

A new perspective on trait differences between native and invasive exotic plants

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Abstract. Functional differences between native and exotic species potentially constitute one factor responsible for plant invasion. Differences in trait values between native and exotic invasive species, however, should not be considered fixed and may depend on the context of the comparison. Furthermore, the magnitude of difference between native and exotic species necessary to trigger invasion is unknown. We propose a criterion that differences in trait values between a native and exotic invasive species must be greater than differences between co-occurring natives for this difference to be ecologically meaningful and a contributing factor to plant invasion. We used a meta-analysis to quantify the difference between native and exotic invasive species for various traits examined in previous studies and compared this value to differences among native species reported in the same studies. The effect size between native and exotic invasive species was similar to the effect size between co-occurring natives except for studies conducted in the field; in most instances, our criterion was not met although overall differences between native and exotic invasive species were slightly larger than differences between natives. Consequently, trait differences may be important in certain contexts, but other mechanisms of invasion are likely more important in most cases. We suggest that using trait values as predictors of invasion will be challenging.

Key words: context dependence; ecological importance; effect size; functional traits; invasion; invasive species; meta-analysis.

INTRODUCTION

Niche models of community assembly and plant invasion suggest that exotic species are poor invaders when they are functionally similar to native species at local scales (Shea and Chesson 2002, Fargione et al. 2003, Gurevitch et al. 2011). Consequently, invasion occurs when niche vacancy exists following disturbances that increase resource availability (Davis et al. 2000, Davis and Pelsor 2001), or when competitors and natural enemies suppress native species performance (Keane and Crawley 2002, Zupping-Dingley 2011). Species able to exploit the available resources invade the community. The ability to exploit available resources depends on functional differences among species, which are considered proportional to invasive ability (Naeem et al. 2000, van Kleunen et al. 2010). Functional differences between native and exotic invasive plant species are typically inferred by quantifying differences in trait values between species (Leishman et al. 2007, Ordonez et al. 2010, Leffler et al. 2011, 2013), but

differences are meaningless unless a minimum difference is known to hasten invasion. Two factors may be critical in determining if invasion can occur: the context of the comparison between the native and exotic species because trait values can be plastic, and differences in trait values relative to other factors that promote invasion (i.e., the importance of trait differences).

While several studies find differences in morphological or physiological traits between exotic invasive and native species (Drenovsky et al. 2008, Schumacher and Roscher 2009, Leffler et al. 2011, 2013), many meta-analyses find equivocal results. Van Kleunen et al. (2010) examined 117 studies and concluded that exotic invasive species differed in growth rate, leaf area, and physiology, and suggested that invasion might be predictable from plant traits. Others have concluded that natives and exotics were similar in carbon-capture strategy (Leishman et al. 2007, 2010), or only differed in a few key areas such as phenotypic plasticity (Daehler 2003). The link between plasticity and the fitness of exotic invasive species, however, is tenuous (Davidson et al. 2011). In a detailed review of specific traits in experimental studies, relatively few traits including spatial growth, fecundity, and resource-use efficiency were consistently higher in invasive species (Pyšek and Richardson 2007). The context-dependent nature of invasion is especially evident regarding soil nitrogen. High soil-nitrogen availability is typically considered a context for exotic plant invasion (Maron and Connors

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1996, Davis and Pelsor 2001, Holdredge et al. 2010) but examples of N having little or a negative influence on exotic abundance can be found (Brandon et al. 2004, Thompsen et al. 2006, Pan et al. 2011). Moreover, studies that describe differences between exotic invasive and native species typically find relatively few traits that differ significantly, or find differences only in select contexts (Leffler et al. 2011, 2013), hence the assertion that traits of invasive species tend to be habitat dependent (Thompson et al. 1995).

A second challenge with attributing invasion to differences in trait values between native and exotic invasive species is that any two species can be expected to differ in several traits. Moreover, the difference in trait value between native and exotic invasive species that will promote invasion is unknown, especially since factors such as order of arrival (Von Holle and Simberloff 2005, Daleo et al. 2009) or presence of natural enemies (Keane and Crawley 2002, Zuppinge-Dingley et al. 2011) can also influence invasion. This argument is akin to suggesting competition can be intense, but not important in structuring a community (Goldberg and Novoplansky 1997). The possibility exists that trait difference may be large, but have little bearing on invasion, and a metric is needed to quantify this importance (i.e., a comparison between invasive and noninvasive exotic species as in Strauss et al. 2006).

Because an absolute minimum trait difference to promote invasion likely does not exist, we propose a relative minimum for differences to potentially be ecologically important. If trait differences between native and exotic invasive species are important for the invasion process, then these differences should be greater than variation among native species already present in the community. If invasion by the exotic is occurring, but the difference between the natives and the exotic is small, then processes other than trait differences must be driving the invasion. Consequently, when variation among co-occurring individuals in a single trait is high, it is unlikely that an exotic species will invade based solely on its value for the same trait. We do not, however, suggest that large differences between exotic invasive and native plants relative to differences among natives is sufficient for invasion, only that this criterion be satisfied for trait differences to be potentially important in the invasion process.

Here, we take a broad-scale perspective in examining the invasive-species literature and ask if the difference between native and exotic invasive species is greater than the difference between two co-occurring natives. We conduct a meta-analysis that simultaneously examines all traits authors found reason to compare between native and exotic invasive species. Specifically, we estimate differences between native and exotic invasive species in various traits and compare those to differences between native species using all possible species pairs in published literature. Studies are further classified by plant functional group, type of study (i.e., field studies,

controlled greenhouse studies, and so forth), biome, and type of trait examined.

METHODS

Citations of relevant literature were gathered from Web of Science, Science Citation Index for publication years 1995–2010 (Appendix A). We used a title search with the following terms: (invas* or nonnat* or nonnat* or alien* or exotic or nonindig* or non-indig*) and (nat* or indig* or non-invas* or noninvas*) and eliminated non-plant studies by searching the resulting titles for animal terms (bird or avian or vertebrate or invertebrate or mammal or insect or rodent or rattus or arthropod). The remaining records were limited to articles rather than reviews in the Web of Science Categories of Ecology, Environmental Science, Plant Science, and Forestry. Papers published in animal ecology journals and marine journals were eliminated. Additional papers were added based on previous experience with the literature to include known studies missed by the search, and from citations within the papers found with the search. In order for a study to be included in the database, it needed to compare a measure of physiology or morphology on an individual plant between one species that was an exotic invasive and another species locally native. The only exception was the inclusion of studies that measured combined biomass on several individuals growing in the same study plot or pot. Data presented in the paper needed to include mean, sample size, and a measure of dispersion for the native and exotic invasive species grown in the same experimental condition or field plot. The complete database included 151 papers and 8117 data points. Seventy-one of those papers also included native–native comparisons yielding an additional 3388 data points. See Appendix B and its Fig. B.1 for additional details.

Data in selected papers were extracted from tables where available, or from graphs using the program Data Thief III (*available online*).⁵ Multiple data points were obtained from a single paper if that paper compared one or more exotic invasive to one or more locally native species, or if the paper examined multiple contexts (e.g., water and N treatment)—an occurrence in nearly every study. In these cases, all possible comparisons between native and exotic invasive species were made, sometimes yielding several hundred data points. Our procedure accounted for the potential dependence of extracting multiple data points from a single study. We employed Hedges' *d* effect-size statistics (Kulmatiski et al. 2008, van Kleunen et al. 2010). Each data point consisted of one effect size, the difference between the mean trait or performance measure of the exotic invasive species (\bar{i}) and the native species (\bar{n}), normalized by the pooled standard deviation (*s*) and a sample-size weighting factor (*j*):

⁵ <http://datathief.org>

$$d = \left(\frac{\bar{i} - \bar{n}}{s} \right) j \quad (1)$$

where

$$s = \sqrt{\frac{(n_n - 1)s_n^2 + (n_i - 1)s_i^2}{n_n + n_i - 2}} \quad (2)$$

n_n and n_i are the sample sizes of the native and exotic invasive species, respectively; s_n^2 and s_i^2 are the variances about the mean of the native and exotic species, respectively, and

$$j = 1 - \frac{3}{4(n_n + n_i - 2) - 1}. \quad (3)$$

The variance of the effect size was calculated as

$$v_d = p \left(\frac{1}{n_n} + \frac{1}{n_i} \right) + (p - 1)d^2 \quad (4)$$

where

$$p = j^2 \left(\frac{n_n + n_i - 2}{n_n + n_i - 4} \right). \quad (5)$$

This form of the variance is considered an unbiased estimate (Kulmatiski et al. 2008) when sampling dependence is present (Gleser and Olkin 1994). We used the absolute value of effect size in our analyses because the data set includes traits where an advantage to the exotic invasive species might be gained by having a high value for the trait (e.g., RGR [relative growth rate], SLA [specific leaf area]) or a low value of the trait (e.g., leaf thickness). The full data set is available as a Supplement.

We used a linear mixed model to estimate effect size in our analyses. All analysis were conducted in the statistical computing language R, version 3.0.1 (R Development Core Team 2008). Since individual studies provided multiple data points in the data set, we used a data aggregation procedure (function AGG [meta-analysis aggregation, version 0.8] within package MAd) to estimate effect size for each study (Gleser and Olkin 1994). Aggregation was performed by moderator and type of comparison (i.e., comparison between a native and invasive or a comparison between two natives). Separate aggregation and analysis were performed for each moderator we examined including type of studies (field, plot, and pot), study biome (alpine, desert, mediterranean, temperate, tropical; see Appendix B: Fig. B2), functional group (aquatic, forb, grass, shrub, tree, vine), or trait type (aboveground, belowground, or whole plant for growth, morphological, or physiological traits, and reproductive traits). See Appendix B: Fig. B3 for the distributions of all effect sizes for each level of moderator. The meta-analysis was performed using function RMA (meta-analysis via the linear [mixed-effects] model, version 1.6-0) within package METAFOR using the REML

(restricted maximum likelihood) method. Parameter estimates, 95% confidence intervals, and a test of residual heterogeneity (Q_E) based on a χ^2 distribution were extracted from RMA. Moderator significance was examined using a resampling technique (Adams et al. 1997, van Kleunen et al. 2010) to compare the test of moderators (Q_M) from RMA to a null distribution of Q_M values based on 5000 iterations of the RMA function with a random assignment of aggregated effect sizes to moderators. The P value for this test indicates the fraction of Q_M values that are greater (i.e., more heterogeneous) than the original Q_M (Appendix B: Fig. B4). For any of the Q_M tests that were statistically significant, we performed a multiple comparison (function GLHT [general linear hypotheses; version 1.2-17] within package MULTCOMP) to determine at which levels the native–invasive comparison was distinct from the native–native comparison. We used a similar procedure as above, extracting a t value from each multiple comparison in the 5000 iterations, creating a null distribution of t and calculating P as the fraction of t values greater than the original t (Appendix B: Fig. B5). We also used the same data-aggregation procedure (with only native/invasive as a moderator) to compute an effect size for all studies to determine if there was a relationship between whole-study effect size and the number of data points within a study.

Finally, we selected two traits from the non-aggregated complete data set, SLA and growth (including relative and absolute growth rate of leaves, stems, and roots) to highlight our findings by examining distribution of effect size for directional differences assuming both high SLA and growth are beneficial for invasion. These traits were represented in 37 and 27 studies, respectively, and smooth distributions of effect sizes are achieved with a kernel density estimator (function DENSITY within package STATS).

RESULTS

We observed a distinct negative relationship between the aggregated effect size and the number of data points in a study (Fig. 1). Aggregated effect size was nearly one order of magnitude lower in studies that contributed over 100 data points compared to those that contributed fewer than 10 data points; this trend was similar for the native–invasive and native–native comparisons. There is a tendency for studies contributing numerous data points to have a highly right-skewed distribution of individual effect sizes (Fig. 1 inset), suggesting most data points show little difference between native and invasive species.

All tests reveal considerable residual heterogeneity (Q_E , Table 1), indicating that various studies included in this analysis yielded different results. The effect size for the absolute value of the difference between native and exotic invasive species was 0.644 with a 95% confidence interval between 0.564 and 0.724 (Fig. 2a). The effect

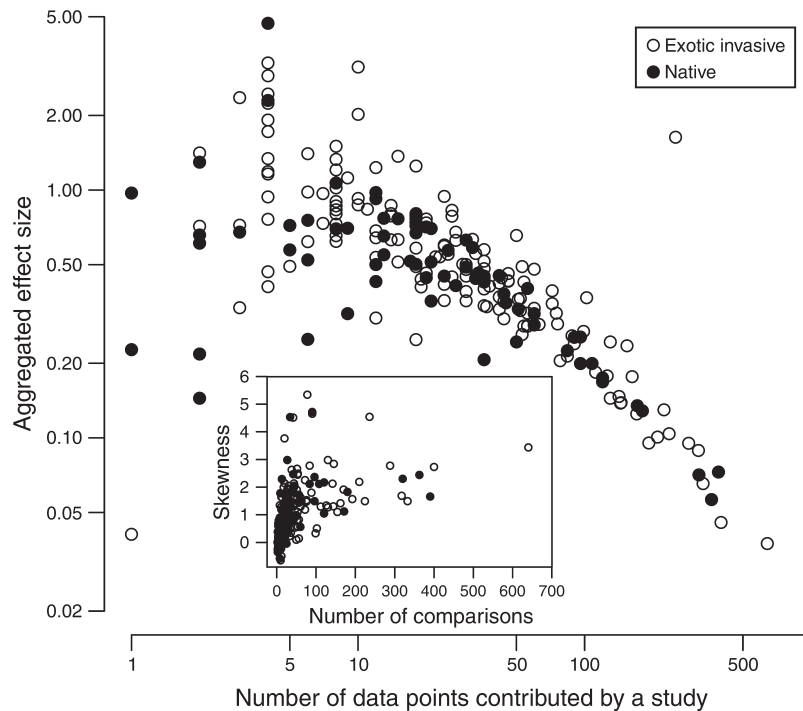


FIG. 1. Relationship between the aggregated effect size and the number of comparisons extracted from a single study; note that the axes are log scale. The inset shows the relationship between skewness of effect-size distribution within a study and the number of comparisons extracted from a single study; note that the axes are on a linear scale.

size for a comparison between two native species from the same studies was 0.500 with a confidence interval between 0.374 and 0.627. While differences between exotic invasive species and native species were greater than differences between two natives, this difference was statistically significant only at $P = 0.07$ (Table 1, Q_M).

Of the four subsequent tests of moderators, only the test of different experimental types yielded a significant result (Fig. 2b, Table 1, $Q_M P = 0.016$); all other tests had $P > 0.350$ (Fig. 2c–e, Table 1). Given the significant Q_M result for “Type,” we performed a multiple comparison and observed a greater effect size for the comparison between exotic invasive and native species (0.899) than between two natives (0.583) with $P = 0.015$ in field studies alone. Other multiple comparison results for Type were not significant.

We examined two traits closely linked to invasion, SLA and growth rate (Fig. 3). Both of these traits were assumed to be advantageous to invasive species consequently we examined directional (i.e., non-absolute value) effect size. In the case of both traits, effect size for the exotic invasive–native comparison and the native–native comparison were nearly zero and the two distributions overlapped considerably. For SLA, the median effect size for the exotic–invasive comparison was 0.25 while the median for the native–native comparison was -0.09 . Median values for growth traits were 0.47 and 0.31, respectively.

DISCUSSION

The trend throughout the analysis presented here is that exotic invasive plants only differ minimally more from native plants than native plants differ from each other. While the trend was toward greater differences between exotic invasive species and native species, that trend was only significant for studies that made comparisons between native and exotic species in the field rather than in manipulated plot or pot experiments. This finding supports the contention that trait-based differences between native and exotic invasive species alone will be a challenging tool to use for prediction of future invasion (Thompson and Davis 2011).

Despite the lack of broad differences between native and exotic invasive species observed here, nearly every study had at least one effect size greater than 2.5 but also

TABLE 1. Tests of residual heterogeneity (Q_E) and moderators (Q_M) for each analysis.

Study	Test				
	Q_E	Q_E df	$Q_E P$	Q_M	$Q_M P^\dagger$
All studies	557.0	217	<0.001	309.2	0.070
Type of study	959.3	279	<0.001	390.0	0.016
Biome study	542.6	207	<0.001	299.3	0.646
Functional group study	503.6	206	<0.001	315.4	0.492
Trait type study	1610	495	<0.001	729.9	0.363

$^\dagger Q_M P$ values are derived from the resampling procedure detailed in Adams et al. (1997).

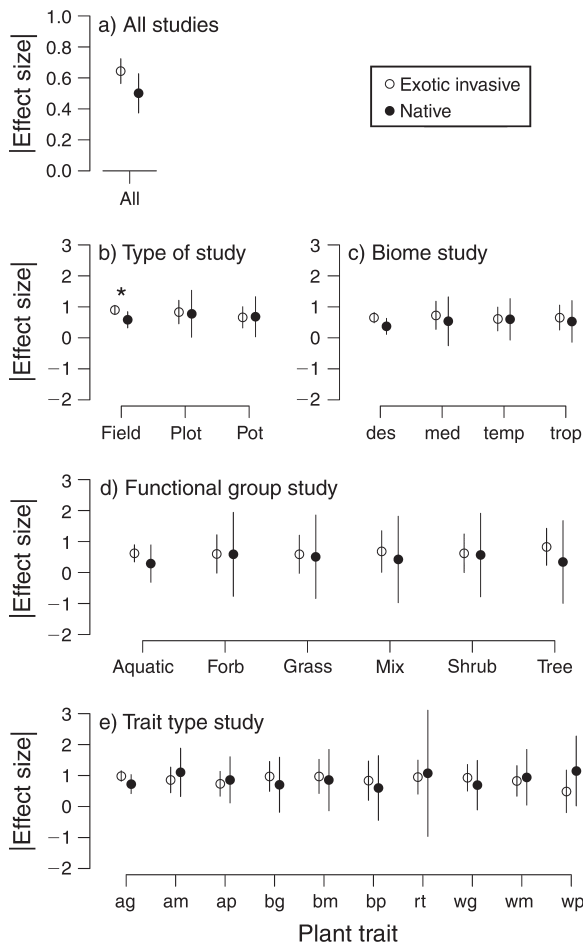


FIG. 2. The absolute value of the effect size (effect size) for (a) all studies, (b) type of study, (c) study biome (des, desert; med, mediterranean; temp, temperate; trop, tropical), (d) functional group, and (e) trait type (ag, aboveground growth; am, aboveground morphology; ap, aboveground physiology; bg, belowground growth; bm, belowground morphology; bp, belowground physiology; rt, reproductive traits; wg, whole-plant growth; wm, whole-plant morphology; wp, whole-plant physiology). Error bars are 95% confidence intervals. The Q statistics for panels (a)–(e) are in Table 1. Note that the y -axis scale for panel (a) differs from others to make error bars apparent.

* $P < 0.05$ for multiple comparison between exotic invasive–native and native–native.

effect sizes smaller than 0.5. For example, from Hamerlynck et al. (2010) we calculated an effect size of 7.9 for the difference in photosynthetic rate between the exotic invasive grass *Eragrostis lehmanniana* and the native grass *Muhlenbergia porteri*, but another observation of stomatal conductance in the same study had an effect size of only 0.002. These dichotomies often depended on the context of the comparison. In James (2008) the authors conclude that leaf nitrogen productivity (NP) is a key trait in annual grass invasion. Effect size for leaf NP ranged between 0.78 and 1.51 between

the invasive *Bromus tectorum* and the native *Elymus elymoides*; and between 0.49 and 2.27 for the invasive *Taeniatherum caput-medusae* and the native *Psuedoroegneria spicata*. Large effect sizes were observed under low nutrient conditions while small effect sizes were calculated from comparisons in a less stressful context.

When effect size was aggregated within studies we observed a negative relationship between it and the number of comparisons (Fig. 1). For example, all effect sizes ($n = 4$) for a comparison of tree height between *Pinus tecunumanii* (exotic) and *Cedrela odorata* (native) were greater than 2.5 (Carpenter et al. 2004) while fewer than 50% of the effect sizes ($n = 333$) in gas exchange and growth traits in a comparison of several native and exotic invasive desert shrubs were greater than 2.5 (Funk and Zachary 2010). This result is similar to a publication bias. Studies with few comparisons may result from a priori selection of species, traits, and contexts with large effect size; or a posteriori selection of species, traits, and contexts for inclusion in publications. That this trend, and the relationship between skewness and number of comparisons (Fig. 1 inset), is similar for native–invasive and native–native comparisons is further evidence that differences between exotic invasive and native plant species are minimal (Thompson et al. 1995, Meiners 2007).

Despite our overall conclusion of minimal difference, exotic invasive species were more distinct from native species than two natives were from each other in non-manipulated field surveys of plant traits (Fig. 2b). These results are derived from 69 of the papers included in the data set, and 50% of the aggregated effect sizes in these studies fall between 0.42 and 1.23. Finding differences in field studies demonstrates that potentially important trait differences exist in situ, lending support to contentions that traits are important in invasion (van Kleunen et al. 2010). Our finding of significant trait differences in field studies points to a potential limitation of our threshold; it only applies at small scales where species directly interact. Since invasion necessarily proceeds at multiple, larger scales (Theoharides and Dukes 2007), other mechanisms of invasion remain important. Future studies should focus more effort on surveying natural communities rather than comparing native and exotic invasive species growing in small plots or greenhouses. These settings only approximate the natural world and plants in such studies do not necessarily interact in a meaningful way.

Specific leaf area (SLA) and growth rate are often linked to invasion (Pyšek and Richardson 2007, Schumacher and Roscher 2009) but we observed nearly identical distributions of effect size for the exotic invasive–native comparison and the native–native comparison. Native species have a similar range of trait values for SLA and growth rate as invading species (Meiners 2007). Consequently, the context in which those traits are expressed is perhaps more important than the traits themselves (Thompson et al. 1995).

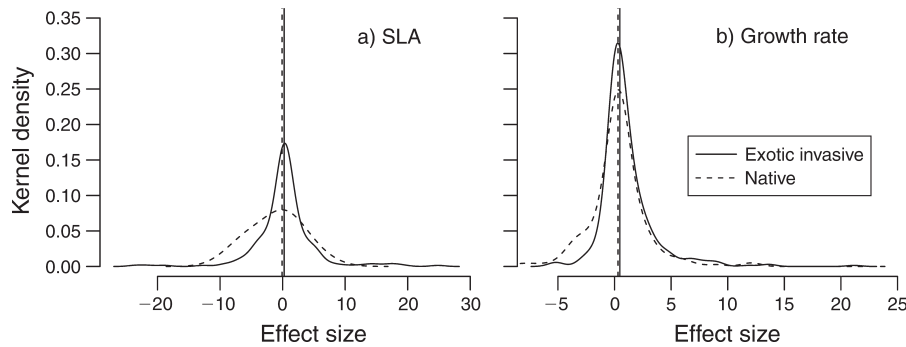


FIG. 3. Distribution of effect size data points for (a) specific leaf area and (b) growth rate; both traits are hypothesized to be greater in exotic invasive species. Vertical lines indicate medians of each distribution. Smooth distributions are achieved with a kernel density estimator.

Recent studies have highlighted the context dependence of leaf traits including photosynthesis and nitrogen-use efficiency (McKown et al. 2013) and root proliferation (Karst et al. 2012).

In our present study we asked if native and exotic invasive species differ, but also attempted to establish a minimum difference that may be ecologically important. We considered a potentially important difference between an exotic invasive and a native to be one significantly greater than that between co-occurring native species. If this criterion is not achieved it is difficult to argue that the difference is important for invasion; other factors that influence invasion such as enemy release (Keane and Crawley 2002, Zuppinger-Dingley et al. 2011), species order of arrival (Daleo et al. 2009), or propagule pressure (Von Holle and Simberloff 2005) could be of equal, or greater importance. This perspective on invasion is analogous to the ecological competition literature that distinguishes between intensity and importance of competition (Goldberg and Novoplansky 1997, Damgaard and Fayolle 2010). Absolute difference between a native and an invasive is akin to intensity, while that value relative to expected difference among species that co-occur is akin to importance. The competition literature highlights the importance of context; while competition may occur, competition is less important for structuring communities in stressful ecosystems than it is under more benign conditions (Callaway et al. 2002, Kikvidze et al. 2006).

Despite our conclusion that trait differences are minimally responsible for invasion, exotic invasive species have clear negative consequences (Vitousek 1990, Vilá et al. 2011). The degree of trait difference between native and exotic invasive plants may be more important in determining the influence of the invasive species on ecosystem functioning rather than in predicting invasion (Vitousek 1990, Strayer 2012). The largest alterations in ecosystem functioning have occurred with dramatic changes in functional group composition. The invasion of annual grasses into the perennial-dominated Intermountain West of North America has greatly increased fire frequency (Chambers et al. 2007) and

caused seasonal spikes in soil NO_3^- that did not exist previously, but are now common (Booth et al. 2003). Similarly, shrub encroachment into desert grasslands and the arctic can greatly alter the carbon balance of these systems (Steltzer et al. 2008, Eldridge et al. 2011).

Our results suggest trait differences between native and exotic invasive species reported in the papers we examined are not solely important for invasion at the broadest scale. Rather, on a case-by-case basis the likely model is a trait \times environment interaction (i.e., context dependence) that can only inform local predictions of probability of invasion. While trait differences may be considerable, only in certain contexts are trait differences likely an important factor contributing to invasion. One such context is the species composition of the native community. A community with few native species may be “under-dispersed” (Gerhold et al. 2011), yielding little difference among natives. Trait differences may be more likely to promote invasion in this scenario than in a community with a trait distribution more representative of the regional species pool; our threshold would be difficult to achieve in communities with considerable trait breadth.

Since native and invasive plants did not differ considerably in traits here, applied ecologists should consider that (1) while a diverse community of functionally distinct species may be most desirable for ecological processes or resilience (Walker et al. 1999, Hooper et al. 2005), diverse communities are not necessarily resistant to invasion due to their trait composition alone (Naeem et al. 2000); (2) species identity (Mokany et al. 2008) may be more important than diversity (Pokorny et al. 2005) in conferring resistance to invasion; (3) designing invasion-resistant communities by choosing species based on their traits (Pywell et al. 2003, Funk et al. 2008) will be challenging; and (4) plant traits may be most useful by contributing to a “probability of invasion” for a species in a certain ecological setting rather predicting invasion per se (Milbau and Stout 2008). Most importantly, preventing invasion requires managers to examine the full suite of

mechanisms by which exotic species can establish (Hobbs and Humphries 1995, James et al. 2010).

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LITERATURE CITED

- Adams, D. C., J. Gurevitch, and M. S. Rosenberg. 1997. Resampling tests for meta-analysis of ecological data. *Ecology* 78:1277–1283.
- Booth, M. S., J. M. Stark, and M. M. Caldwell. 2003. Inorganic N turnover and availability in annual- and perennial-dominated soils in a northern Utah shrub-steppe ecosystem. *Biogeochemistry* 66:311–330.
- Brandon, A. L., D. J. Gibson, and B. A. Middleton. 2004. Mechanisms for dominance in an early successional old field by the invasive non-native *Lespedeza cuneata* (Dum. Cours.) G. Don. *Biological Invasions* 6:483–493.
- Callaway, R. M., et al. 2002. Positive interactions among alpine plants increase with stress. *Nature* 417:844–848.
- Carpenter, F. L., J. D. Nichols, and E. Sandi. 2004. Early growth of native and exotic trees planted on degraded tropical pasture. *Forest Ecology and Management* 196:367–378.
- Chambers, J. C., B. A. Roundy, R. R. Blank, S. E. Meyer, and A. Whittaker. 2007. What makes Great Basin sagebrush ecosystems invulnerable by *Bromus tectorum*? *Ecological Monographs* 77:117–145.
- Daehler, C. C. 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics* 34:183–211.
- Daleo, P., J. Alberti, and O. Iribarne. 2009. Biological invasions and the neutral theory. *Diversity and Distributions* 15:547–553.
- Damgaard, C., and A. Fayolle. 2010. Measuring the importance of competition: a new formulation of the problem. *Journal of Ecology* 98:1–6.
- Davidson, A. M., M. Jennions, and A. B. Nicotra. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters* 14:419–431.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528–534.
- Davis, M. A., and M. Pelsor. 2001. Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters* 4:421–428.
- Drenovsky, R. E., C. A. Martin, M. R. Falasco, and J. J. James. 2008. Variation in resource acquisition and utilization traits between native and invasive perennial forbs. *American Journal of Botany* 95:681–687.
- Eldridge, D. J., M. A. Bowker, F. T. Maestre, E. Roger, J. F. Reynolds, and W. G. Whitford. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. *Ecology Letters* 14:709–722.
- Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences USA* 100:8916–8920.
- Funk, J. L., E. E. Cleland, K. N. Suding, and E. S. Zavaleta. 2008. Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution* 23:695–703.
- Funk, J. L., and V. A. Zachary. 2010. Physiological responses to short-term water and light stress in native and invasive plant species in southern California. *Biological Invasions* 12:1685–1694.
- Gerhold, P., M. Pärtel, O. Tackenberg, S. M. Hennekens, I. Bartish, J. H. J. Schaminée, A. J. F. Fergus, W. A. Ozinga, and A. Prinzing. 2011. Phylogenetically poor plant communities receive more alien species, which more easily coexist with natives. *American Naturalist* 177:668–680.
- Gleser, L. J., and I. Olikin. 1994. Stochastically dependent effect sizes. Pages 339–356 in H. Cooper, L. V. Hedges, and J. C. Valentine, editors. *The handbook of research synthesis*. Russell Sage Foundation, New York, New York, USA.
- Goldberg, D., and A. Novoplansky. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85:409–418.
- Gurevitch, J., G. A. Fox, G. M. Wardle, Inderjit, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14:407–418.
- Hamerlynck, E. P., R. L. Scott, M. S. Moran, T. O. Keefer, and T. E. Huxman. 2010. Growing season ecosystem and leaf-level gas exchange of an exotic and native semiarid bunchgrass. *Oecologia* 163:561–570.
- Hobbs, R. J., and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. *Conservation Biology* 9:761–770.
- Holdredge, C., M. D. Bertness, E. von Wettberg, and B. R. Silliman. 2010. Nutrient enrichment enhances hidden differences in phenotype to drive a cryptic plant invasion. *Oikos* 119:1776–1784.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- James, J. J. 2008. Leaf nitrogen productivity as a mechanism driving the success of invasive annual grasses under low and high nitrogen supply. *Journal of Arid Environments* 72:1775–1784.
- James, J. J., B. S. Smith, E. A. Vasquez, and R. L. Sheley. 2010. Principles for ecologically based invasive plant management. *Invasive Plant Science and Management* 3:229–239.
- Karst, J. D., P. R. Belter, J. A. Bennett, and J. F. Cahill, Jr. 2012. Context dependence in foraging behavior of *Achillea millefolium*. *Oecologia* 170:925–933.
- Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17:164–170.
- Kikvidze, Z., L. Khetsuriani, D. Kikodze, and R. M. Callaway. 2006. Seasonal shifts in competition and facilitation in subalpine plant communities of the central Caucasus. *Journal of Vegetation Science* 17:77–82.
- Kulmatiski, A., K. H. Beard, J. R. Stevens, and S. M. Cobbold. 2008. Plant–soil feedbacks: a meta-analytical review. *Ecology Letters* 11:980–992.
- Leffler, A. J., J. J. James, and T. A. Monaco. 2013. Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. *Oecologia* 171:51–60.
- Leffler, A. J., T. A. Monaco, and J. J. James. 2011. Nitrogen acquisition by annual and perennial grass seedlings: testing the role of performance and plasticity to explain plant invasion. *Plant Ecology* 212:1601–1611.
- Leishman, M. R., T. Haslehurst, A. Ares, and Z. Baruch. 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. *New Phytologist* 176:635–643.
- Leishman, M. R., V. P. Thompson, and J. Cooke. 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. *Journal of Ecology* 98:28–42.
- Maron, J. L., and P. G. Connors. 1996. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* 105:302–312.
- McKown, A. D., R. D. Guy, M. S. Azam, E. C. Drewes, and L. K. Quamme. 2013. Seasonality and phenology alter functional leaf traits. *Oecologia* 172(3):653–665.

- Meiners, S. J. 2007. Native and exotic plant species exhibit similar population dynamics during succession. *Ecology* 88: 1098–1104.
- Milbau, A., and J. C. Stout. 2008. Factors associated with alien plant transitioning from casual, to naturalized, to invasive. *Conservation Biology* 22:308–317.
- Mokany, K., J. Ash, and S. Roxburgh. 2008. Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology* 96:884–893.
- Naem, S., J. M. H. Knops, D. Tilman, K. M. Howe, T. Kennedy, and S. Gale. 2000. Plant diversity increases resistance to invasion in the absence of covarying factors. *Oikos* 91:97–108.
- Ordóñez, A., I. J. Wright, and H. Olf. 2010. Functional differences between native and alien species: a global-scale comparison. *Functional Ecology* 24:1353–1361.
- Pan, J. J., D. Ammerman, and R. J. Mitchell. 2011. Nutrient amendments in a temperate grassland have greater negative impacts on early season and exotic plant species. *Plant Ecology* 212:853–864.
- Pokorny, M. L., R. L. Sheley, C. A. Zabinski, R. E. Engel, T. J. Svejcar, and J. J. Borkowski. 2005. Plant functional group diversity as a mechanism for invasion resistance. *Restoration Ecology* 13:448–459.
- Pyšek, P., and D. M. Richardson. 2007. Traits associated with invasive alien plants: Where do we stand. Pages 97–125 in W. Nentwig, editor. *Biological Invasions*. Springer-Verlag, Berlin, Germany.
- Pywell, R. F., J. M. Bullock, D. B. Roy, L. Warman, K. J. Walker, and P. Rothery. 2003. Plant traits as predictors of performance in ecological restoration. *Journal of Applied Ecology* 40:65–77.
- R Development Core Team. 2008. R: a language and environment for statistical computing, version 3.0.1. R Foundation for Statistical Computing, Vienna, Austria.
- Schumacher, J., and C. Roscher. 2009. Differential effects of functional traits on aboveground biomass in semi-natural grasslands. *Oikos* 118:1659–1668.
- Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution* 17:170–176.
- Steltzer, H., R. A. Hufbauer, J. M. Welker, M. Casalis, P. F. Sullivan, and R. Chimner. 2008. Frequent sexual reproduction and high intraspecific variation in *Salix arctica*: implications for a terrestrial feedback to climate change in the High Arctic. *Journal of Geophysical Research: Biogeosciences* (2005–2012) 113:G03S10.
- Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences USA* 103:5841–5845.
- Strayer, D. 2012. Eight questions about invasions and ecosystem functioning. *Ecology Letters* 15:1199–1210.
- Theoharides, K. A., and J. S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176:256–273.
- Thompson, M. A., J. D. Corbin, and C. M. D'Antonio. 2006. The effect of soil nitrogen on competition between native and exotic perennial grasses from northern coastal California. *Plant Ecology* 186:23–35.
- Thompson, K., and M. A. Davis. 2011. Why research on traits of invasive plants tells us very little. *Trends in Ecology and Evolution* 26:155–156.
- Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? *Ecography* 18: 390–402.
- van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13:235–245.
- Vilá, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarošík, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pyšek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- Vitousek, P. M. 1990. Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57:7–13.
- Von Holle, B., and D. Simberloff. 2005. Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology* 86:3212–3218.
- Walker, B., A. Kinzig, and J. Langridge. 1999. Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems* 2: 95–113.
- Zuppinger-Dingley, D., B. Schmid, Y. Chen, H. Brandl, M. G. A. van der Heijden, and J. Joshi. 2011. In their native range, invasive plants are held in check by negative soil-feedbacks. *Ecosphere* 2:article 54.

SUPPLEMENTAL MATERIAL

Appendix A

Citations for all literature included in the meta-analysis data set ([Ecological Archives E095-026-A1](#)).

Appendix B

Additional methods and descriptions of the data set, maps showing locations of studies in the data set, and additional results of statistical analysis, including distributions of effect size for each moderator and null distributions for Q_M statistics and multiple comparisons ([Ecological Archives E095-026-A2](#)).

Supplement

Data set used in the meta-analysis including effect size, variance, all moderator variables, and indication of authors and publication years for each datum ([Ecological Archives E095-026-S1](#)).