

# Predicting invasiveness and range size in wetland plants using biological traits: a multivariate experimental approach

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## Summary

1. Predicting invasion potential across a wide range of plant species using only their biological traits is often challenging. We present a novel approach, aligning species along a multivariate axis of putative invasiveness traits. The traits were quantified in a common garden in which we manipulated two critical variables thought to strongly influence invasiveness: herbivory and resource availability.

2. We used principal component analysis (PCA) to characterize 20 species based on seven key traits (percentage germination, specific leaf area, seed mass, above-ground biomass, below-ground biomass, response to fertilization and response to herbivory). We then assessed whether the linear combination of traits identified by axis 1 of the PCA could predict invasiveness.

3. Axis 1 of the trait-based PCA explained nearly 40% of variation in two literature-based invasiveness scores; thus, we considered it to be useful as a trait-based invasiveness index. Literature-based invasiveness was greatest in large species (both above-ground and below-ground) with high percentage germination, small positive responses to fertilization and small negative responses to herbivory.

4. Contrary to expectations from the enemy release hypothesis, species that were native to our region and highly invasive elsewhere were associated with only weak responses to insect herbivory. This suggests that invasion potential may be highest in species that are insensitive to herbivore pressure, rather than species benefitting the most from enemy release.

5. Native range size is often an effective predictor of invasiveness, although the underlying mechanisms are unclear; we therefore compared the predictive ability of range size versus biological traits. Our trait-based index was a better predictor of invasiveness than range size, while also explaining nearly 20% of the variation in longitudinal range size.

6. *Synthesis.* We present a novel method for using traits to quantify invasiveness that appears to have broad predictive utility. Our results explicitly link biological traits to range size and global invasiveness, perhaps reflecting a general ecological strategy in plants. Following additional testing, this simple method could be utilized in a pre-introduction screening protocol, and we provide practical recommendations for doing so.

**Key-words:** dispersal ability, enemy release hypothesis, insect herbivory, invasion ecology, invasiveness traits, native range size, Nitrogen fertilization, predicting invasibility, principal component analysis, weed assessment protocols

## Introduction

Predicting *a priori* the likelihood of an introduced plant species becoming invasive is a goal of many ecologists (Mack 1996; Williamson & Fitter 1996; Reichard & Hamilton 1997; Prinzing *et al.* 2002; Hayes & Barry 2008). Identifying intrinsic biological traits that correlate strongly with invasiveness

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could make prediction a reality, deepen our understanding of why certain species become invasive and save millions of dollars in control costs annually (Pimentel *et al.* 2000). However, few of the previous attempts to identify invasiveness traits can be applied successfully across a broad range of species (but see Rejmánek 1996).

Two distinct approaches are commonly used to identify traits that separate invasive from non-invasive plant species: collecting trait data from individuals grown in a common-garden environment and collecting trait data from large databases or floras. Both methods have strengths and weaknesses. For example, quantifying traits from plants in a common garden minimizes environmental-based trait variation and makes trait comparisons more tractable, but most such studies focus on only a few species ( $\leq 6$  in 90% of studies reviewed by van Kleunen, Weber & Fischer 2010). In contrast, collecting trait values from databases and floras often permits assessing a relatively large number of species (from tens to hundreds; for example, Rejmánek & Richardson 1996; Reichard & Hamilton 1997). Unfortunately, the trait data that are most relevant to invasiveness are often unavailable (Pyšek & Richardson 2007) or reported only using broad categories (e.g. mode of dispersal, presence of clonal growth), which may decrease predictive ability because critical within-species trait variation is overlooked. When quantitative trait data from these sources are reported (e.g. height, seed mass), all intraspecific variation from throughout a species' range is typically reduced to its midpoint (Goodwin, McAllister & Fahrig 1999), and this may poorly characterize species with broad environmental tolerances (Prinzing *et al.* 2002).

Regardless of the approach, the design of trait comparison experiments is often not ideal for making broad inferences about traits and invasiveness. First, although a recent meta-analysis of trait comparison studies (van Kleunen, Weber & Fischer 2010) found that invasives had higher trait values than natives and non-invasives in nearly every performance category tested (including physiological efficiency, fitness, size, growth rate and shoot allocation; >20 traits from 111 studies), determining which particular traits contribute the most to invasiveness in a broad sense is problematic, especially because comparison species may not be randomly selected (Vilà & Weiner 2004). Second, although most weed assessment protocols used by managers and quarantine officials score species along a continuum of invasive potential (Whitney & Gabler 2008), most trait comparison studies assess trait differences between dichotomous species groups (e.g. invasive versus non-invasive or native). Such groupings simplify comparisons, but they ignore the fact that invasive potential varies continuously among species (Richardson & Pyšek 2006). Finally, by considering multiple traits as if they were independent, most trait comparison studies ignore the complexities of among-trait correlations. Explicit consideration of these relationships may better distinguish species based on trait data and improve our ability to predict invasive potential (e.g. Küster *et al.* 2008).

We present a novel approach for predicting invasiveness from trait data in an attempt to address the limitations noted

above. We conducted a common-garden experiment, quantifying putative invasiveness traits for 20 herbaceous wetland species that vary widely in their invasive potential and accounting for among-trait correlations explicitly via a multivariate analytical framework. We emphasized traits that are related to rapid growth, large size, increased competitiveness, good dispersal ability and high reproductive capacity (Pyšek & Richardson 2007; van Kleunen, Weber & Fischer 2010), predicting that highly invasive species would be characterized by greater germination percentages, higher specific leaf areas (SLA), more above-ground and below-ground biomass and smaller seeds (thus increased dispersal ability) when compared to less invasive species. We aligned our species along a single principal component axis to quantify variation in multivariate invasiveness trait space, using an independent set of invasiveness scores (described below) to test the predictive value of our trait-based scores.

In addition to the benefits noted above, quantifying traits in a common garden also allowed us to experimentally manipulate two key variables that have been empirically linked to invasiveness: resource supply and escape from natural enemies (Suding, LeJeune & Seastedt 2004; Carpenter & Cappuccino 2005). Oddly, this has rarely been attempted for multispecies comparisons, despite the fact that trait differences between invasives and non-invasives may only become apparent when enemies and resource supply vary across a habitat. Indeed, Burns (2006) confirmed that trait differences between invasive and non-invasive Commelinaceae are only pronounced at high nutrient availability and Schierenbeck, Mack & Sharitz (1994) found that invasive *Lonicera japonica* only produces more above-ground biomass than native *Lonicera sempervirens* in the presence of herbivory. Thus, in addition to the traits listed above, we also predicted that our most invasive species would grow the most in response to fertilization and release from herbivory, with native species exhibiting greater release from herbivory than introduced species (*sensu* Carpenter & Cappuccino 2005).

Native range size is another character that often correlates strongly with invasiveness (Goodwin, McAllister & Fahrig 1999; Pyšek *et al.* 2009), although the underlying mechanisms remain unclear. Species adapted to regionally common habitats may encounter similar conditions beyond their native range (Gaston 2003), or they may simply have an increased likelihood of being transported to a new region (Goodwin, McAllister & Fahrig 1999). Clearly, neither mechanism represents an inherent biological trait, although large native ranges likely correspond to key traits or trait variations that promote widespread distributions. Because native range size is ultimately an emergent property, largely dependent on a species' biological traits (Gaston 2003), native range size itself has serious shortcomings as a predictor of invasiveness if the ultimate goal is understanding the mechanisms underlying invasion success. Here, we address the relationship between biological traits and range size, first assessing their relative importance as predictors of invasiveness and then exploring the mechanistic link between biological traits, native range size and invasiveness.

Below we build on previous attempts to predict invasiveness from traits in hopes of addressing the limitations described above. We quantified seven potential invasiveness traits and aligned 20 wetland species along a putative invasiveness traits index using principal component analysis (PCA). We then tested whether quantifying trait-based variation in this way could be a useful method for assessing invasion potential by evaluating whether trait-based scores predicted independently derived invasiveness scores using data from two compendia of weedy and invasive species (Holm *et al.* 1979; Randall 2002). Finally, we assessed the relative importance of biological traits and native range size as predictors of invasive potential.

## Materials and methods

### SPECIES SELECTION

Wetlands are particularly susceptible to invasions (Galatowitsch, Anderson & Ascher 1999; Zedler & Kercher 2004); thus, our initial test of this approach focused on wetland species only (see Table S1 in Supporting Information). We included species that occur primarily in wetlands [Facultative Wetland indicator species according to Reed (1988)]; species that occur in Pennsylvania, where our experiment was located (based on the USDA Plants Database; <http://plants.usda.gov>); and species for which seed was either commercially available (16 spp.) or could be collected locally (4 spp.). Most of our purchased seed came from restoration nurseries who provided wild-collected accessions and accessions that are likely to be found in natural populations. We used no horticultural cultivars, and many of our species were collected from multiple populations (see Table S1 for details). Our species vary widely in invasiveness, from ubiquitous invaders (e.g. *Echinochloa crus-galli*, *Phalaris arundinacea*, *Typha latifolia*) and species with more localized invasions (e.g. *Myosotis scorpioides*, *Mimulus ringens*) to species that are rarely problematic outside their native range (e.g. *Bromus ciliatus*, *Briza minor*). We used non-native and native species, and both groups exhibit a similar range of invasiveness (see, e.g. Randall 2002).

### DESIGN OF THE COMMON-GARDEN EXPERIMENT

We assessed plant traits across a range of growing conditions by crossing three levels of nitrogen fertilization (0, 8 and 16 g N m<sup>-2</sup>) with two levels of insect herbivory (present or absent). We randomly assigned treatments to six wading pools (1.5 m diameter) in each of three experimental blocks (18 pools total). Every pool contained all 20 species, each in its own 3.8-L nursery pot. Pots were partially submerged in water (8–12 cm), so the soil surface stayed wet without flooding the developing seedlings. Pots received 3.5 L of a 1 : 3 sand/topsoil mixture to facilitate harvesting root biomass.

On 18 June 2007, we fertilized pots with nitrogen (as an aqueous solution of urea) and 8 g m<sup>-2</sup> each of P<sub>2</sub>O<sub>5</sub> and K<sub>2</sub>O. On 20 June, we sowed each pot with *c.* 100 seeds of a single species except the two for which we had limited seeds (*Myosotis scorpioides* and *Mentha spicata*, 50 per pot). Seeds were not pre-treated before sowing. Following germination, one healthy seedling in the centre of each pot was retained; all remaining seedlings and subsequent germinants were removed. Insect herbivory was controlled by spraying every 7–10 days with a broad-spectrum insecticide (AsanaXL; DuPont, Wilmington, DE, USA) that kills insects without affecting

plant growth (Carson & Root 2000). All plants were grown at the Pymatuning Laboratory of Ecology in north-western Pennsylvania, USA.

### TRAIT QUANTIFICATION

We calculated percentage germination based on the number of seedlings harvested throughout the growing season. We harvested plants on 6 October, collecting the most recently developed fully expanded leaf for quantifying SLA (m<sup>2</sup> kg<sup>-1</sup>) and measuring leaf area using an LI-3000 (LI-COR Biosciences, Lincoln, NE, USA). We separated below-ground from above-ground biomass and weighed both after drying to a constant weight. We quantified seed mass, but where we could not reliably weigh seeds (*Calamagrostis canadensis*, *Juncus effusus*, *Scirpus cyperinus*, *Penthorum sedoides* and *M. ringens*), we used published values from our source seed catalogues; this corresponded well to our own measurements where the comparison could be made ( $r = 0.96$ ,  $P < 0.001$ ,  $n = 13$ ).

For each species, we calculated least squares mean values for biomass, SLA and percentage germination, using general linear mixed models in SAS v.8.01 (SAS Institute, Inc.; Cary, NC, USA) to account for variation across our experimental treatments. We considered species identity, fertilization and insect herbivory (plus all interactions) as fixed effects and block as a random effect. We derived two additional response traits using least squares mean total biomass (above-ground plus below-ground): fertilization response (biomass at high N divided by biomass at low N) and response to herbivory (biomass with herbivores divided by biomass without herbivores). Both ratios were natural log-transformed to approach normality (Hedges, Gurevitch & Curtis 1999) and facilitate interpretation. Prior to analysis, biomass and percentage germination values were transformed to approximate a normal distribution [ $\log_{10}(Y + 1)$  and arcsine ( $Y^{0.5}$ ), respectively]. Throughout the text, means  $\pm$  standard errors are reported unless stated otherwise.

### INVASIVENESS TRAIT INDEX DERIVATION AND ASSESSMENT

We performed PCA on the matrix of 20 species and seven traits with PC-ORD v. 4.01 (MJM Software Design, Gleneden Beach, OR, USA), using correlations in our association matrix. Raw data for the PCA were standardized least squares means, means or natural log-transformed response ratios. We evaluated whether axis 1 of the trait-based PCA could serve as an 'invasiveness traits index' by regressing it against two literature-based assessments of invasiveness, based on two compendia of weedy and invasive species (Holm *et al.* 1979; Randall 2002). Because the sign of a PCA axis is arbitrary, and to facilitate interpretation of axis 1 as an invasiveness traits index, we have reversed the sign of axis 1 values throughout, giving more invasive species higher index values (see Appendix S1 for original numerical output of the PCA). To clearly distinguish literature-based assessments from our independently derived invasiveness traits index, we refer to the former as 'realized invasiveness' from this point on.

In *A Geographical Atlas of World Weeds* (GAWW; Holm *et al.* 1979), 6400 species are categorized based on their impact on crop production for every country in which they have been identified as a weed. We calculated realized invasiveness scores for our 20 species by assigning each of the categories in GAWW a numerical value (serious weed = 4; principal weed = 3; common weed = 2; weed of unknown importance = 1) and summing across all countries in which a species was listed. Alternative weighting schemes did not affect our

results. We used linear regression to predict GAWW-based realized invasiveness from our invasiveness traits index.

A *Global Compendium of Weeds* (GCW; Randall 2002) is the most comprehensive reference of invasive plant species available, including 18 146 taxa that are problematic in native vegetation or agricultural settings. Each species' account in GCW includes a list of references that identify a species as invasive or weedy. Such lists are informative because prior invasiveness is often a good predictor of future invasiveness in a new region (Reichard & Hamilton 1997; Kolar & Lodge 2001). We used linear regression to predict the number of references in GCW from our invasiveness traits index. For both GAWW and GCW, realized invasiveness scores were natural log-transformed after adding one to improve normality; species excluded from either volume were given scores of zero (i.e. not invasive) and included in the analysis.

Although these metrics of realized invasiveness are useful, they also have weaknesses; thus, we conducted *post hoc* analyses to examine the effect of two potentially important sources of bias in our data. First, because most references included in GCW come from relatively few countries (among our species, 40% on average are from the US or Australia), we recalculated GCW-based scores, allowing only one reference per country. Second, both GCW- and GAWW-based scores are based in part on the number of invaded countries, even though political boundaries need not coincide with physical barriers to invasive species spread. We therefore recalculated scores from both compendia by aggregating nearby countries to assess patterns at regional and sub-continental scales. In every case, results based on these alternative literature-based scores were consistent with our original analyses (see Appendix S2 for details).

To account for phylogenetic non-independence, we also used phylogenetically independent contrasts (PIC; Garland, Harvey & Ives 1992) to assess relationships between biological traits and realized invasiveness. We conducted PIC using the AOT module in Phylocom 4.1 (Webb, Ackerly & Kembel 2008), setting branch lengths equal to 1 and using literature to resolve our phylogeny (Barker *et al.* 2001; Bremer *et al.* 2009; Schneider *et al.* 2009). Finally, we conducted two additional sets of analyses after using our invasiveness traits index (PCA axis 1) as the sole predictor of invasiveness: (i) we assessed whether axes 2–6 of the PCA explained significant variation in realized invasiveness scores using multiple linear regression, and (ii) we used individual traits as predictors using univariate and multiple linear regressions to assess whether our multivariate approach had simply identified one or two key traits that are critical for invasive species success.

We used a leave-one-out jackknife procedure to validate our method, repeating analyses 20 times using all possible 19-species data sets to extract two sets of metrics. First, we conducted trait-based PCA and regressed GCW- and GAWW-based realized invasiveness against axis 1 scores (as above) for each jackknife data set to assess variability in  $r^2$  among data sets. Second, for each jackknife data set, we used the linear combination of trait scores from the 19-species PCA along with the omitted species' standardized trait means to manually calculate where the omitted species would fall along axis 1 of the PCA (its estimated invasiveness traits index score). We calculated prediction intervals for linear regression at the omitted species' estimated invasiveness traits index score for GCW- and GAWW-based realized invasiveness using regression solutions from the corresponding jackknife data set. For each species, we then assessed whether its observed realized invasiveness scores fell within prediction intervals calculated from the jackknife replicate in which it was omitted. As a benchmark, we also assessed whether observed realized invasiveness

scores fell within the prediction intervals from our full 20-species regressions.

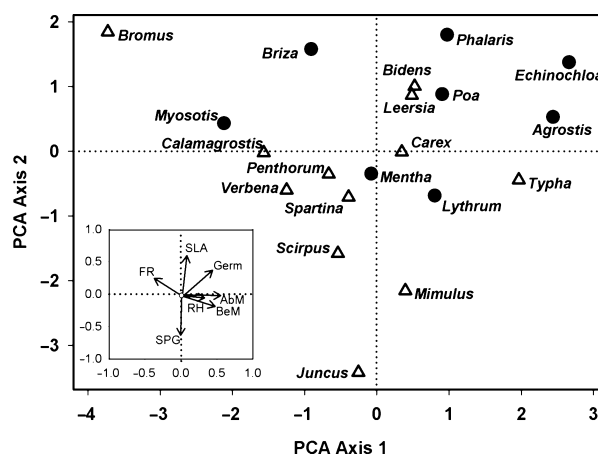
## ASSESSING RELATIONSHIPS AMONG TRAITS, RANGE SIZE AND INVASIVENESS

Lastly, we used linear regressions to explore relationships among biological traits, native range size and realized invasiveness. We estimated native range sizes using three databases: USDA Plants (<http://plants.usda.gov>), USDA-ARS GRIN Taxonomy ([www.ars-grin.gov/cgi-bin/npgs/html/queries.pl](http://www.ars-grin.gov/cgi-bin/npgs/html/queries.pl)) and Flora Europaea (<http://rbg-web2.rbge.org.uk/FE/fe.html>). We estimated the longitudinal and latitudinal extent of a species' native range based on the countries, provinces or states in which it was reported as native. We assumed that occupancy at the edge of a range extended to the centre of that country, province or state, and we subtracted 50° from the longitudinal range of five species whose native distribution spans the Atlantic Ocean (Table S1).

## Results

### TRAIT-BASED INVASIVENESS SCORES

Based on our putative invasiveness traits index (PCA axis 1), species that were bigger (both above- and below-ground), had higher germination percentages and responded the least to insect herbivores had scores  $>0$  (Fig. 1). Species that

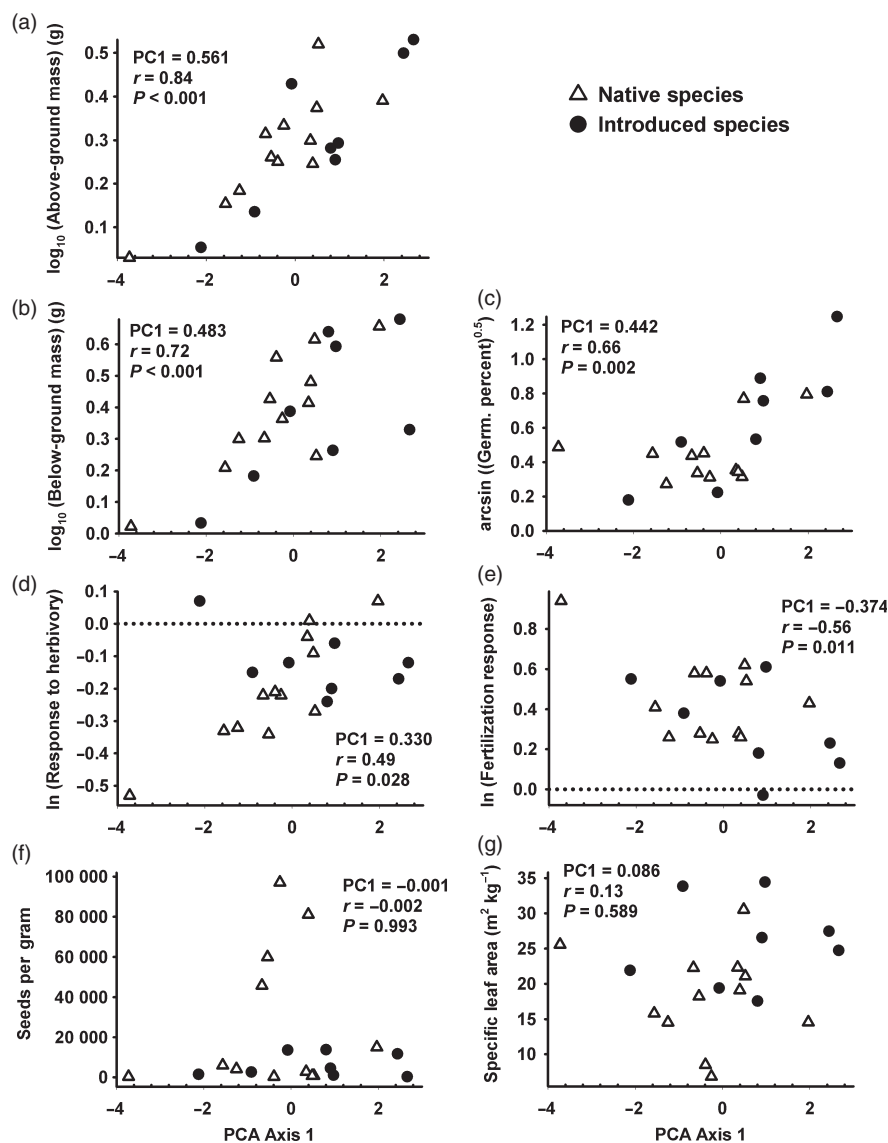


**Fig. 1.** Principal component analysis (PCA) of 20 herbaceous wetland species and seven traits that are associated with invasiveness. PCA axis 1 corresponds to our invasiveness traits index, with invasiveness increasing left to right. Species are identified by genus, with native species (open triangles) and introduced species (closed circles) interspersed along axis 1 (see Table S1 for full names of all species). Axis 1 explained 31.6% of the total variance extracted from our data set and axis 2 explained 24.8%. The inset graph shows the location of individual traits in multivariate space (AbM, above-ground biomass; BeM, below-ground biomass; Germ, germination fraction; FR, fertilization response; RH, response to herbivory; SLA, specific leaf area; SPG, seeds per gram). In the inset graph, note that an increase in response to herbivory (RH) represents a shift from large negative trait values to values approaching zero as PCA axis 1 scores increase (see Fig. 2d). The scale in the inset graph is equal to that in the main graph, although the range is reduced.

benefitted the most from nitrogen amendments and for which insect herbivores decreased their biomass the greatest had scores  $< 0$  (Figs 1 and 2). Axis 1 accounted for 31.6% of explained trait variation.

Native and introduced species formed a relatively homogeneous group according to the traits we measured. Six of seven trait values did not differ between these species groups (Table S2), and neither did their invasiveness traits index scores (introduced:  $0.59 \pm 0.57$ , native:  $-0.39 \pm 0.41$ ;  $t_{18} = -1.44$ ,  $P = 0.17$ ). Only SLA was significantly greater in introduced versus native species, although this difference was non-significant based on sequential Bonferroni corrections for multiple comparisons (see Table S2). Despite

having similar mean values for their response to herbivory, native and introduced species did differ in their relationship between response to herbivory and the invasiveness traits index. Although response to herbivory correlated well with PCA axis 1 for natives, this relationship did not hold for introduced species [Fig. 2d; correlations between the invasiveness traits index and response to herbivory: native species  $r = 0.88$ ,  $P \leq 0.001$ , 95% CI (0.63, 0.97); introduced species  $r = -0.56$ ,  $P = 0.15$ , 95% CI (-0.91, 0.23)]. All other correlations between the invasiveness traits index and individual traits were similar for native and introduced species (based on overlapping 95% CI; data not shown, but see Fig. 2).

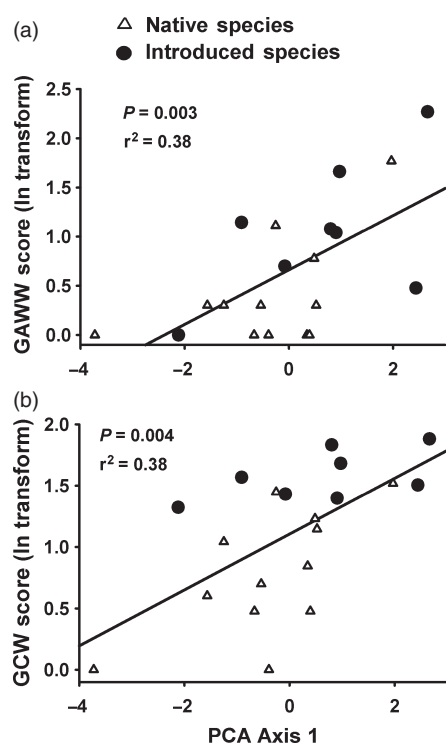


**Fig. 2.** Scatterplots of the invasiveness traits index [principal component analysis (PCA) Axis 1] versus individual traits that comprise it. The axis 1 coefficients (PC1) are given for each trait. Note that correlations were conducted on data as shown and PCA was conducted using centred and standardized trait values. Native species (open triangles) and introduced species (closed circles) had similar mean values for all traits except specific leaf area, which was higher for introduced species (see text). Dotted lines in (d) and (e) denote values of zero, which corresponds to no treatment effects for a given response (e.g. no response to enemy release in panel d). Negative responses to herbivory (in d) indicate that insect herbivores decreased standing crop biomass. Positive fertilization responses (in e) indicate increased biomass following nitrogen additions of  $16 \text{ g m}^{-2}$  (relative to no added N).

## RELATING TRAITS TO LITERATURE-BASED REALIZED INVASIVENESS

Our invasiveness traits index explained nearly 40% of the variation in realized invasiveness based on GAWW and GCW, and species with the highest invasiveness traits index values included our most notorious invaders (Fig. 3). Phylogenetically independent contrasts confirmed these findings, explaining up to 51% of the variation in realized invasiveness (Fig. S1). No other PCA axis explained significant variation in realized invasiveness, and all individual traits were poor or inconsistent predictors of realized invasiveness compared to our invasiveness traits index (Appendix S3).

Model validation based on our leave-one-out jackknife procedure indicated substantial consistency in our results. The amount of explained variation in realized invasiveness varied little among replicates (mean  $r^2$  for GCW =  $0.37 \pm 0.033$ ; mean  $r^2$  for GAWW =  $0.37 \pm 0.026$ ), dropping significantly ( $> 2$  SE) only when *Echinochloa crus-galli* was omitted (GAWW  $r^2 = 0.25$ ; GCW  $r^2 = 0.26$ ). Axis 1 of each 19-species PCA consistently accounted for *c.* 30% of explained trait variation (mean =  $31.9\% \pm 0.25$ , range = 29.1–33.7%). Based on the omitted species' estimated invasiveness index scores, observed GCW-based realized invasiveness scores fell within prediction intervals in 19 of 20 cases; this is identical to findings from the full data set. Observed GAWW-based realized invasiveness scores also fell within their prediction intervals in 19 of 20 cases; for the full data set, all 20 scores did so.



**Fig. 3.** Relationships between the invasiveness traits index [principal component analysis (PCA) Axis 1] and literature-based invasiveness from (a) Holm *et al.*'s (1979) *A Geographical Atlas of World Weeds* and (b) Randall's (2002) *A Global Compendium of Weeds*.

## BIOLOGICAL TRAITS, RANGE SIZE AND INVASIVENESS

Our invasiveness traits index explained nearly 20% of the variation in longitudinal range extent ( $r^2 = 0.19$ ,  $F_{1,19} = 4.29$ ,  $P = 0.05$ ) but was unrelated to latitudinal range extent ( $r^2 = 0.07$ ,  $F_{1,19} = 1.38$ ,  $P = 0.26$ ). Furthermore, compared to our trait-based index, latitudinal range extent and longitudinal range extent were poor predictors of realized invasiveness (Table 1). Adding the invasiveness traits index to models including both range size metrics increased the explained variation in realized invasiveness by 45% (adjusted  $R^2$  values rose by  $\geq 50\%$ ); based on Akaike weights, these models were roughly three times more likely than models with range size as the only predictors. In the full models, longitudinal extent was a marginally significant predictor of GCW-based invasiveness, and neither range size metric explained GAWW-based invasiveness.

## Discussion

We demonstrate for the first time the predictive value of aligning species along a multivariate axis of putative invasiveness traits. The linear combination of a few key traits, quantified from plants grown in a simple and inexpensive common garden, explained substantial variation in realized invasiveness for a phylogenetically diverse group of species. To our knowledge, this is also the first study to experimentally quantify response to herbivory by multiple invasive plant species in their native range. The relationship between response to herbivory and our invasiveness traits index indicated weak negative responses by our most invasive species and strong negative responses by less invasive ones. This pattern was most pronounced in species native to our region, suggesting that the species most likely to become invasive are the least sensitive to herbivory in their native range, rather than those experiencing the greatest pressure from herbivores there. This does not support the enemy release hypothesis but is consistent with recent reviews questioning the extent to which enemy release contributes to invasion success (Colautti *et al.* 2004; Chun, van Kleunen & Dawson 2010). Finally, our trait-based index predicted invasiveness better than native range size did. Although native range size is often used successfully to predict invasiveness in plants (Goodwin, McAllister & Fahrig 1999; Pyšek *et al.* 2009), the underlying mechanisms are unclear. In contrast, our results appear to link key biological traits to native range size and, subsequently, to global invasiveness.

## INTERPRETATION AND IMPLICATIONS OF AN INVASIVENESS TRAITS INDEX

Our method uses PCA simply to quantify the major axis of variation in multiple invasiveness traits. That such a metric explains substantial variation in two independent assessments of global invasiveness is novel, and we hypothesize that it may predict invasive potential in a more general sense. As an alternative statistical approach, we could have used

**Table 1.** Multiple regression results and model fit statistics ( $R^2$  and adjusted  $R^2$ ) for models predicting realized invasiveness from latitudinal and longitudinal range extent, both including and excluding our invasiveness traits index (PCA Axis 1)

	Full model		Model parameters		
			PCA Axis 1	Latitude	Longitude
<b>GCW</b>					
$F_{3,16}$	5.62	$t$	2.28	-1.27	2.10
$P$	<b>0.008</b>	$P$	<b>0.036</b>	0.224	0.052
$R^2$	0.51	$\beta$ (SE)	0.17 (0.07)	-0.10 (0.008)	0.005 (0.002)
Adj. $R^2$	0.42	Std $\beta$	0.445	-0.326	0.581
$AIC_C$	-23.84				
$w_i$	0.733				
$F_{2,17}$	4.67	$t$	-	-1.32	2.84
$P$	<b>0.024</b>	$P$	-	0.204	<b>0.011</b>
$R^2$	0.35	$\beta$ (SE)	-	-0.12 (0.009)	0.007 (0.002)
Adj. $R^2$	0.28	Std $\beta$	-	-0.379	0.815
$AIC_C$	-21.82				
$w_i$	0.267				
<b>GAWW</b>					
$F_{3,16}$	5.74	$t$	2.32	0.19	1.32
$P$	<b>0.007</b>	$P$	<b>0.034</b>	0.849	0.205
$R^2$	0.52	$\beta$ (SE)	0.200 (0.086)	0.002 (.010)	0.004 (0.003)
Adj. $R^2$	0.43	Std $\beta$	0.450	0.050	0.364
$AIC_C$	-16.81				
$w_i$	0.748				
$F_{2,17}$	4.71	$t$	-	-0.013	2.10
$P$	<b>0.024</b>	$P$	-	0.990	0.051
$R^2$	0.36	$\beta$ (SE)	-	0.000 (.011)	0.006 (0.003)
Adj. $R^2$	0.28	Std $\beta$	-	-0.004	0.600
$AIC_C$	-14.64				
$w_i$	0.252				

PCA, principal component analysis. Realized invasiveness scores are based on *A Global Compendium of Weeds* (GCW; Randall 2002) or *A Geographical Atlas of World Weeds* (GAWW; Holm *et al.* 1979). Unstandardized and standardized slopes ( $\beta$ ) are both shown, as are small-sample bias-corrected Akaike Information Criteria ( $AIC_C$ ) and Akaike weights ( $w_i$ ). Significant results ( $P < 0.05$ ) are in bold.

constrained ordination (e.g. redundancy analysis or discriminant function analysis) to describe the major axes of trait-based variation while simultaneously minimizing the variance in realized invasiveness scores. Constrained ordinations have been used to predict invasiveness in the past (e.g. Rejmánek & Richardson 1996; Reichard & Hamilton 1997), but because constrained ordinations are designed to explain variation in one or more response variables, inferences regarding predictor variables are specific to those responses. Although our method does require further testing, we think it has promise as a general invasiveness predictor, largely because it is derived independently of external invasiveness data.

The generality we would expect from a broadly informative trait-based invasiveness index is supported by Schlaepfer *et al.* (2010), who conducted a multi-species trait-based PCA using many of the same traits we recorded. As in our analysis, axis 1 of their PCA accounted for just over 30% of the explained trait variation and was closely related to above-ground biomass, below-ground biomass and percentage germination. Together, these results suggest that invasiveness represents a general ecological strategy that can be assessed quantitatively and along which multiple species may be aligned (i.e. Pianka 1970; Grime 1977; Westoby 1998). Inva-

siveness has often been described as a continuous character (Baker 1974; Richardson & Pyšek 2006; Schlaepfer *et al.* 2010), yet most assessments consider invasiveness in dichotomous terms only. By explicitly recognizing this among-species variation, and by viewing invasiveness as a general ecological strategy, we hypothesize that predicting future invaders will become easier and that our fundamental understanding of invasion biology will be strengthened.

#### SPECIFIC TRAITS ASSOCIATED WITH INVASIVENESS

Our invasiveness traits index describes the major axis of variation in the putative invasiveness traits we quantified. The component scores for these traits in relation to our index provide information about how they co-vary within our set of species; thus, they cannot be used simply to infer the relative importance of individual traits for invasive potential. Nevertheless, assessing which traits were and were not closely tied to our index (based on eigenvector loadings on PCA axis 1 or, equivalently, on correlations between individual traits and the invasiveness traits index) may provide a better understanding of why it was such a successful predictor of realized invasiveness, while also illuminating future research directions in this area.

Our invasiveness traits index was most closely tied to absolute plant size (see also Schlaepfer *et al.* 2010). Plant size is a common component of both invasiveness and competitive ability (Gaudet & Keddy 1988; Williamson & Fitter 1996; van Kleunen, Weber & Fischer 2010), because whether they are native or introduced, large plants can often suppress their neighbours by overtopping them and pre-empting both above-ground and below-ground resources (Carson & Pickett 1990; Stevens *et al.* 2004). In contrast, metrics of relative biomass accumulation were less important components of our index. Although fertilization response was related to our index, it was in the opposite direction of what we had expected, with small species experiencing greater relative increases in biomass than large species. Specific leaf area, which is correlated with relative growth rates, was not related to our index. With respect to invasiveness, these patterns suggest that the ability to increase dramatically in size may be less important than simply being large. In other words, small-statured plants that double or triple in size with added nitrogen may realize no net benefits if they remain smaller than inherently larger species. This pattern is found in natural systems, where inherently large species are more likely than small ones to increase in abundance following nutrient additions (Carson & Pickett 1990; Stevens *et al.* 2004; Pennings *et al.* 2005; Liancourt, Viard-Cretat & Michalet 2009).

The enemy release hypothesis predicts that enemies reduce the fitness of native species more than introduced ones (Keane & Crawley 2002), which is inconsistent with the similar mean response to herbivory we observed for the two groups in our study. However, because our experiment utilized herbivores occurring naturally at our study site, we cannot separate the effects of specialist and generalist herbivores, and we cannot exclude the possibility that herbivores specializing on our introduced species were present. More importantly, the enemy release hypothesis also predicts that species experiencing the greatest release from their enemies will be the most invasive (Keane & Crawley 2002). A key assumption underlying this prediction is that herbivores regulate populations of invasive species in their native range, yet particularly for the native species in our study the largest, most invasive ones had the weakest response to herbivory (i.e. their enemy release potential was the lowest). This pattern is in accordance with recent reviews suggesting that enemy release may not be a critical determinant of invasiveness (Colautti *et al.* 2004; Chun, van Kleunen & Dawson 2010). Instead, our findings indicate an association between invasiveness and relative insensitivity to herbivores, because species introduced to our region (all of which have successfully established populations here) and species native to our region that are invasive elsewhere all had fairly minimal responses to herbivory. We note that our findings may in part reflect a distinction between quantitative and qualitative assessments of invasiveness. Because species vary widely in invasiveness, categorizing them as either invasive or non-invasive (e.g. Colautti *et al.* 2004; Liu & Stiling 2006; Chun, van Kleunen & Dawson 2010) could obscure important variation in enemy susceptibility and how it varies with resource supply (Cronin, Tonsor & Carson 2010). Nonetheless, our results may help explain why there seems to be little evidence for the

enemy release hypothesis. Further experiments that quantify enemy release while also accounting for variation in invasiveness are needed to truly test the generality of these findings.

Percentage germination was a significant component of our invasiveness traits index, which is consistent with previous studies demonstrating the importance of traits promoting establishment from seed (Pyšek & Richardson 2007; van Kleunen, Weber & Fischer 2010). In addition, percentage germination is our only example of an individual trait that was significantly related to realized invasiveness, predicting scores from GAWW, our compendium that is most biased towards agricultural weeds (see Appendix S3). This suggests that percentage germination itself is a key predictive trait in disturbed or agricultural habitats. In more natural settings, where dense vegetation could limit invader establishment regardless of germination success, this trait may be less indicative of invasive potential.

#### NATIVE RANGE SIZE, TRAITS AND INVASIVENESS

Our invasiveness traits index was a better predictor of realized invasiveness than native range size, while also explaining nearly 20% of the variation in longitudinal range extent. Most other studies that have emphasized the importance of range size in predicting a species' invasive potential ignore the biological traits underlying both characteristics. Yet a species' range size is at least partially a consequence of its traits and how those traits impact performance in the local environment (Gaston 2003; Pyšek & Richardson 2007). We suggest that our data represent an explicit link between traits, range size and invasiveness, whereby significant variation in both native range size and invasiveness can be explained by a few key traits. Recently, Pyšek *et al.* (2009) also found that global invasiveness in plants native to Central Europe is explained both by biological traits and by distribution characteristics within the Czech Republic. In their regression tree analyses, traits were significant predictors of invasiveness, both directly and indirectly (with indirect effects mediated by the direct effect of traits on native distributions). Thus, distinguishing between native range size and biological traits as predictors of invasiveness and evaluating the inherent relationship between these two sets of characters may both be needed to accurately assess the mechanisms underlying invasiveness. We contend that future invasiveness assessments using native range size as a predictor should also explicitly consider biological traits and the inherent dependence of range size on those traits.

Our invasiveness traits index explained variation in longitudinal but not latitudinal range extent, suggesting there may be a useful distinction between these two metrics of native range size with respect to invasiveness traits. Much emphasis is often placed on latitudinal range, which generally reflects a species' climatic limits, but longitudinal extent may be a useful representation of a species' ability to disperse and establish populations across the landscape within those limits. Indeed, Quinn, Gaston & Arnold (1996) reported that longitudinal extent was a better metric than latitudinal extent for identifying rare butterflies and mollusks in Britain. Although nobody to our knowledge has separately assessed the relation-



ships between native longitudinal and latitudinal extent versus invasive potential or invasiveness traits, doing so may broaden our understanding of range size as it relates to biological invasions.

#### BUILDING ON OUR APPROACH

We did not record two biological traits that are commonly strong predictors of invasiveness in plants, plant height and the degree to which species spread clonally (Pyšek & Richardson 2007). We predict that adding these traits would have increased the explained variation in realized invasiveness from 40% to higher amounts, and we recommend they be included in future studies. Although most of the species in our short-term experiment are perennial and thus did not flower, including an estimate of reproductive output could also have improved our predictive ability. However, this may be one example of a trait that is better assessed using literature-based estimates to minimize the likelihood of introduced species escaping from the common garden itself.

Our ability to predict realized invasiveness from trait data may have been enhanced by all of our species sharing a common habitat (Thompson, Hodgson & Rich 1995; Williamson 2001; Thuiller *et al.* 2006; van Kleunen, Weber & Fischer 2010). Despite the fact that our study included a phylogenetically diverse group of species, the traits conferring invasive potential in waterlogged and often eutrophic habitats may differ substantially from traits predicting invasiveness in forest understories or xeric grasslands. Indeed, when Richardson, Cowling & Le Maitre (1990) used trait data to predict the invasion potential of *Pinus* species in the fynbos region of South Africa, they credited the habitat-specific approach in part for their high degree of success. Our approach is also habitat specific, but in contrast we were able to predict invasiveness across a phylogenetically broad group of species. Additional study will be needed to determine the predictive limits of our approach across habitats.

Extending the generality of our approach will also require quantifying traits across multiple locations and years to assess sensitivity to within-species trait variation. We expect relatively minor temporal effects because growing conditions in a common garden should be similar across years. Regional variation in trait values is likely to play a larger role; however, because PCA is robust to variation in data precision (Legendre & Legendre 1998), this may not be a serious limitation, particularly if interspecific trait variation significantly outweighs intraspecific variation.

One of our eventual goals in developing this methodology is successfully applying it to new species, using trait-based invasiveness index scores to assess invasion potential prior to introduction. Calculating new index scores from our current PCA is straightforward. Once the appropriate trait data have been collected from a new species, its mean trait values would be standardized relative to our original data set of species-specific trait means (provided in Appendix S1). The new species' invasiveness traits index score would then be calculated by multiplying each standardized trait mean by its

axis 1 coefficient (PC1 in Fig. 2) and summing across all seven traits. Assessing whether such trait-based index scores can successfully predict invasion potential in new sets of species will provide a critical test of this method's utility.

#### Conclusion

We present a novel method for aligning species based on their variation in multiple putative invasiveness traits. This index explains substantial variation in independent assessments of realized invasiveness, and we suggest it may have even broader predictive power. We stress the importance of quantifying traits in an experimental setting that permits an assessment of how these traits respond to key biotic and abiotic conditions (e.g. herbivore pressure and nutrient availability), building on previous similar work (Schierenbeck, Mack & Sharitz 1994; Burns 2006; Schlaepfer *et al.* 2010). We anticipate that this method could be improved and subsequently utilized as part of a large-scale pre-introduction screening program.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** Phylogenetically independent contrasts for the relationships between our invasiveness traits index (PCA Axis 1) and literature-based invasiveness.

**Table S1.** Species used to calculate the trait-based invasiveness index.

**Table S2.** Trait means (and standard errors) for native versus introduced species from the common-garden experiment.

**Appendix S1.** Trait means and numerical output from principal component analysis.

**Appendix S2.** Assessments of bias in realized invasiveness scores.

**Appendix S3.** Alternative methods for predicting realized invasiveness from trait data.

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