antonio and Vitousek 1992). A prime example of this human-mediated invasion is the marketing of named cultivars displaying the highest levels of persistence. When these cultivars are marketed it leads to broad dispersion of propagules, an influential factor in the spread and infilling of invasive plants (Warren et al. 2013). These anthropogenic selection and dispersion pathways violate the assumptions of ecological diffusion models for the introduction and spread of nonnative species (Chivers and Leung 2012; Skellam 1951).

Exotic forages have been developed through the process of selecting cultivars displaying strong persistence mechanisms and breeding to develop large quantities of seed for commercial distribution, and at times selecting lines with even stronger persistence. This human-accelerated plant breeding for very specific persistence traits differs from other invasive plants due to the intentional selection and introduction. The dispersion of exotic forages is also atypical in that private and public land managers have spread seed sources across large areas for forage establishment and in remote areas for wildlife food plots. As a comparison, leafy spurge (*Euphorbia esula* L.) invasion has a spectrum of negative ecological effects including reducing native plant species richness (DiTomaso 2009). However, the introduction and dispersion of *E. esula* has not been driven by plant breeders or managers introducing plant seed sources in an attempt to enhance production (Butler and Cogan 2004).

Bridge the Gap Between Disconnected Disciplines and Interests. We argue that ecologists should consider the disciplinary disconnectedness associated with invasions of exotic forage plants and facilitate dialogue and collaboration between those who study and manage invasive plants and those who introduce and breed exotic forage plants. A partial list of disciplines includes agronomic plant breeders who select and breed exotic forage plants, livestock producers and wildlife managers who cultivate exotic forage plants to address forage quantity

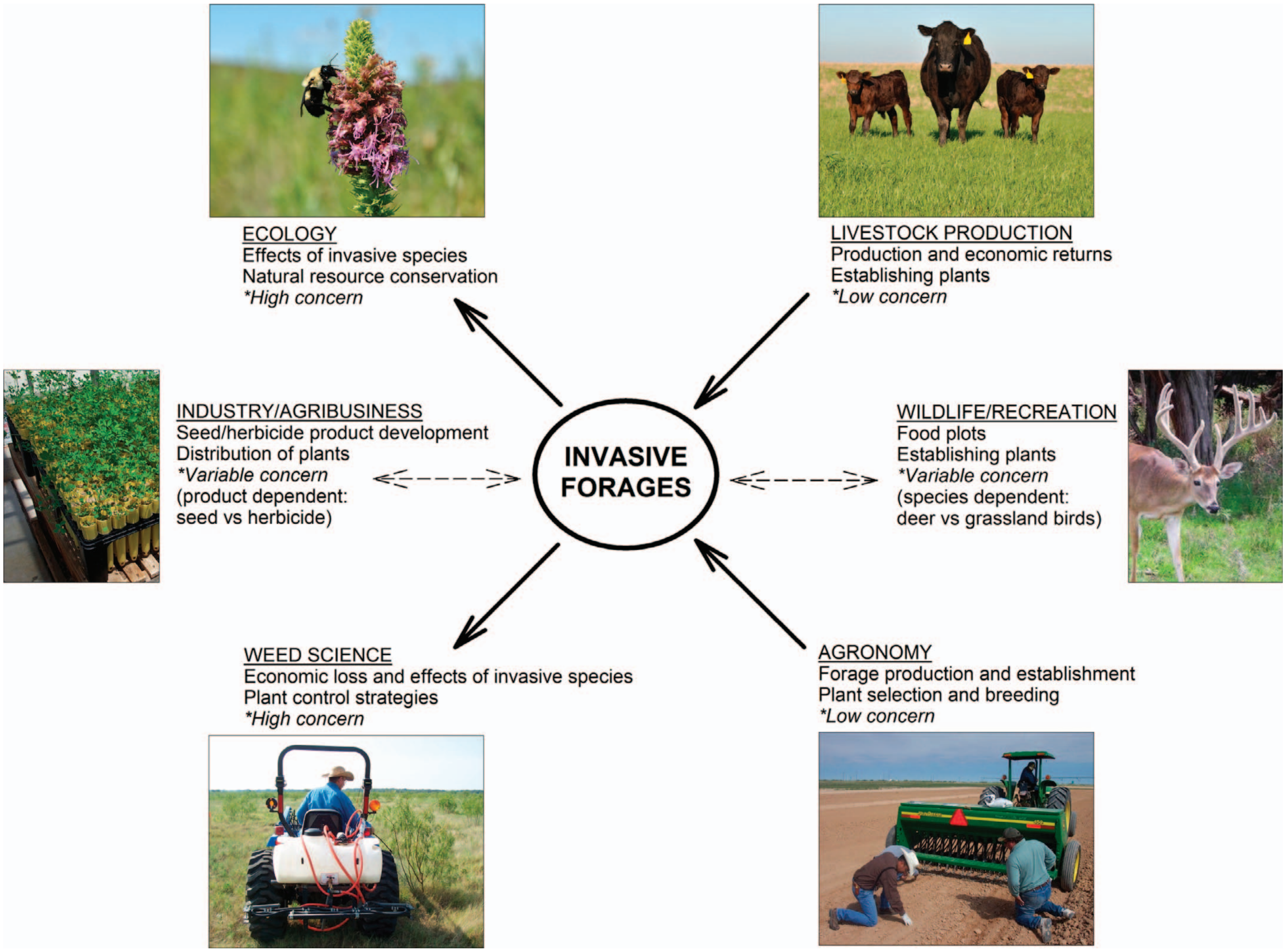

Figure 2. Subject matter disciplines, level and source of concern, and pathways associated with development, establishment, and management of exotic forages. Unidirectional solid arrows going from a discipline toward invasive forages represent disciplines interested in forage breeding with a low concern about invasion potential. Unidirectional solid arrows going from invasive forages to a discipline represent disciplines interested in the potential negative ecological effects with a high concern about invasion potential. Multidirectional dashed arrows represent disciplines that are interested in forage breeding and invasion potential depending on different goals or objectives.

and quality deficits, ecologists and weed scientists managing invasive plants, and private industry (which is concerned with both sides of this issue by producing and distributing seed or developing and marketing herbicides) (Figure 2).

An example of disconnectedness is in Alabama, where *L. cuneata* is promoted for forage and restoration, but is also listed by the state invasive plant council as invasive (Alabama Invasive Plant Council 2012; Ball and Mosjidis 2007). This disconnect is represented largely by production agriculture on one side and conservation of natural resources on the other side. The fallacy of this dichotomy is that grasslands and rangelands are complex landscapes with multi-functionality for agriculture and conservation. Thus, we suggest a focused initiative that integrates subject matter disciplines and public and private interests to promote awareness and cross-disciplinary collaboration with the goal of developing innovative solutions.

Innovative solutions are critical due to the expanse of established exotic forages, potential positive benefits of these species, and the risk of off-target negative impacts and poor success of controlling invasions (Kettenring and Adams 2011; Vilà et al. 2011). Examples of innovative solutions include developing strategies to maximize spatial detection and treatment efficacy (Emry et al. 2011) and optimizing herbivore utilization and plant phenology with temporally and spatially discrete prescribed fires (Cummings et al. 2007). We also suggest that exotic forages be considered by ecologists as a special subset of invasive plants that merit as much scientific attention as other subsets of plants such as invasive woody species (Mason et al. 2009; Twidwell et al. 2013) and accidental introductions (Butler and Cogan 2004).

Reconsider Regulation, Policy Development, and Funding Priorities. The invasion potential of exotic forages highlighted in this study suggests that the role of government oversight in approving new forage varieties for release deserves to be reconsidered. Enforcement and development of more rigorous screening protocols to prevent broad introductions and minimize invasion risk are among the actions that should be implemented, and have also been suggested for exotic perennial grasses cultivated for bioenergy production and horticulture (Barney 2014; Doughtery et al. 2014; Matlaga and Davis 2013). Science and policy must also be transparently and actively engaged so research funding priorities are compatible with both conservation and production. Research funded in part by the U.S. Department of Agriculture also reflects conflicting goals. For example, research on forage characteristics of Old World bluestems (Cui et al. 2013) and control of invasive Old World bluestems (Robertson et al. 2013) conflicts, and both studies were conducted in the Southern Great Plains of the United States. State-and-transition models used to guide management of ecological sites must also increase attention paid to the invasion of exotic herbaceous plants as only 13% of current Ecological Site Descriptions account for these species (Twidwell et al. 2013). This dichotomy suggests that communication should be improved at all levels of research funding and priority development.

Conflicting priorities and guidelines are also a problem at the federal technical assistance level, specifically with recommendations for establishing habitat in the Conservation Reserve Program (CRP) on U.S. private lands. For example, Kansas required CRP planting mixes of C_4 native species as opposed to many other states that allowed C_3 or C_4 exotic monocultures (many using exotic forages assessed in this study) (USDA 2004). Subsequently, Kansas has reported stronger positive effects on grassland bird population recovery associated with habitat requirements and arthropod prey abundance (McIntyre and Thompson 2003; Rodgers and Hoffman 2004).

Integrate Restoration, Conservation, and Production in Native Plant Communities. An integrated approach is needed to quantify the economic and ecological value of native plant communities compared to exotic forage monocultures. This type of cost–benefit analysis (CBA) and ecological economics would provide monetary equivalents to ecological goods and services that are potentially sacrificed with invasions of exotic forage plants. These goods and services might include biodiversity, pollinators, wildlife habitat, soil and water conservation, and fire behavior, among others (Pimentel et al. 2005). Such a systematic CBA approach would provide an objective method for making decisions that optimize interests of agriculture and conservation while minimizing risk of invasion and cascading ecological effects.

Research also needs to move beyond quantifying only agronomic impact or only ecological impact. Quantitative assessments of social benefits such as increased profit margins, labor, input requirements, and efficiencies are needed for comparison against ecological costs. A recent review of improved tropical forages reported that of 98 studies reviewed, only 21% quantified economic impact, only 7% quantified ecological impact, and only 2% quantified social impact (White et al. 2013). The temporal impact of exotic forages has also been neglected in research as less than 20% of the studies reviewed by White et al. (2013) provided quantitative estimates of longer-term economic impacts. Quantifying the economic, ecological, and social impacts will enhance our ability to embrace the complexity of these multi-functioning landscapes, especially landscapes that are particularly threatened by exotic forage.

The challenges driving the issue of exotic forage invasion are numerous and complex. This study has identified several, including inadequate and incomprehensive scientific knowledge, disconnectedness between stakeholders, contradictory policy and funding, and a lack of quantitative data of the tradeoffs between native and exotic species, among others. An additional challenge is the cost of using native plants compared to exotic plants as native plant seed sources are not as available or as affordable. Currently the cost of seed for a mix of native tallgrasses (big bluestem [*Andropogon gerardii* Vitman], switchgrass [*Panicum virgatum* L.], little bluestem [*Schizachyrium scoparium* (Michx.) Nash], and yellow Indiangrass [*Sorghastrum nutans* (L.) Nash ex Small]) compared to three exotic forages (*L. cuneata*, *S. arundinaceus*, and perennial ryegrass [*Lolium perenne* (L.)]) is 1.3 time to 8.3 time higher per unit area (Hancock Seed Company 2013). Cumulatively, these challenges suggest a need to reconsider native plants for restoration and reseeding that requires additional understanding of managing native plants for production agriculture, how native plant communities assemble after exotic plant invasion, and how different native species perform in restorations (Martin and Wilsey 2012; Pywell et al. 2003). Ultimately, the gap between production agriculture and conservation of natural resources must be bridged so we can objectively consider the socio-ecological complexities of exotic forages.

Realizing the Magnitude and Complexity of Exotic Forage Invasion. Our systematic review and meta-analyses of the most common exotic forages in North America revealed the negative effect that exotic forage introduction and invasion can have in transforming terrestrial ecosystems. The evidence in this study has practical application for many scientific disciplines, such as agronomy, weed science, animal science, wildlife, and conservation biology. As our global population continues to grow exponentially it places an increasing demand on food production, and consequently on how to manage grasslands and rangelands. Because these lands are complex multi-functioning landscapes that are critical to agricultural production and biodiversity conservation, our study will help stakeholders strike a balance between deriving food products and maintaining native plant communities and ecosystem goods and services.

Acknowledgments

Appreciation is extended to authors contributing to the larger body of work upon which this project builds. We also thank Dr. Norma Fowler, University of Texas, for providing additional unpublished data from her study. This article was made possible by support from the Iowa State Wildlife Grants program with the U.S. Fish and Wildlife Service Wildlife and Sport Fish Restoration Program (U-2-R-1) and the Oklahoma Agricultural Experiment Station.

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Received October 22, 2014, and approved April 27, 2015.

Associate Editor for this paper: Lisa J. Rew, Montana State University.