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**Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment
of richness?**

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92 **Classification.** Biological Sciences

94 *“it is not only winds, currents, and birds that aid the migration of plants; man primarily takes
care of this” (von Humboldt, 1805).*

Abstract

96 Invasions have increased the size of regional species pools, but are typically assumed to reduce
native diversity. However, global-scale tests of this assumption have been elusive because of the
98 focus on exotic species richness, rather than relative abundance. This is problematic because low
invader richness can indicate invasion resistance by the native community or, alternatively,
100 dominance by a single exotic species. Here, we used a globally-replicated study to quantify
relationships between exotic richness and abundance in grass-dominated ecosystems in 13
102 countries on six continents, ranging from salt marshes to alpine tundra. We tested effects of
human land use, native community diversity, herbivore pressure, and nutrient limitation on
104 exotic plant dominance. Despite its widespread use, exotic richness was a poor proxy for exotic
dominance at low exotic richness, because sites that contained few exotic species ranged from
106 relatively pristine (low exotic richness and cover) to almost completely exotic-dominated (low
exotic richness but high exotic cover). Both exotic cover and richness were predicted by native
108 plant diversity (native grass richness) and land use (distance to cultivation). Although climate
was important for predicting both exotic cover and richness, climatic factors predicting cover
110 (precipitation variability) differed from those predicting richness (maximum temperature and
temperature in the wettest quarter). Herbivory and nutrient limitation did not predict exotic
112 richness or cover. Exotic dominance varied most among regions (subcontinents), whereas cover
was greatest in areas with low native grass richness at the site- or regional-scale. Although this
114 could reflect native grass displacement, a lack of biotic resistance is a more likely explanation,
given that grasses comprise the most aggressive invaders. These findings underscore the need to

116 move beyond richness as a surrogate for the extent of invasion, because this metric confounds
mono-dominance with invasion resistance. Monitoring species' relative abundance will more
118 rapidly advance our understanding of invasions.

Human commerce and migration have breached biogeographic barriers, initiating an
unprecedented period of global species migration and homogenization that has intrigued
biologists for over 200 years (Candolle & Sprengel, 1821, Darwin, 1859, Elton, 1958, Levine &
D'Antonio, 2003, Mack, 2003, Mooney & Cleland, 2001, Qian & Ricklefs, 2006, von
Humboldt, 1805). Introduced species currently comprise 20% of some continental floras and 60-
80% of some island floras (Vitousek *et al.*, 1997). Invasions can alter basic ecosystem processes,
such as water and nutrient cycling, fire frequency, and sediment transport (Levine *et al.*, 2003,
Lodge, 1993, Mills *et al.*, 1994, Seabloom & Wiedemann, 1994, Vitousek *et al.*, 1997, Vitousek,
1990), and the associated losses in ecosystem goods and services have been valued at almost 120
billion dollars per year in the USA alone (Pimentel *et al.*, 2005). While exotic species dominate
some ecosystems, other ecosystems remain dominated by native species (Candolle & Sprengel,
1821, Darwin, 1859, Elton, 1958, Mack, 1989, von Humboldt, 1805), raising a broadly relevant
ecological question: why do exotic plants dominate some locations while other locations remain
largely pristine? Centuries after it was posed, this question remains unresolved largely due to a
lack of comprehensive, standardized data collected globally across a diversity of community
types.

The distribution of invasions may reflect the historical contingencies of evolution, or it may arise
deterministically. For example, species that evolved on large and species-rich continents may be
inherently competitively superior (Darwin, 1859, Sax & Brown, 2000, van Kleunen *et al.*,
2011), and recent work has shown that a single suite of European species dominates many
invaded grasslands worldwide (Firn *et al.*, 2011). Conversely, some ecosystems may be
particularly vulnerable to invasion, such as those with low diversity or high levels of disturbance,

grazing, introduction of exotic species, or human activity (Crawley, 1987, Davis *et al.*, 2000,
144 Melbourne *et al.*, 2007, Rejmanek, 2003, Sax & Brown, 2000, Seabloom *et al.*, 2006, Shea &
Chesson, 2002).

146 Selection during the invasion process also may create strong biases in exotic species' traits that
give the exotics a preferential advantage in certain environments (Gonzalez *et al.*, 2010,
148 Seabloom *et al.*, 2006, van Kleunen *et al.*, 2011). For example, species that are well adapted to
human-dominated landscapes are more likely to be introduced by human colonists either
150 intentionally (e.g., domestic plants and animals) or unintentionally (e.g., weeds, pests, and
pathogens) (Candolle & Sprengel, 1821, Mack, 1989, Mack, 2003, Sax & Brown, 2000, von
152 Humboldt, 1805) and thus may become invasive when introduced into human-dominated
landscapes with high nutrient supply rates, grazing, or disturbance (Antonelli *et al.*, 2011, Davis
154 *et al.*, 2000, Gonzalez *et al.*, 2010, Mack, 1989, Parker *et al.*, 2006, Seabloom *et al.*, 2009). To
the degree that invasions arise as a result of human alteration of an ecosystem, the success of
156 species invasions may be more driven by a species ability to exploit human dominated
landscapes as opposed to the direct effect of a species' provenance.

158 Syntheses and meta-analyses have found that exotic richness is often higher in fertile areas where
human population, economic activity, habitat conversion, and species introduction rates are the
160 highest (Balmford *et al.*, 2001, Fridley *et al.*, 2007, Rejmanek, 2003, Sax *et al.*, 2002, Scott *et*
al., 2001, Seabloom *et al.*, 2006, Taylor & Irwin, 2004, Williams *et al.*, 2005). However, we
162 currently have little understanding of the patterns of exotic dominance, even though it is likely to
be functionally more significant than richness (Levine *et al.*, 2003, Lodge, 1993, Mills *et al.*,
164 1994, Parker *et al.*, 1999, Seabloom & Wiedemann, 1994, Vitousek *et al.*, 1997), because
dominant species have the highest impact on essential ecosystem functions such as primary

166 productivity (Grime, 1998, Hurlbert, 1997). This focus on exotic richness is driven mostly by
data availability rather than conservation priorities that often recognize the importance of exotic
168 abundance (Catford *et al.*, 2012).

Many exotic species are relatively benign and their establishment may result in a net increase in
170 diversity with negligible impacts on the native community (Davis, 2003, Firn *et al.*, 2011, Sax *et al.*,
et al., 2002). In contrast, notorious invaders (e.g., spotted knapweed, purple loosestrife, and kudzu)
172 may occur in nearly monospecific stands, and the highest dominance of exotics can occur at sites
with low exotic diversity due to the presence of one or two highly aggressive species (Catford *et al.*
174 *et al.*, 2012). Thus, although it is often used as a proxy (e.g., Seabloom *et al.*, 2006, Vitousek *et al.*,
1997), we hypothesize that exotic richness is a highly inconsistent predictor of exotic dominance.
176 Furthermore, we expect a nonlinear relationship, as exotic richness is bounded at 0 species, and
relative exotic cover (exotic cover divided by total cover) is bounded between 0 and 100%.

178 We focus on herbaceous-dominated ecosystems (e.g., grasslands, steppes, old fields, and
pastures), because they are globally distributed and play a key role in the biosphere. Grasslands
180 account for about 35% of the Earth's ice-free land mass and net primary production (Chapin *et al.*,
et al., 2002, Conant, 2010). With widespread conversion for multiple anthropogenic uses, including
182 70% of global agriculture, grasslands rank among the most critically endangered biomes
(Henwood, 2010, Hoekstra *et al.*, 2005, Ramankutty *et al.*, 2008). Grasslands provide an
184 opportunity to examine fundamental processes that underlie global patterns of invasion. Within
the span of the last two centuries, exotic species have overtaken vast expanses of grasslands in
186 Australia, South America, and parts of North America (Firn *et al.*, 2011, Mack, 1989, Mack &
Thompson, 1982). In contrast, other areas have apparently remained resistant to invasion (e.g.,
188 southern Africa and the central North American Great Plains) (Mack & Thompson, 1982).

We start by examining the relationship between exotic species establishment (exotic richness) and dominance (exotic cover) and test whether exotic richness, a measure widely used in global analyses of exotic invasion (Catford *et al.*, 2012, Fridley *et al.*, 2004), is a reasonable surrogate for exotic dominance. We then quantify variability in exotic cover that is associated with biogeographic regions (i.e., subcontinents) and ecosystem types (e.g., annual grasslands, mesic grasslands, or alpine tundra). We then test whether this variability is associated with the following factors that have been hypothesized or demonstrated to mediate the establishment or dominance of exotic species: **1. human land use** (e.g., agricultural history and proximity to roads, towns, and rivers)(Gelbard & Harrison, 2003, Rejmanek, 2003, Seabloom *et al.*, 2006), **2. environmental gradients** (e.g., precipitation, elevation, and aboveground biomass) (Balmford *et al.*, 2001, Seabloom *et al.*, 2006, Williams *et al.*, 2005), **3. diversity or composition of the native flora** (e.g., total diversity and diversity of key species groups) (Fargione *et al.*, 2003, Fridley *et al.*, 2007, Stohlgren *et al.*, 2003), **4. herbivore pressure** (change in biomass in response to excluding vertebrate herbivores)(Mack, 1989, Parker *et al.*, 2006, Seabloom *et al.*, 2005, Seabloom *et al.*, 2009), and **4. nutrient limitation** (change in biomass in response to fertilization) (Davis *et al.*, 2000, Huenneke *et al.*, 1990, Seabloom, 2007). We use the results of experimental nutrient additions and fencing treatments to directly assess nutrient limitation and herbivore pressure.

Materials and methods

Study System

This work is conducted within the context of the Nutrient Network (NutNet), a globally replicated study of grassland ecosystems. The data in this study are collected from 62 sites

located in 13 countries (Argentina, Australia, Canada, China, Estonia, Germany, India, Portugal,
212 South Africa, Switzerland, Tanzania, United Kingdom, USA) on 6 continents (Australia [N = 7],
Africa [N=4], Asia [N=2], Europe [N = 9], North America [N = 39], South America [N = 1];
214 Figure 1, Table A1). We had the highest replication in North America, and these sites also had a
large degree of variation in their degree of invasion. We account for within-continent variability
216 with a regional categorical variable nested within continent. Specifically, we divided the North
American sites into four regions based on longitudinal mountain ranges (Sierras/Cascades,
218 Rockies, and Appalachians): Pacific Coast, Intermountain West, Central, and Atlantic Coast.
These regions broadly correspond with the regions of temperate grasslands and invasions used
220 by Mack (1989) and the biomes used by Olson et al. (2001).

Sites were selected without respect to the dominance of native or exotic species. All sites are
222 dominated by herbaceous species and represent a wide range of ecosystem types including alpine
tundra, annual grasslands, mesic grasslands, montane meadows, old fields, salt marshes, savanna,
224 semi-arid grasslands, shortgrass prairie, shrub steppes, and tallgrass prairie. Sites span wide
ranges of elevation (0 to 4241 m), mean annual precipitation (211 to 2072 mm yr⁻¹), mean annual
226 temperature (0.3 to 23.7 C), latitude (38 degrees S to 59 degrees N), and aboveground
productivity (26 to 1408 g m⁻² yr⁻¹).

228 The lead scientist at each site provided latitude and elevation data, and climate data for each site
were derived from the WorldClim database (version 1.4; <http://www.worldclim.org/bioclim>)
230 (Hijmans *et al.*, 2005). In our models we used the following climate variables (BIO designator
indicates the variable code in the WorldClim database): mean annual temperature (degrees C;
232 BIO1), mean maximum temperature of the warmest month (BIO5), mean minimum temperature
of the warmest month (BIO5), mean annual precipitation (mm per year; BIO12), precipitation

234 seasonality (coefficient of variation in precipitation among months; BIO15), temperature
seasonality (standard deviation of temperature among months; BIO4), mean temperature in the
236 wettest quarter (degrees C; BIO8). This suite of climate variable summarizes the mean and
seasonality of temperature and precipitation and the seasonal synchrony of rainfall and
238 temperature (i.e., does most of the rain fall during hot or cool times of the year?).

In addition, each scientist provided detailed data on the agricultural history of each site. Here we
240 included two variables summarizing the cultivation and grazing history of each site. To do this,
we created an ordered variable summarizing the time since each site had been grazed by
242 domestic livestock: (0) Never grazed, (1) 30 or more years since grazing, (2) 10 to 29 years since
grazing, (3) 1 to 9 years since grazing, and (4) Currently grazed. We constructed a similar metric
244 for cultivation with the following categories: (0) Never cultivated, (1) 30 or more years since
cultivation, and (2) less than 30 years since cultivation. We used aerial photos of each site
246 (maps.google.com) to assess geographic features associated with invasion including distance to
the nearest road, coast, and river, and cultivated land as well as the population of the nearest
248 town or city. Proximity to coastlines, rivers, roads, agricultural land, and human populations
centers have all been associated with species invasions (Forman & Alexander, 1998, Mikkelson
250 *et al.*, 2007, Rejmanek, 2003, Seabloom *et al.*, 2006, Small & Cohen, 2004, Taylor & Irwin,
2004).

252 An observational study was conducted at all sites prior to the start of the experimental
treatments. Most sites (N=40) were sampled in three replicate blocks each composed of ten 5×5
254 m plots for a total of 30 plots per site. Note that at some sites, replication varied: 10 sites had less
than 30 plots (range of 10 to 27 plots per site) and 10 sites had more than 30 plots (range of 31 to
256 60 plots per site). The total data set was composed of 1,889 individual observations including

variable replication at some sites. While most sites collected data in 2007 (N=39), data from
258 additional sites were collected in 2008 (N=10), 2009 (N=3), 2010 (N=3), 2011 (N=2), 2012
(N=3), 2013 (N=2).

260 At a subset of the sites (N=39), we conducted a replicated experiment that allowed us to estimate
herbivore pressure and nutrient limitation. The experiment was a full factorial combination of
262 nutrient addition (Control or Fertilized) and consumer density (Control or Fenced) for a total of 4
treatments. Fences were 2.1 m tall, and designed to exclude large aboveground mammalian
264 herbivores, including ungulates. The first 90 cm was 1 cm woven wire mesh with a 30 cm
outward-facing flange stapled to the ground to exclude digging animals; climbing and
266 subterranean animals potentially could access plots. Nutrient addition rates and sources were: 10
g N m⁻² yr⁻¹ as timed-release urea, 10 g P m⁻² yr⁻¹ as triple-super phosphate, 10 g K m⁻² yr⁻¹ as
268 potassium sulfate and 100 g m⁻² yr⁻¹ of a micronutrient mix (6% Ca, 3% Mg, 12% S, 0.1% B, 1%
Cu, 17% Fe, 2.5% Mn, 0.05% Mo, and 1% Zn). N, P, and K were applied annually; the
270 micronutrient mix was applied once at the start of the study to avoid toxicity of largely immobile
micronutrients.

272 Ammonium nitrate was used as the nitrogen source in 2007, however urea was used in all
subsequent years due to difficulties in procuring ammonium nitrate. We tested whether various
274 nitrogen sources could alter community responses by conducting an experiment comparing the
two nitrogen sources (timed-release urea, and ammonium nitrate) at four NutNet sites
276 (Bunchgrass, Hopland, Lookout, and Mclaughlin; Table A1). At each site, we established a fully
randomized complete block design with 3 treatments (Control and 10 g of N added as either
278 timed-release urea or ammonium nitrate) and 3 blocks (9 plots per site and 36 plots total). Each
plot was 2 x 2 m. We applied the treatments in spring 2009 and sampled the cover and biomass

280 of the plots in 2010 as described below. We found no difference in richness or total live biomass
among the nitrogen sources based on a mixed effects model with site and block within site
282 treated as random effects ($p = 0.374$ for biomass and $p=1.000$ for richness).

Sampling. Areal cover of all species was estimated visually to the nearest 1% in a 1 m^2 quadrat in
284 each 5×5 m plot. Typically there were 30 cover plots per site. Cover was estimated
independently for each species so that total summed cover exceeded 100% for multilayer
286 canopies. At some sites with strongly seasonal communities, cover was estimated twice during
the year and the maximum cover of each species was used in the analyses. Lead scientists at each
288 site provided the provenance of each species that occurred at their sites. Across the study sites,
some species occurred in both their native and exotic range (Firn *et al.*, 2011). Aboveground
290 biomass was collected in two 10×100 cm strips (0.2 m^2 in each plot) clipped at peak biomass in
each 5×5 -m plot for an average 30 biomass samples per site. Biomass was sorted to functional
292 group (i.e. grass, forb, legume, bryophyte, litter), and the current year's production was dried to
constant mass at 60°C , and weighed to the nearest 0.01 g.

294 *Statistical Analyses.* All analyses were conducted using R version 2.15 (R Development Core
Team, 2010). We examined the relationship between exotic richness and cover and the following
296 bioclimatic drivers: elevation (m), mean annual precipitation (MAP; mm yr^{-1}), seasonal
precipitation variability (coefficient of variation in monthly precipitation), mean annual
298 temperature (C), mean minimum annual temperature (C), mean maximum annual temperature
(C), seasonal temperature variability (standard deviation in mean monthly temperature),
300 temperature in the wettest quarter (C), aboveground dead biomass (g m^{-2}), and aboveground live
biomass ($\text{g m}^{-2} \text{ yr}^{-1}$). We tested whether the richness of local flora (i.e., cumulative number of

302 species at each site) was correlated with exotic establishment or dominance by including site-
level native species richness. We also included the richness of native species of different lifespan
304 (annual or perennial) and lifeform (grasses, forbs, and woody plants). There were insufficient
data at one site to fully classify species by lifeform and lifespan, and this sites was not included
306 in regressions including these variables.

We tested whether exotic richness or cover were related to herbivore pressure or nutrient
308 limitation at each of the experimental sites (N=39) after a single year of treatment (Fencing or
Fertilization). We calculated the treatment effects after a single year as the best direct measure of
310 the herbivore effects and nutrient limitation independent of compositional changes and species
extinctions that become increasingly important after multiple years of treatments. We estimated
312 herbivore pressure as the change in live biomass resulting from fencing calculated as the log
ratio $\log(B_f/B_{f+})$, where B_f is the live biomass in control plots and B_{f+} is the live biomass in
314 fenced plots after one year of fencing treatment. We estimated nutrient limitation by calculating
the change in live biomass resulting from nutrient addition calculated as the log ratio
316 $\log(B_{nut+}/B_{nut-})$, where B_{nut-} is the live biomass in unfertilized plots and B_{nut+} is the live biomass in
fertilized plots after one year of nutrient addition treatments.

318 We calculated exotic cover as a relative measure by summing cover of all exotic species and
dividing by the summed cover of all species. We modeled the cover of exotic species as a
320 proportion ranging from 0 to 1.0 using generalized linear models with logit link and binomial
error (i.e., logistic regression), and modeled exotic richness (number of exotic species per m²)
322 using a log link and Poisson errors (i.e., Poisson regression). All regression models started with
the following variables: elevation (log m); precipitation (mm yr⁻¹); seasonal precipitation and
324 temperature variation; mean, maximum, and minimum annual temperature (C); aboveground live

biomass ($\log \text{ g m}^{-2} \text{ yr}^{-1}$); aboveground dead biomass ($\log \text{ g m}^{-2}$); richness of native species,
326 native annuals, native grasses, native forbs, native woody plants, herbivore pressure (i.e., fencing
effect on biomass); nutrient limitation (fertilization effect on biomass); years since last grazing
328 and cultivation; distance to the nearest road, river, cultivated land, and coast; and the population
of the nearest town.

330 We used quasi-likelihood to adjust for over- or under-dispersion in the data. It is not possible to
calculate AIC or similar likelihood based statistics from quasi-likelihood models (Venables &
332 Ripley, 2003), so we reduced the models using backwards selection and Type II sums of squares
to include only those variables explaining significant amount of variation using the F statistic.

334 We also conducted the analyses using transformations for the richness (square root) and
proportion exotic cover (arcsine square root), and results were qualitatively similar. Finally, we
336 had similar results analyzing the plot-scale data using mixed-effects models with site as a
random effects (Pinheiro & Bates, 2000).

338 We were missing data on live biomass at 4 sites, fencing and fertilization effects on biomass at
23 sites, and cultivation or grazing history at 26 sites. Biomass, fencing effects, fertilization
340 effects, cultivation history, grazing history, and land-use data were not present in any of the of
the final statistical models (i.e., the parsimonious models after selection), so we present results of
342 models fit to the larger data set excluding these variables. Results did not differ qualitatively
across these different subsets of the data.

344 **Results**

Across sites ranging from salt marshes to alpine tundra (Figure 1; Table A1), we documented
346 1,477 species from 102 families. The 191 exotic species comprised 34 families. We were unable

to classify the provenance of 129 taxa due to either taxonomic or provenance uncertainties (9%
348 of the total species). Unclassified species comprised 7% of the cover in the total data set, and we
have no reason to expect that unclassified species were biased with regards to their provenance.
350 Relative exotic cover ($100 \times \text{exotic cover} / \text{total cover}$) varied from 0 to 100% at both the plot ($n =$
1,924) and site scales ($n = 62$). Exotic richness ranged from 0 to 46 species at the site scale
352 (cumulative exotic richness) and 0 to 20 species at the plot scale (i.e., mean exotic richness m^{-2}).
Note that hereafter we only analyze mean exotic richness at the plot scale, as the mean plot scale
354 richness is highly correlated with cumulative exotic richness across all plots at each site ($r =$
0.84, $p < 0.001$).

356 Exotic cover and exotic richness were positively correlated at the site and plot scale (Figure 2;
Table 1), however the relationship was strongly nonlinear. In addition, exotic cover was highly
358 variable at low levels of species richness. For example, while sites with an average of 10 or more
exotic species were always dominated by exotic species ($> 80\%$ exotic cover), sites with less
360 than 3 exotic species spanned the range from 0 to 96% exotic cover. As a result of the higher
variance in exotic cover at sites with low exotic richness, the residuals around the regressions
362 were much larger at low levels exotic richness (Inset Figure 2). Thus, exotic richness provides a
lower bound on exotic dominance, but exotic richness does not discern between sites with a few
364 sparse invaders (low exotic richness and cover) and those dominated by a few highly abundant
exotic species (low exotic richness but high exotic cover).

366 Most of the variability in exotic richness and cover at the plot scale was due to differences
among regions and ecosystems; there was almost no variability accounted for by differences
368 among continents (Figure 3), as even highly invaded continents had areas dominated by native
species (e.g., the Central Great Plains of North America; Figure 1 & 5). Exotic cover varied most

370 strongly among regions (44%). While exotic richness also had significant variation among
regions (30% of variance), it varied much more among sites within a single ecosystem in a
372 region (42% of variance). In terms of regional variation in exotic cover, all sites in Africa, Asia,
and Europe were dominated by native species, as measured by richness or cover, whereas all
374 sites on the Pacific coast of North America were highly invaded (Figure 4A). Variation among
different ecosystems was equally strong. Alpine, montane, salt marsh, and shrub steppe sites had
376 less than 10% exotic cover, whereas annual grasslands had more than 75% exotic cover (Figure
4B).

378 In part, these differences among regions and ecosystems reflect underlying biotic, climatic, and
human land use gradients. Site-level means of exotic cover and richness were lowest in areas
380 with a diverse native grass flora (number of grass species at a site) and at sites located far from
cultivated agricultural fields (Table 2). Exotic cover was also higher in areas with consistent
382 precipitation (low variance among months), and exotic richness was higher at hot (high
maximum temperature) sites near the coast that have a cool wet-season.

384 The strong and consistent effects of native grass richness likely reflect the dominance of grasses,
as a group. Native grasses comprised the highest percent of native plant cover (mean = 46.9% ±
386 3.5% SEM). Forbs were the next most abundant group (mean = 35.1% ± 3.3% SEM). In
contrast, average forb diversity (mean = 16.9 ± 1.9 SEM species m⁻²) was higher than grasses
388 (mean = 6.2 ± 0.7 SEM species m⁻²). The strong negative relationship between native grass
richness and exotic species cover also could occur if exotic cover and native grass richness were
390 driven by the same underlying factors. To test this possibility, we compared models of exotic
cover and native grass richness that did not use the diversity of the native flora as an explanatory
392 variable. Although both responded to climate, the strength and direction of factors controlling

native grass richness were different than those driving exotic cover (Table A2), providing little
394 evidence for a shared latent factor.

The following variables were not included in any of the reduced models: minimum annual
396 temperature (C); aboveground live biomass ($\log \text{ g m}^{-2} \text{ yr}^{-1}$); aboveground dead biomass ($\log \text{ g m}^{-2}$); richness of native species, native annuals, native grasses, native forbs, native woody plants,
398 herbivore pressure (i.e., fencing effect on biomass); nutrient limitation (fertilization effect on biomass); years since last grazing and cultivation; distance to the nearest road, river; and the
400 population of the nearest town. Thus, while native community flora, climate, and land use all influence exotic cover and richness, only a few of these commonly used factors were ever
402 retained in models. Herbivore pressure and nutrient limitation of productivity were never correlated with global measures of exotic richness or cover.

404 **Discussion**

Using data from a multi-continent, replicated study, we found exotic richness to be an
406 inconsistent predictor of exotic dominance at sites with low exotic richness. While sites with many exotic species were uniformly exotic dominated, sites with few exotic species could either
408 be largely native or completely dominated by one or two exotic species. In grasslands, much of this variation arose from differences among regions within continents (the Atlantic and Pacific
410 coasts of North America were highly invaded, but the Midwest was not) and ecosystem types (annual grasslands, savannas, pastures, old fields were dominated by exotics). Region and
412 ecosystem type are interrelated. For example, all of the Atlantic coast sites are old fields or savanna and 57% of the Pacific coast sites are annual grasslands or savanna. Human land use,
414 native community diversity, and environmental gradients (i.e., climate) were all correlated with

invasion. Specifically, the strongest predictor of exotic richness and cover was the number of
416 native grass species present in the site or regional flora, with more native grass species
negatively correlated with exotic grass richness. In addition, exotic richness and cover were both
418 higher at sites that were close to cultivated land. Climate also played a role in determining
invasion, however climatic effects were different for exotic and native richness. Exotic cover
420 was highest in sites that had low rainfall seasonality, while exotic richness was highest at sites in
hot areas (high maximum temperature) with a pronounced cool and wet season.

422 Despite the historical and continued focus on exotic richness (Fridley *et al.*, 2007), we found that
exotic richness was only an effective predictor of exotic dominance when exotic richness was
424 very high (i.e., greater than 10 exotic species per m²). Exotic richness could not resolve the
difference between two distinct types of sites with low exotic species richness: those sites that
426 are relatively pristine with a few rare exotic species and those that are dominated by a few highly
dominant exotic species. Thus, examination of only exotic richness hinders our understanding of
428 drivers of invasion by confounding these qualitatively different site types, both with low exotic
richness. The poor predictive capacity of exotic richness suggests the need for efforts like the
430 work presented here that measure exotic dominance in standard and comparable ways across
many sites.

432 The importance of native grass richness as a predictor of exotic cover suggests that evolutionary
history may be a critical component in understanding invasions. Interestingly, it is the diversity
434 of grasses and not diversity *per se* that appears to mediate the dominance of exotic species. In
addition, we find the strongest relationship between exotic cover and cover of the most abundant
436 group of native plants (i.e. grasses) as opposed to the most diverse (i.e. forbs). Exotic grasses are
particularly effective invaders and tend to be more abundant in their invasive range (Firn *et al.*,

438 2011), and colonization by new species can be impeded by presence of resident species that are
functionally similar (Fargione *et al.*, 2003). Regions that have evolved diverse grass floras may
440 be more likely to contain native species that overlap the niches of a particularly effective group
of invaders (i.e., grasses), conferring invasion resistance. Ultimately, drawing inferences about
442 diversity-invasibility relationships using observational data requires caution, because of possible
covariates that may confound causal native exotic richness relationships (Fridley *et al.*, 2007,
444 Rejmanek, 2003).

Given the wide range of environmental conditions spanned by this work and the diversity of
446 exotic taxa represented across these sites, we did not expect to find consistent environmental
drivers of exotic species richness and cover. Nevertheless, we did find that both exotic cover and
448 richness were increased by the propinquity of cultivated lands. In addition, exotic richness was
higher in coastal areas. Human endeavors, including agriculture, undoubtedly increase invasion
450 as has been shown in many other studies (Antonelli *et al.*, 2011, Davis *et al.*, 2000, Gelbard &
Harrison, 2003, Gonzalez *et al.*, Mack, 1989, Parker *et al.*, 2006, Rejmanek, 2003, Scott *et al.*,
452 2001, Seabloom *et al.*, 2009, Seabloom *et al.*, 2006, Taylor & Irwin, 2004, Williams *et al.*,
2005).

454 Studies replicated at the regional, as opposed to the global scale, have found higher exotic
richness in low-lying coastal areas (Alexander *et al.*, 2011, Rejmanek, 2003, Seabloom *et al.*,
456 2006, Williams *et al.*, 2005); however indirect factors like coastal proximity and elevation are
often highly correlated with many potential invasion-drivers including native richness, species
458 introduction rates, ecosystem productivity, human population, and conversion of land to human-
dominated uses (Balmford *et al.*, 2001, Rejmanek, 2003, Scott *et al.*, 2001, Seabloom *et al.*,

460 2002, Seabloom *et al.*, 2006, Williams *et al.*, 2005). While we found more exotic species at sites
near coastlines, elevation was not included in the best model of exotic dominance or richness.

462 We did not find a detectable impact of large herbivore pressure on exotic occurrence and
dominance. However, other studies have shown that preferential consumption of native plants by
464 herbivores may increase invasions (Orrock *et al.*, 2008, Orrock *et al.*, 2009, Seabloom *et al.*,
2009), although the strength and direction of herbivore effects are contingent upon the amount of
466 shared evolutionary history between herbivores and plants (Mack, 1989, Parker *et al.*, 2006,
Verhoeven *et al.*, 2009). At a broader scale, the areas in our study that are highly invaded are
468 concordant with those highlighted by Mack (1989) as possibly lacking an evolutionary history
with congregating, hoofed grazers during the Holocene, such as Australia and the Pacific coast of
470 North America. In contrast, sites with high native grass diversity and low cover of exotics have a
long history of grazing by hoofed mammals, such as Eurasia, Africa, and the Central Great
472 Plains of North America (Mack, 1989).

While it is clear that biological invasions have altered many of the world's ecosystems and
474 precipitate significant economic costs (Levine *et al.*, 2003, Lodge, 1993, Mills *et al.*, 1994,
Pimentel *et al.*, 2005, Seabloom & Wiedemann, 1994, Vitousek *et al.*, 1997, Vitousek, 1990),
476 we still have little ability to make general predictions about which species will have the greatest
impacts as invaders and which areas are likely to be the most impacted (Catford *et al.*, 2012, Firn
478 *et al.*, 2011, Parker *et al.*, 1999, Seabloom *et al.*, 2003). The search for general drivers of
invasion at the global scale has been hindered by the lack of consistent, globally replicated data
480 on exotic abundance, and a resulting overemphasis on exotic richness as a surrogate for impact.
Here we show that exotic richness is only an effective predictor of exotic dominance when
482 richness is exceptionally high; overall, exotic richness represents a poor proxy for the impact,

assessed here via exotic cover, of exotic species on native communities. Our global-scale
484 observations bridge the gap between mechanistic studies at single sites and meta-analyses of
global patterns of exotic richness, shedding new light on the drivers and outcomes of global
486 invasions.

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496 References

- Alexander J. M., Kueffer C., Daehler C. C., Edwards P. J., Pauchard A., Seipel T., Consortium
498 M. (2011) Assembly of nonnative floras along elevational gradients explained by
directional ecological filtering. *Proceedings of the National Academy of Science USA*.
- 500 Antonelli A., Humphreys A. M., Lee W. G., Linder H. P. (2011) Absence of mammals and the
evolution of New Zealand grasses *Proceedings Royal Society B*, 278, 695-701.
- 502 Balmford A., Moore J. L., Brooks T., Burgess N., Hansen L. A., Williams P., Rahbek C. (2001)
Conservation conflicts across Africa. *Science*, 291, 2616-2619.

- 504 Candolle A. P. D., Sprengel K. P. J. (1821) *Elements of the philosophy of plants: containing the*
506 *principles of scientific botany with a history of the science, and practical illustrations.* ,
Edinburgh, W. Blackwood.
- Catford J. A., Vesk P. A., Richardson D. M., Pysek P. (2012) Quantifying levels of biological
508 invasion: towards the objective classification of invaded and invisable ecosystems.
Global Change Biology, 18, 44-62.
- 510 Chapin F. S., A. M. P., Mooney H. A. (2002) *Principles of terrestrial ecosystem ecology* New
York : Springer
- 512 Conant R. T. (2010) Challenges and opportunities for carbon sequestration in grassland systems:
A technical report on grassland management and climate change mitigation. pp Page,
514 Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- Crawley M. J. (1987) What Makes A Community Invasible? In: *Colonization, succession, and*
516 *stability : the 26th Symposium of the British Ecological Society held jointly with the*
Linnean Society of London. (eds Gray AJ, Crawley MJ, Edwards PJ) pp Page, Oxford
518 Oxfordshire ; Boston, Blackwell Scientific Publications.
- Darwin C. A. (1859) *On the orgin of species. or the preservation of favoured races in the*
520 *struggle for life*, London, John Murray, Albermarle Street.
- Davis M. A. (2003) Biotic globalization: Does competition from introduced species threaten
522 biodiversity? *Bioscience*, 53, 481-489.

- 524 Davis M. A., Grime J. P., Thompson K. (2000) Fluctuating resources in plant communities: a
general theory of invasibility. *Journal of Ecology*, 88, 528-534.
- Elton C. S. (1958) *The ecology of invasions by animals and plants*, London, England, Methuen.
- 526 Fargione J., Brown C. S., Tilman D. (2003) Community assembly and invasion: An experimental
test of neutral versus niche processes. *Proceedings of the National Academy of Sciences*
528 *of the United States of America*, 100, 8916-8920.
- Firn J., Moore J. L., Macdougall A. S., Borer E. T., Seabloom E. W., Hillerislambers J., . . .
530 Buckley Y. M. (2011) Abundance of introduced species at home predicts abundance
away in herbaceous communities. *Ecology Letters*, 14, 274-281.
- 532 Forman R. T. T., Alexander L. E. (1998) Roads and their major ecological effects. *Annual*
Review of Ecology and Systematics, 29, 207-+.
- 534 Fridley J. D., Brown R. L., Bruno J. E. (2004) Null models of exotic invasion and scale-
dependent patterns of native and exotic species richness. *Ecology*, 85, 3215-3222.
- 536 Fridley J. D., Stachowicz J. J., Naeem S., Sax D. F., Seabloom E. W., Smith M. D., . . . Von
Holle B. (2007) The invasion paradox: Reconciling pattern and process in species
538 invasions. *Ecology*, 88, 3-17.
- Gelbard J. L., Harrison S. (2003) Roadless habitats as refuges for native grassland diversity.
540 *Ecological Applications*, 13, 404-415.

- Gonzalez A. L., Kominoski J. S., Danger M., Ishida S., Iwai N., Rubach A. (2010) Can
542 ecological stoichiometry help explain patterns of biological invasions? *Oikos*, 119, 779-
790.
- 544 Grime J. P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder
effects. *Journal of Ecology*, 86, 902-910.
- 546 Henwood W. D. (2010) Toward a strategy for the conservation and protection of the world's
temperate grasslands. *Great Plains Research*, 20, 121-134.
- 548 Hijmans R. J., Cameron S. E., Parra J. L., Jones P. G., Jarvis A. (2005) Very high resolution
interpolated climate surfaces for global land areas. *International Journal of Climatology*,
550 25, 1965-1978.
- Hoekstra J. M., Boucher T. M., Ricketts T. H., Roberts C. (2005) Confronting a biome crisis:
552 global disparities of habitat loss and protection. *Ecology Letters*, 8, 23-29.
- Huenneke L. F., Hamburg S. P., Koide R., Mooney H. A., Vitousek P. M. (1990) Effects of Soil
554 Resources on Plant Invasion and Community Structure in Californian Serpentine
Grassland. *Ecology*, 71, 478-491.
- 556 Hurlbert S. H. (1997) Functional importance vs keystoneity: Reformulating some questions in
theoretical biocenology. *Australian Journal of Ecology*, 22, 369-382.
- 558 Levine J. M., D'antonio C. M. (2003) Forecasting biological invasions with increasing
international trade. *Conservation Biology*, 17, 322-326.

- 560 Levine J. M., Vila M., D'antonio C. M., Dukes J. S., Grigulis K., Lavorel S. (2003) Mechanisms
underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of*
562 *London Series B-Biological Sciences*, 270, 775-781.
- Lodge D. M. (1993) Biological invasions: Lessons for ecology. *Trends in Ecology & Evolution*,
564 8, 133-137.
- Macdougall A. S., Bennett J. R., Firn J., Seabloom E. W., Borer E. T., Lind E. M., . . . Pierre K.
566 J. L. (In Review) Human-mediated drivers of diversity underlie the invasion paradox.
- Mack R. N. (1989) Temperate grasslands vulnerable to plant invasion: characteristics and
568 consequences. In: *Biological invasion: a global perspective*. (eds Drake JA, Mooney HA,
Dicastri F, Groves RH, Kruger FJ, Rejmanek M, Williamson M) pp Page. New York,
570 New York, USA, John Wiley and Sons.
- Mack R. N. (2003) Plant naturalizations and invasions in the eastern United States: 1634-1860.
572 *Annals of the Missouri Botanical Garden*, 90, 77-90.
- Mack R. N., Thompson J. N. (1982) Evolution in Steppe with Few Large, Hoofed Mammals.
574 *American Naturalist*, 119, 757-773.
- Melbourne B. A., Cornell H. V., Davies K. F., Dugaw C. J., Elmendorf S., Freestone A. L., . . .
576 Yokomizo H. (2007) Invasion in a heterogeneous world: resistance, coexistence or
hostile takeover? *Ecology Letters*, 10, 77-94.
- 578 Mikkelsen G. M., Gonzalez A., Peterson G. D. (2007) Economic Inequality Predicts Biodiversity
Loss. *Plos One*, 2.

- 580 Mills E. L., Leach J. H., Carlton J. T., Secor C. L. (1994) Exotic species and the integrity of the
Great Lakes: Lessons from the past. *Bioscience*, 44, 666-676.
- 582 Mooney H. A., Cleland E. E. (2001) The evolutionary impact of invasive species. *Proceedings of
the National Academy of Sciences of the United States of America*, 98, 5446-5451.
- 584 Olson D. M., Dinerstein E., Wikramanayake E. D., Burgess N. D., Powell G. V. N., Underwood
E. C., . . . Kassem K. R. (2001) Terrestrial ecoregions of the worlds: A new map of life
586 on Earth. *Bioscience*, 51, 933-938.
- Orrock J. L., Witter M. S., Reichman O. J. (2008) Apparent competition with an exotic plant
588 reduces native plant establishment. *Ecology*, 89, 1168-1174.
- Orrock J. L., Witter M. S., Reichman O. J. (2009) Native Consumers and Seed Limitation
590 Constrain the Restoration of a Native Perennial Grass in Exotic Habitats. *Restoration
Ecology*, 17, 148-157.
- 592 Parker I. M., Simberloff D., Lonsdale W. M., Goodell K., Wonham M., Kareiva P. M., . . .
Goldwasser L. (1999) Impact: Toward a Framework for Understanding the Ecological
594 Effects of Invaders. *Biological Invasions*, 1, 3-19.
- Parker J. D., Burkepile D. E., Hay M. E. (2006) Opposing effects of native and exotic herbivores
596 on plant invasions. *Science*, 311, 1459-1461.
- Pimentel D., Zuniga R., Morrison D. (2005) Update on the environmental and economic costs
598 associated with alien-invasive species in the United States. *Ecological Economics*, 52,
273-288.

- 600 Pinheiro J. C., Bates D. M. (2000) *Mixed Effects Models in S and S-Plus*, Springer.
- Qian H., Ricklefs R. E. (2006) The role of exotic species in homogenizing the North American
602 flora. *Ecology Letters*, 9, 1293-1298.
- R Development Core Team (2010) R: A language and environment for statistical computing pp
604 Page, R Foundation for Statistical Computing, Vienna, Austria.
- Ramankutty N., Evan A. T., Monfreda C., Foley J. A. (2008) Farming the planet: 1. Geographic
606 distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles*,
22, 1-19.
- 608 Rejmanek M. (2003) The rich get richer - responses. *Frontiers in Ecology and the Environment*,
1, 122-123.
- 610 Sax D. F., Brown J. H. (2000) The paradox of invasion. *Global Ecology and Biogeography*, 9,
363-371.
- 612 Sax D. F., Gaines S. D., Brown J. H. (2002) Species invasions exceed extinctions on islands
worldwide: A comparative study of plants and birds. *American Naturalist*, 160, 766-783.
- 614 Scott J. M., Davis F. W., Mcghee R. G., Wright R. G., Groves C., Estes J. (2001) Nature
reserves: Do they capture the full range of America's biological diversity? *Ecological*
616 *Applications*, 11, 999-1007.
- Seabloom E. W. (2007) Compensation and the stability of restored grassland communities.
618 *Ecological Applications*, 17, 1876-1885.

- 620 Seabloom E. W., Bjornstad O. N., Bolker B. M., Reichman O. J. (2005) The spatial signature of
environmental heterogeneity, dispersal, and competition in successional grasslands.
Ecological Monographs, 75, 199-214.
- 622 Seabloom E. W., Borer E. T., Martin B. A., Orrock J. L. (2009) Effects of long-term consumer
manipulations on invasion in oak savanna communities. *Ecology*, 90, 1356-1365.
- 624 Seabloom E. W., Dobson A. P., Stoms D. M. (2002) Extinction rates under nonrandom patterns
of habitat loss. *Proceedings of the National Academy of Sciences of the United States of*
626 *America*, 99, 1129-11234.
- Seabloom E. W., Harpole W. S., Reichman O. J., Tilman D. (2003) Invasion, competitive
628 dominance, and resource use by exotic and native California grassland species.
Proceedings of the National Academy of Sciences of the United States of America, 100,
630 13384-13389.
- Seabloom E. W., Wiedemann A. M. (1994) Distribution and Effects of *Ammophila-Breviligulata*
632 Fern (American Beachgrass) on the Foredunes of the Washington Coast. *Journal of*
Coastal Research, 10, 178-188.
- 634 Seabloom E. W., Williams J. W., Slayback D., Stoms D. M., Viers J. H., Dobson A. P. (2006)
Human impacts, plant invasion, and imperiled, plant species in California. *Ecological*
636 *Applications*, 16, 1338-1350.
- Shea K., Chesson P. (2002) Community ecology theory as a framework for biological invasions.
638 *Trends in Ecology & Evolution*, 17, 170-176.

- Small C., Cohen J. E. (2004) Continental physiography, climate, and the global distribution of
640 human population. *Current Anthropology*, 45, 269-277.
- Stohlgren T. J., Barnett D. T., Kartesz J. T. (2003) The rich get richer: patterns of plant invasions
642 in the United States. *Frontiers in Ecology and the Environment*, 1, 11-14.
- Taylor B. W., Irwin R. E. (2004) Linking economic activities to the distribution of exotic plants.
644 *Proceedings of the National Academy of Sciences of the United States of America*, 101,
17725-17730.
- 646 Van Kleunen M., Weber E., Fischer M. (2011) A meta-analysis of trait differences between
invasive and non-invasive plant species. *Ecology Letters*, 13, 235-245.
- 648 Venables W. N., Ripley B. D. (2003) *Modern Applied Statistics with S*, Springer.
- Verhoeven K. J. F., Biere A., Harvey J. A., Van Der Putten W. H. (2009) Plant invaders and
650 their novel natural enemies: who is naive? *Ecology Letters*, 12, 107-117.
- Vitousek P., M., D'antonio C., M., Loope L., L., Rejmanek M., Westbrooks R. (1997) Introduced
652 species: a significant component of human-caused global change. *New Zealand Journal
of Ecology*, 21, 1-16.
- 654 Vitousek P. M. (1990) Biological Invasions and Ecosystem Processes: Towards an Integration of
Population Biology and Ecosystem Studies. *Oikos*, 57, 7-13.
- 656 Von Humboldt A. (1805) Essay on the geography of plants. In: *Foundations of biogeography :*
classic papers with commentaries. (eds Lomolino MV, Sax DF, Brown JH) pp Page.,
658 University of Chicago Press.

Williams J. W., Seabloom E. W., Slayback D., Stoms D. M., Viers J. H. (2005) Anthropogenic
660 impacts upon plant species richness and net primary productivity in California. *Ecology*
Letters, 8, 127-137.

662

Table 1. Results of logistic regression of exotic cover on exotic richness at the site scale (N=62).

666 Tests of significance are based on quasi-likelihood due to significant under- or over-dispersion in the data. Estimated dispersion parameter was 0.52.

Source	Estimate	S.S.	D.F.	F	p
Exotic Richness	0.5629	26.209	1	50.428	<0.0001
Residuals		31.184	60		

670 **Table 2.** Final regression model of exotic cover and exotic richness at the site scale (N=62)
 explained by environmental covariates. Tests of significance are based on quasi-likelihood due to
 672 significant over- or under-dispersion in the data. Only the reduced model is shown. The full
 model included elevation (m); precipitation (mm yr⁻¹); seasonal precipitation and temperature
 674 variation; mean, maximum, and minimum annual temperature (C); aboveground live biomass
 (log g m⁻² yr⁻¹); aboveground dead biomass (log g m⁻²); richness of native species, native
 676 annuals, native grasses, native forbs, native woody plants, herbivore pressure (i.e., fencing effect
 on biomass); nutrient limitation (fertilization effect on biomass); years since last grazing and
 678 cultivation; distance to the nearest road, river, cultivated land, and coast; and the population of
 the nearest town. Estimated dispersion parameter for quasi-likelihood was 0.70 for exotic cover
 680 and 2.15 for exotic richness.

Response	Source	Estimate	S.S.	D.F.	F	p
Exotic Cover	Native Grass Richness	-0.362	16.92	1	24.3	0.000
	Precipitation Variation	0.050	6.93	1	10.0	0.003
	Distance to Cultivation	-1.022	3.37	1	4.8	0.032
	Residuals		39.62	57		
Exotic Richness	Native Grass Richness	-0.163	36.93	1	17.2	0.000
	Distance to Coast	-0.511	22.03	1	10.3	0.002
	Maximum Temperature	0.117	20.56	1	9.6	0.003
	Temp. Wettest Quarter	-0.048	9.44	1	4.4	0.041
	Distance to Cultivation	-0.338	9.44	1	4.4	0.041
	Residuals		118.20	55		

Figure Legends

682 **Figure 1.** Nutrient Network sites included in the current analyses. Observational sites only have
a single year of data and no experimental manipulations. Experimental sites have one year of
684 pre-treatment data in addition to data after the start of the fencing and nutrient-addition
treatments. Gray shaded circles are proportional to exotic cover.

686 **Figure 2:** Logistic regression showing relationship between exotic richness and mean cover of
exotic species in 1,924 plots in 62 grassland sites in 13 countries. Small open circles are plot-
688 scale data and larger gray circles show site means. Solid line shows predicted relationship based
on a logistic regression of the plot-scale data for exotic cover and richness ($F= 49.5$; $p < 0.001$).
690 Inset shows the absolute value of the regression residuals.

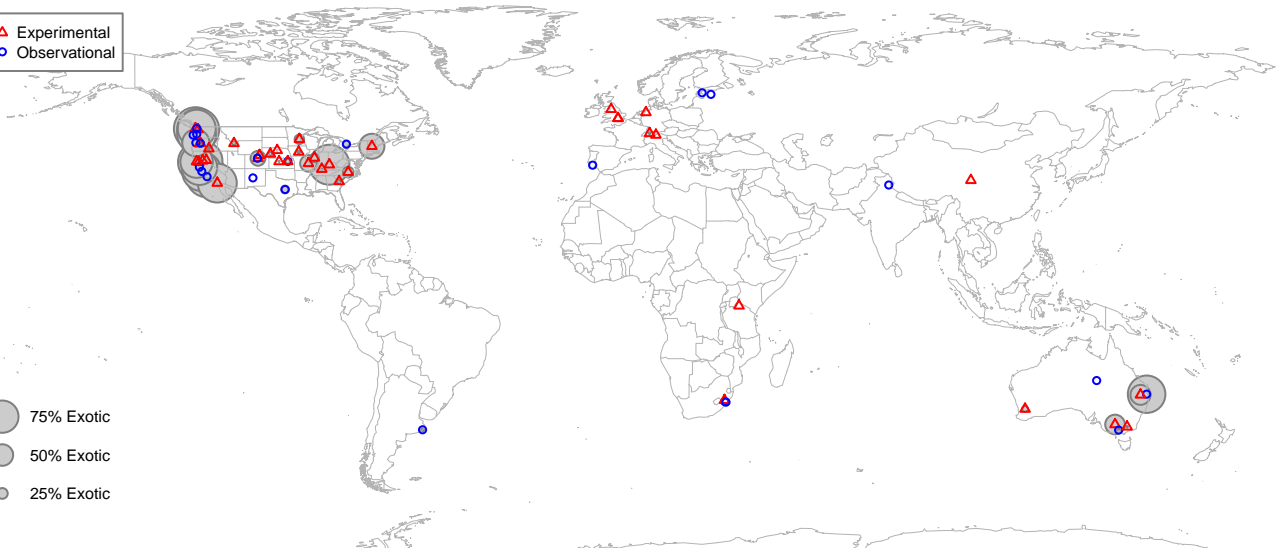
Figure 3: Variance components analysis showing distribution of variance in exotic richness and
692 exotic cover (percent of total) among 1,924 plots sampled at 62 sites in 13 countries. Sources of
variation are the following nested terms: continent, region, ecosystem, site, block, and plot
694 (residual) level variation.

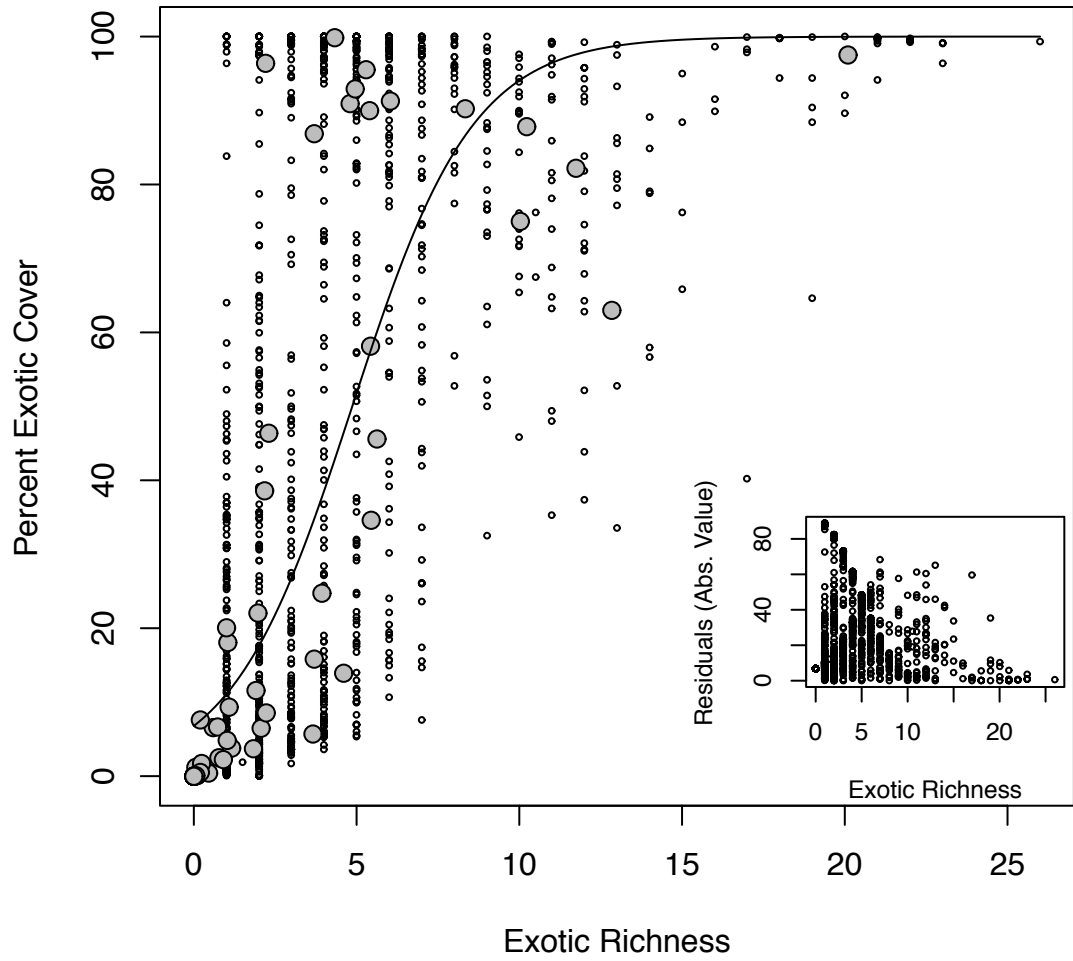
Figure 4: Exotic cover (percent of total) by region (A.) and ecosystem (B.) at 62 sites in 13
696 countries. Pacific-coast, central, intermountain-west, and Atlantic-coast are regions within North
America. Error bars are 1 SEM and numbers in parentheses are the number of sites in each
698 category.

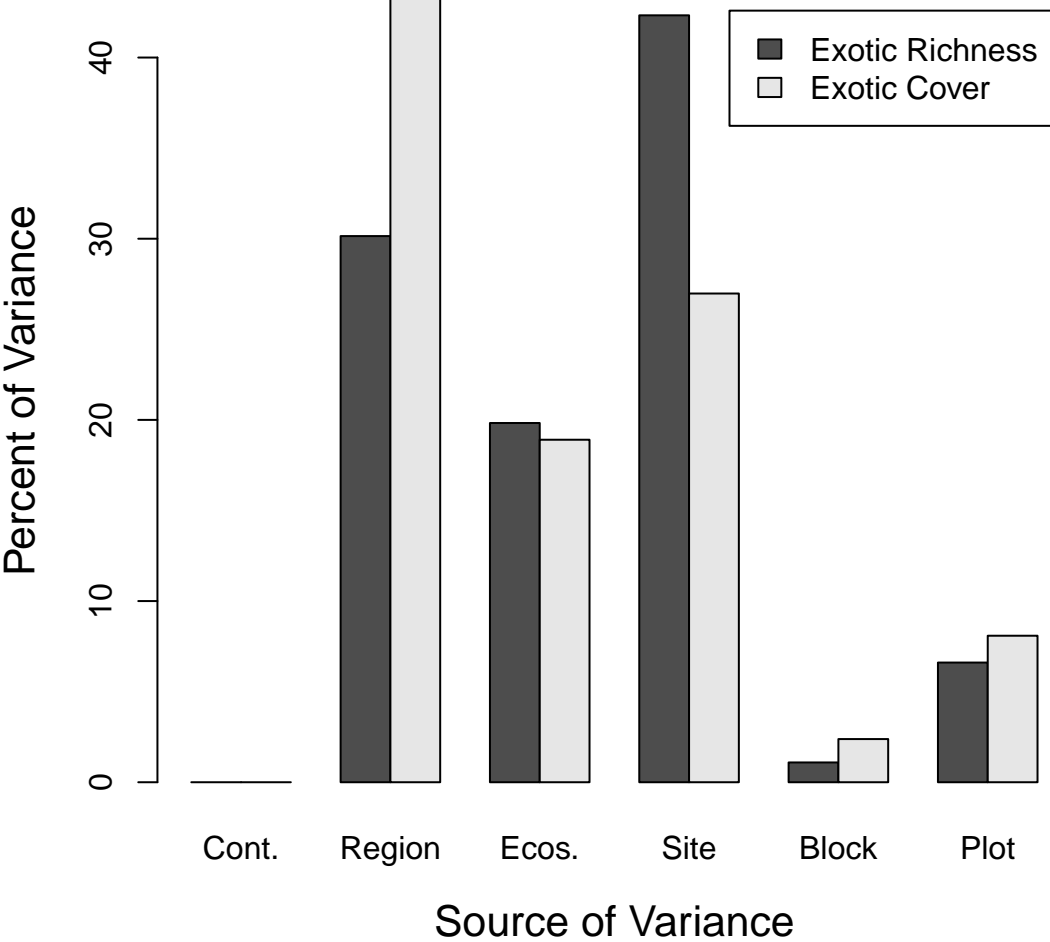
Figure 5: Regressions showing relationship between mean cover and richness of exotic species
700 and the total richness of native grass species at 62 grassland sites in 13 countries. Regression
lines for percent cover are logistic regressions and for richness are Poisson regressions.

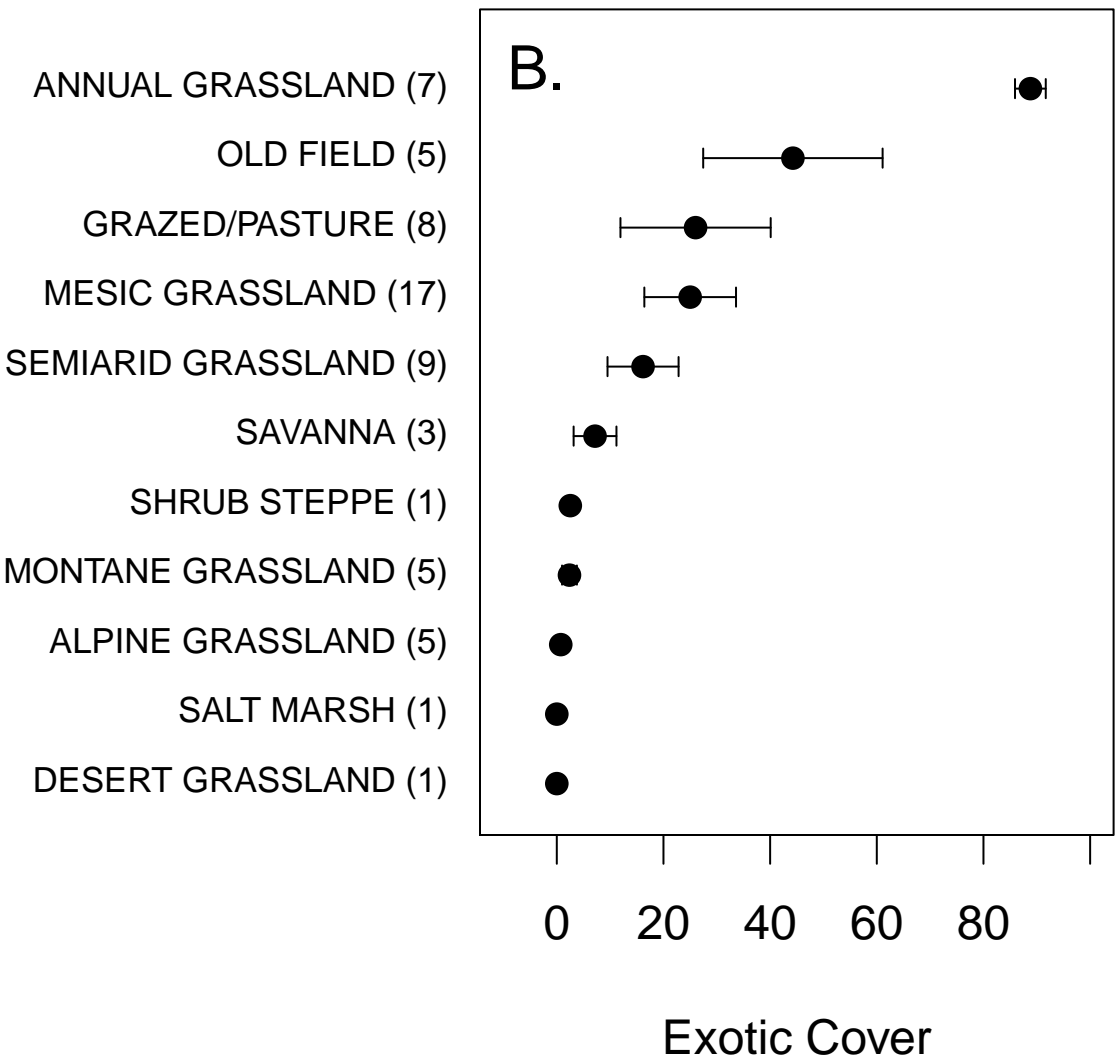
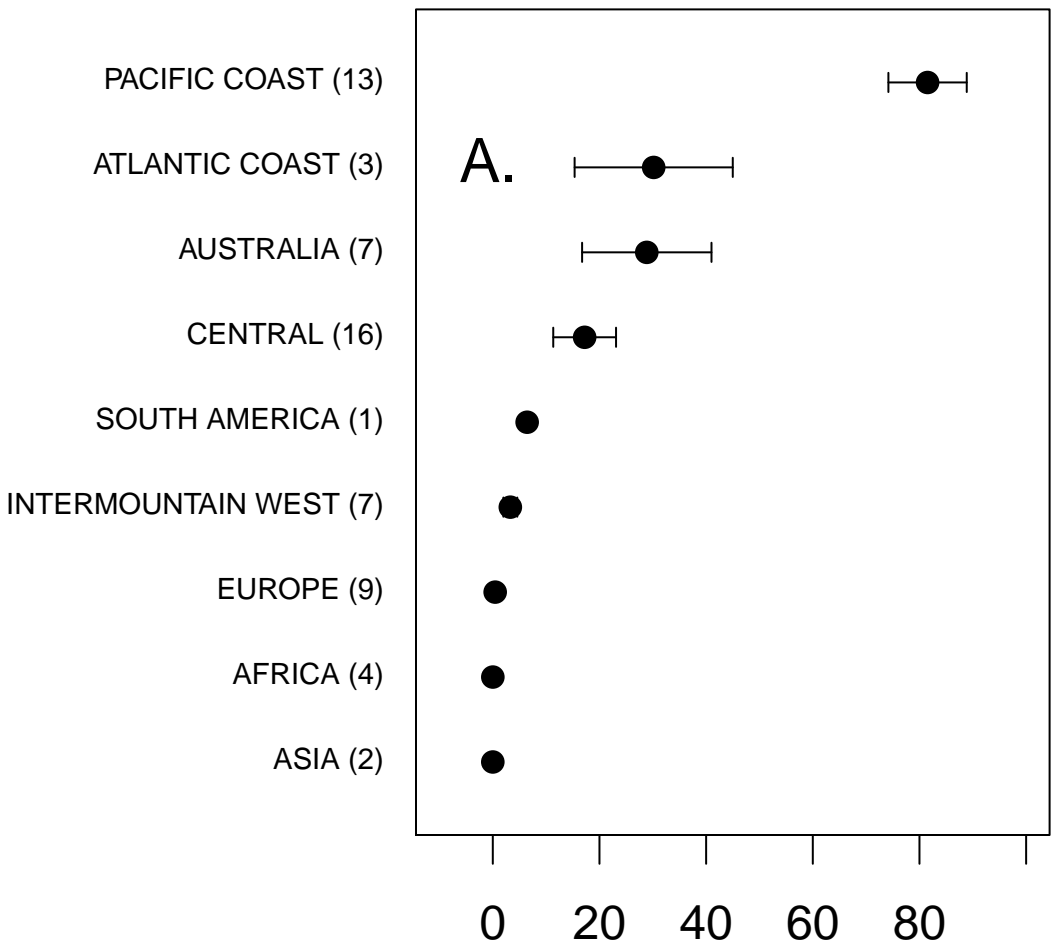
△ Experimental
○ Observational

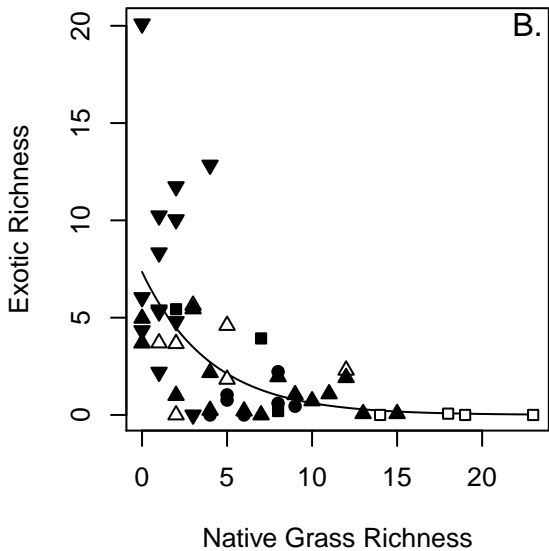
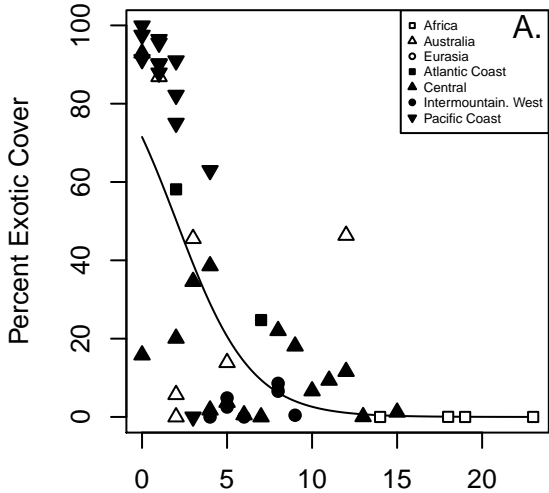
● 75% Exotic
● 50% Exotic
● 25% Exotic











Supplementary Online Appendices

2 **Table A1:** Study sites included in analyses. Pretreatment observational data were collected at all sites. Subsequent fertilization and
 4 fencing were only conducted at experimental sites. Study type indicates if sites had observation data only (Obs.) or observational and
 experimental fencing and fertilization data (Exp.).

Site	Name	Continent	Region	Country	Ecosystem	Lat.	Lon.	Elev. (m)	Precip. (mm)	Study Type	Number of Plots	First Sample Year
1	Serengeti	Africa	Africa	Tanzania	Savanna	-2.25	34.51	1536	854	Exp.	30	2008
2	Mt Gilboa	Africa	Africa	South Africa	Montane Grassland	-29.28	30.29	1748	926	Exp.	30	2010
3	Summerveld	Africa	Africa	South Africa	Mesic Grassland	-29.81	30.72	679	939	Obs.	30	2010
4	Ukulunga	Africa	Africa	South Africa	Mesic Grassland	-29.67	30.40	842	880	Obs.	30	2009
5	Azi	Asia	Asia	China	Alpine Grassland	33.67	101.87	3500	667	Exp.	30	2007
6	Kibber (Spiti)	Asia	Asia	India	Alpine Grassland	32.32	78.01	4241	504	Obs.	30	2011
7	Bogong	Australia	Australia	Australia	Alpine Grassland	-36.87	147.25	1760	1592	Exp.	30	2009
8	Burrawan	Australia	Australia	Australia	Semiarid Grassland	-27.73	151.14	425	683	Exp.	30	2008
9	Derrimut	Australia	Australia	Australia	Semiarid Grassland	-37.81	144.79	38	574	Obs.	30	2007
10	Ethabuka (South Site)	Australia	Australia	Australia	Grazed Pasture	-23.64	138.40	104	211	Obs.	28	2013
11	Kinypanial	Australia	Australia	Australia	Semiarid Grassland	-36.20	143.75	90	426	Exp.	30	2007
12	Mt. Caroline	Australia	Australia	Australia	Savanna	-31.78	117.61	285	330	Exp.	40	2008
13	Pinjarra Hills	Australia	Australia	Australia	Grazed Pasture	-27.53	152.92	38	1133	Obs.	30	2013
14	Fruebuel	Europe	Europe	Switzerland	Grazed Pasture	47.11	8.54	995	1355	Exp.	30	2008
15	Val Mustair	Europe	Europe	Switzerland	Alpine Grassland	46.63	10.37	2320	1098	Exp.	30	2008
16	Papenburg	Europe	Europe	Germany	Old Field	53.09	7.47	0	783	Exp.	10	2007
17	Elva	Europe	Europe	Estonia	Semiarid Grassland	58.26	26.35	64	616	Obs.	10	2012
18	Kirikukyla	Europe	Europe	Estonia	Mesic Grassland	58.71	23.80	8	601	Obs.	30	2012
19	Companhia das Lezirias	Europe	Europe	Portugal	Grazed Pasture	38.00	-8.00	200	554	Obs.	31	2012
20	Heronsbrook (Silwood Park)	Europe	Europe	United Kingdom	Mesic Grassland	51.41	-0.64	60	692	Exp.	30	2007
21	Lancaster	Europe	Europe	United Kingdom	Grazed Pasture	53.99	-2.63	180	1322	Exp.	26	2008
22	Rookery (Silwood Park)	Europe	Europe	United Kingdom	Mesic Grassland	51.41	-0.64	60	706	Exp.	30	2007
23	Koffler Scientific Reserve	North America	Central	Canada	Grazed Pasture	44.02	-79.54	301	815	Obs.	36	2010
24	Cowichan	North America	Pacific Coast	Canada	Old Field	48.46	-123.38	50	764	Exp.	30	2007
25	Hanover	North America	Atlantic Coast	USA	Old Field	43.42	-72.14	271	1033	Exp.	30	2007
26	Savannah River	North America	Atlantic Coast	USA	Savanna	33.34	-81.65	71	1194	Exp.	20	2007
27	Duke Forest	North America	Atlantic Coast	USA	Old Field	36.01	-79.02	141	1163	Exp.	30	2007
28	Barta Brothers	North America	Central	USA	Semiarid Grassland	42.24	-99.65	767	597	Exp.	30	2007
29	Boulder South Campus	North America	Central	USA	Semiarid Grassland	39.97	-105.23	1633	425	Exp.	20	2008
30	Chichaqua Bottoms	North America	Central	USA	Mesic Grassland	41.79	-93.39	275	855	Exp.	54	2009
31	Cedar Creek LTER	North America	Central	USA	Mesic Grassland	45.40	-93.20	270	750	Exp.	50	2007
32	Cedar Point Biological Station	North America	Central	USA	Semiarid Grassland	41.20	-101.63	965	445	Exp.	60	2007
33	Hall's Prairie	North America	Central	USA	Mesic Grassland	36.87	-86.70	194	1282	Exp.	30	2007
34	Konza LTER	North America	Central	USA	Mesic Grassland	39.07	-96.58	440	877	Exp.	30	2007
35	KonzaN1B	North America	Central	USA	Mesic Grassland	39.08	-96.56	440	878	Obs.	12	2007

36	Saline Experimental Range	North America	Central	USA	Semiarid Grassland	39.05	-99.10	440	607	Exp.	30	2008
37	Sevilleta LTER	North America	Central	USA	Desert Grassland	34.36	-106.69	1600	252	Obs.	40	2007
38	Shortgrass Steppe LTER	North America	Central	USA	Semiarid Grassland	40.82	-104.77	1650	365	Exp.	30	2007
39	Spindletop	North America	Central	USA	Grazed Pasture	38.14	-84.50	271	1140	Exp.	30	2007
40	Temple	North America	Central	USA	Mesic Grassland	31.04	-97.35	184	871	Obs.	26	2007
41	Trelease	North America	Central	USA	Mesic Grassland	40.08	-88.83	200	982	Exp.	30	2008
42	Tyson	North America	Central	USA	Old Field	38.52	-90.56	169	997	Exp.	40	2007
43	Bunchgrass (Andrews LTER)	North America	Intermountain West	USA	Montane Grassland	44.28	-121.97	1318	1647	Exp.	30	2007
44	Buttercup (Andrews LTER)	North America	Intermountain West	USA	Montane Grassland	44.28	-121.96	1500	1718	Obs.	30	2007
45	Hart Mountain	North America	Intermountain West	USA	Shrub steppe	42.72	-119.50	1508	272	Exp.	30	2007
46	Lookout (Andrews LTER)	North America	Intermountain West	USA	Montane Grassland	44.21	-122.13	1500	1898	Exp.	30	2007
47	Niwot Ridge LTER	North America	Intermountain West	USA	Alpine Grassland	39.99	-105.38	3050	439	Obs.	40	2007
48	Sagehen Creek UCNR	North America	Intermountain West	USA	Montane Grassland	39.43	-120.24	1920	882	Exp.	30	2007
49	Sheep Experimental Station	North America	Intermountain West	USA	Grazed Pasture	44.24	-112.20	910	262	Exp.	40	2007
50	American Camp	North America	Pacific Coast	USA	Mesic Grassland	48.47	-123.01	41	557	Obs.	30	2007
51	Elliott Chaparral	North America	Pacific Coast	USA	Annual Grassland	32.88	-117.05	200	331	Exp.	30	2008
52	Finley NWR	North America	Pacific Coast	USA	Mesic Grassland	44.41	-123.28	68	1104	Obs.	19	2007
53	Glacial Heritage	North America	Pacific Coast	USA	Mesic Grassland	46.87	-123.03	33	1311	Obs.	30	2007
54	Hastings UCNR	North America	Pacific Coast	USA	Annual Grassland	36.20	-121.55	750	702	Obs.	30	2007
55	Hopland REC	North America	Pacific Coast	USA	Annual Grassland	39.01	-123.06	598	1127	Exp.	27	2007
56	Jasper Ridge Biological Preserve	North America	Pacific Coast	USA	Annual Grassland	37.41	-122.24	120	592	Obs.	30	2007
57	Leadbetter Point	North America	Pacific Coast	USA	Salt Marsh	46.61	-124.05	2	2072	Obs.	30	2007
58	McLaughlin UCNR	North America	Pacific Coast	USA	Annual Grassland	38.86	-122.41	642	867	Exp.	30	2007
59	Sedgwick Reserve UCNR	North America	Pacific Coast	USA	Annual Grassland	34.70	-120.02	550	521	Obs.	30	2007
60	Sierra Foothills REC	North America	Pacific Coast	USA	Annual Grassland	39.24	-121.28	197	935	Exp.	30	2007
61	Smith Prairie	North America	Pacific Coast	USA	Mesic Grassland	48.21	-122.62	62	597	Exp.	30	2007
62	Mar Chiquita	South America	South America	Argentina	Mesic Grassland	-37.72	-57.42	6	838	Obs.	30	2011

6 **Table A2.** Final regression model of exotic cover and exotic richness at the site scale (N=62) explained by environmental covariates.
 8 Tests of significance are based on quasi-likelihood due to significant over- or under-dispersion in the data. Only the reduced model is
 10 shown. The full model included elevation (m); precipitation (mm yr⁻¹); seasonal precipitation and temperature variation; mean,
 maximum, and minimum annual temperature (C); aboveground live biomass (log g m⁻² yr⁻¹); aboveground dead biomass (log g m⁻²).
 Estimated dispersion parameter for quasi-likelihood was 0.56 for exotic cover, 4.24 for exotic richness, and 3.10 for native grass
 richness.

Response	Source	Estimate	Type II S.S.	D.F.	F	p
Exotic Cover	Mean Annual Temp.	0.227	8.03	1	14.3	0.000
	Temp. Wettest Quarter	-0.133	7.08	1	12.6	0.001
	Residuals		33.17	59		
Exotic Richness	Temp. Driest Quarter	0.065	51.78	1	12.2	0.001
	Residuals		254.36	60		
Native Grass Richness	Elevation	0.447	33.89	1	10.9	0.002
	Temp. Wettest Quarter	0.040	34.95	1	11.3	0.001
	Residuals		179.78	58		

14 **Table A3.** Author contributions to manuscript.

Full Name	Wrote the paper, e.g. contributed substantially to at least one section of the paper	Analyzed data, e.g. generated models (statistical and/or mathematical), figures, tables, maps, diagrams etc.	Developed and framed research questions for specific study using Nutrient Network data	Nutrient Network coordinators, e.g. designed experiments, coordinates network data collection and compilation, and garners funding.	Contributed substantially to data analyses, e.g. provided comments and suggestions	Contributed to paper writing, e.g. provided comments and suggestions	Collected Data
Eric Seabloom	X	X	X	X	X	X	X
Elizabeth Borer			X	X	X	X	X
Yvonne Buckley					X	X	X
Elsa Cleland			X		X	X	X
Kendi Davies					X	X	X
Jennifer Firn			X		X	X	X
W. Stanley Harpole			X	X	X	X	X
Yann Hautier					X	X	X
Eric M. Lind				X	X	X	X
Andrew MacDougall			X		X	X	X
John L. Orrock					X	X	X
Suzanne M Prober					X	X	X
Peter Adler						X	X
Juan Alberti							X
T. Michael Anderson							X
Jonathan D. Bakker						X	X
Lori A. Biederman							X
Dana M. Blumenthal						X	X
Cynthia S. Brown						X	X
Lars Brudvig						X	X
Maria Caldeira							X
Chengjin Chu							X
Michael J. Crawley					X		X
Pedro Daleo							X
Ellen I. Damschen							X
Carla M Dantonio						X	X
Nicole M. DeCrappeo							X
Chris R. Dickman							X
Guozhen Du							X
Philip A Fay						X	X
Paul Frater						X	X
Daniel S. Gruner						X	X
Nicole Hagenah						X	X

Andy Hector						X	X
Aveliina Helm							X
Helmut Hillebrand							X
Kirsten S. Hofmocker						X	X
Hope C. Humphries							X
Oscar Iribarne							X
Virginia L. Jin							X
Adam Kay						X	X
Kevin P Kirkman						X	X
Julia A. Klein						X	X
Johannes M. H. Knops						X	X
Kimberly J. La Pierre						X	X
Laura M. Ladwig							X
John G. Lambrinos							X
Andrew DB Leakey						X	X
Qi Li							X
Wei Li							X
Rebecca McCulley						X	X
Brett Melbourne							X
Charles Mitchell						X	X
Joslin L. Moore						X	X
John Morgan						X	X
Brent Mortensen						X	X
Lydia R. O'Halloran				X			X
Meelis Pärtel						X	X
Jesús Pascual							X
David Pyke						X	X
Anita C. Risch						X	X
Roberto Salguero-Gómez						X	X
Mahesh Sankaran							X
Martin Schuetz						X	X
Anna Simonsen							X
Melinda Smith							X
Carly Stevens						X	X
Lauren Sullivan						X	X
Glenda M. Wardle							X
Elizabeth M. Wolkovich						X	X
Peter D. Wragg						X	X
Justin Wright							X
Louie Yang						X	X