

Biodiversity, photosynthetic mode, and ecosystem services differ between native and novel ecosystems

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Abstract Human activities have caused non-native plant species with novel ecological interactions to persist on landscapes, and it remains controversial whether these species alter multiple aspects of communities and ecosystems. We tested whether native and exotic grasslands differ in species diversity, ecosystem services, and an important aspect of functional diversity ($C_3:C_4$ proportions) by sampling 42 sites along a latitudinal gradient and conducting a controlled experiment. Exotic-dominated grasslands had drastically lower plant diversity and slightly higher tissue N concentrations and forage quality compared to native-dominated sites. Exotic sites were strongly dominated by C_4 species at southern and C_3 species at northern latitudes with a sharp transition at $36\text{--}38^\circ$, whereas native sites contained $C_3:C_4$ mixtures. Large differences in $C_3:C_4$ proportions and temporal niche partitioning were found between

native and exotic mixtures in the experiment, implying that differences in $C_3:C_4$ proportions along the latitudinal gradient are caused partially by species themselves. Our results indicate that the replacement of native- by exotic-dominated grasslands has created a management tradeoff (high diversity versus high levels of certain ecosystem services) and that models of global change impacts and C_3/C_4 distribution should consider effects of exotic species.

Keywords Exotic species · Invasive species · C_3 photosynthesis · C_4 photosynthesis · $C_4:C_3$ proportions

Introduction

Human alteration of ecosystems is causing exotic-dominated plant communities, consisting of recently assembled non-native species with potentially novel ecological interactions, to persist on nearly one-third of the Earth's terrestrial surface (Hobbs et al. 2006; Kulmatiski 2006; Ellis 2011; Wilsey et al. 2011). Community- and ecosystem-level

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consequences of single exotic species invasions have been well studied (e.g., Vitousek 1990; Levine et al. 2003; Vilà et al. 2011; Pyšek et al. 2012). For example, Vilà et al. (2011) concluded from their meta-analysis that on average, single exotic species invasions result in decreased plant diversity, but that ecosystem processes can increase, decrease, or remain unchanged. In many systems, however, multiple species have been introduced, and they could have greater collective impacts than would be supposed from studying individual species.

The impacts of multiple interacting exotic species on community and ecosystem processes have only recently been considered (e.g., Wilsey et al. 2009, 2011; Mascaro et al. 2012). Wilsey et al. (2009, 2011) and Isbell and Wilsey (2011a) found in common garden experiments that diversity declined to a lower level in exotic-species communities than paired native communities. This decline did not consistently lead to reduced biomass production (Wilsey et al. 2011; Isbell and Wilsey 2011b). Multiple species invasions in forests of Hawaii, however, have resulted in more diverse exotic-dominated sites with increased productivity compared to native-dominated sites (Mascaro et al. 2012). Thus, over broad spatial scales, where identities and abundances of multiple exotics vary across landscapes, the effects of many exotic species could accumulate to have community- and ecosystem-level effects that are important to biodiversity conservation, ecosystem functioning, and management of ecosystem services.

Functional diversity of plant communities is an important index of ecosystem functioning. For example, plant species with the C_3 versus C_4 mode of photosynthesis differ in many ways, including temperature growth optima, water and N use efficiency, and C uptake, all of which can greatly affect element cycling and seasonal patterns of maximum growth (e.g., Teeri and Stowe 1976; Ode et al. 1980; Monson and Williams 1982; Tieszen et al. 1997; Sage and Monson 1999). Having a mixture of C_3 and C_4 species is an important functional aspect of diverse communities that often accounts for increased productivity with richness (Tilman et al. 1997). The proportion of C_4 species in the community can alter other community-level traits such as tissue C:N ratios (Sage and Monson 1999) which influence decomposition rates and the timing of growth to affect higher trophic levels. Information on C_3 : C_4 proportions also is important to predictions of climate change effects on community structure. For example, simulation models based on the correlation between climate and C_3 and C_4 abundances in native-dominated communities predict that warming will favor C_4 over C_3 grass species in rangelands of North and South America (Epstein et al. 2002). The proportion of C_3 biomass increases linearly with latitude in native-dominated systems (e.g., Epstein et al. 1997), but it is largely unknown

how this relationship changes in the now more common situation of exotic species dominance.

Here, we extend earlier work to test for differences in diversity, including an important aspect of functional diversity (C_3 : C_4 proportions), and relationships between diversity and ecosystem services between exotic- and native-dominated grasslands. We tested for differences along a latitudinal gradient and in an ongoing companion experiment. The long-term, controlled experiment (see Wilsey et al. 2009, 2011) allowed us to test whether any differences in functional diversity could be at least partially due to species themselves rather than to co-varying factors. We measured multiple aspects of communities and ecosystems that are considered to be important to diversity and ecosystem services (“the benefits people receive from ecosystems”) in grasslands and rangelands (e.g., Millennium Ecosystem Assessment 2005; Doll et al. 2009; Potts et al. 2010; Isbell et al. 2011). We sampled plant species richness and diversity, C_3 : C_4 proportions, aboveground net primary productivity (ANPP), multiple aspects of forage quality to herbivores including N concentration, and potential pollinator (bee) abundances, richness, and diversity at all native and exotic sites (e.g., Millennium Ecosystem Assessment et al. 2005; Doll et al. 2009; Potts et al. 2010). We hereafter refer to plant diversity and all other measures collectively as “diversity and ecosystem services” for simplicity. This is because, although not all of these measures are direct measures of final ecosystem services (e.g., Mace et al. 2012), the ability to simultaneously manage all of these measures at high levels would be desirable for meeting goals of biodiversity conservation and provisioning of ecosystem services (Daily 1997; Nelson et al. 2009; Zaveleta et al. 2010; Isbell et al. 2011; Mace et al. 2012).

Trade-offs among management decisions could occur if exotic-dominated systems have lower levels of plant diversity or some ecosystem services but higher levels of others compared to native systems (Tallis et al. 2008; Nelson et al. 2009). Specifically, we tested whether (1) plant diversity was lower and C_3 : C_4 proportions differed in exotic than native grasslands across the latitudinal gradient, and (2) whether any differences in diversity between native and exotic grasslands were associated with differences in the ecosystem services. We predicted that diversity would be lower in exotic-dominated systems, consistent with the decline in diversity observed in experimental communities of exotic compared to native species (Wilsey et al. 2009, 2011; Isbell and Wilsey 2011a), and that diversity declines would be associated with an increase in productivity and, possibly, other ecosystem service levels that could lead to management trade-offs (Rout and Callaway 2009). For example, most exotic plant species of grasslands were intentionally introduced by humans, often in order to increase forage production and quality for livestock (Mack

and Lonsdale 2001). Consequently, ecosystems may be impacted according to the species traits involved with their introduction (Liao et al. 2008; van Kleunen et al. 2010). Finally, we used data from experimental communities to test the prediction that exotic species themselves (and not co-varying factors) alter functional diversity.

Materials and methods

Latitudinal gradient

Site selection

We sampled 21 native- and 21 exotic-dominated ($n = 21$) grasslands of differing species composition from Minnesota to central Texas throughout the tallgrass prairie region, USA in 2010 and 2011. Sites were owned by a variety of private or public organizations. Point-intercept sampling of random locations within each site (described below) confirmed that all selected grasslands were either exotic or native dominated (see “Results”). Native and exotic sites had various land-use histories such as previous haying, grazing, or burning. No exotic sites were purposefully being managed for high exotic proportions to our knowledge. Native sites were never plowed, while exotic sites were previously plowed, previously unplowed but invaded, or owners/managers were uncertain of long-term land-use histories. To minimize impacts of uncontrolled variables on native-exotic comparisons, we used the following criteria for selecting sites. Sites were included if: (1) they were dominated by native or exotic species; (2) for each native site, an exotic-dominated site was in the same geologic region and was located at approximately the same latitude; (3) the site was not plowed within the last 7 years (for exotics only, natives were never plowed); (4) sites were not grazed or hayed the year of sampling. Other possible native grassland sites were excluded from our study if we could not locate an exotic match based on area or other factors mentioned above. Sites were constrained longitudinally to enable comparisons across latitude and one exotic and one native site was sampled per day. Exotic and native sites at a given latitude were separated by 0.6- to 26-km distance (mean 8 km) and sites ranged in size from 1.4 to 17.6 ha (mean 6.5 ha) and 1.1–55.8 ha (mean 11 ha), respectively.

Diversity and ecosystem services

We measured variables that are important to diversity and ecosystem services in grasslands and rangelands, including plant species richness and diversity (Mace et al. 2012), $C_3:C_4$ proportions, aboveground productivity, multiple aspects of forage quality, and bee (i.e., potential pollinator)

abundances, species richness, and diversity (Millennium Ecosystem Assessment et al. 2005). Sampling took place at peak biomass for native grasslands in the area. Plant species abundances at each site were sampled using a point-intercept method, results of which are highly correlated with biomass [mean r^2 across 35 species = 0.89, in Wilsey et al. (2011) experiment]. Thus, all relative abundance data are considered to be relative biomass estimates. The method consisted of dropping 1-m-long pins perpendicular to the ground at each outside corner of a 20×50 -cm frame in 25 randomly sampled locations (totaling 100 pin drops per site), and counting the number of pin hits per species. Species were designated as either native or exotic using national references when possible (49 % of species) (Flora of North America 1993), and regional references for the rest (Great Plains Flora Association 1986; Gleason and Cronquist 1991; Eilers and Roosa 1994; Diggs et al. 1999; Yatskievych 2006). We were unable to identify 3 % of species to C_3 or C_4 status and 5 % of species to native or exotic status based on the available plant material, and these were removed from proportion C_3 and proportion exotic variables, respectively. Species within the genera *Carex* and *Melilotus* were combined due to difficulty of verifying species in the field. Proportion of exotic biomass at each site was calculated as the number of exotic species hits divided by total number of hits.

Diversity and ecosystem services were measured at each site and multiple samples were averaged within sites (the unit of observation) to avoid pseudoreplication. Species richness was measured as the total number of species hit by pins at each site, and Simpson’s diversity ($1/D$) was estimated by aggregating all point-intercept data into one site-level measurement. Peak aboveground biomass (g/m^2) was sampled by clipping five randomly placed 20×50 -cm quadrats, drying plant material at $65^\circ C$ for 48 h and weighing dried biomass. Live and standing dead material was combined in each quadrat to obtain an estimate of net primary productivity. Standing dead was assumed to be produced during the current growing season, so by adding it to peak biomass, we were able to come up with a more complete estimate of NPP than peak biomass alone (Scurlock et al. 2002). Forage quality was assessed by measuring C:N ratios, crude protein ($N \times 6.25$), and two different aspects of digestibility from subsamples of dried, green biomass from clipped plots. C and N content was measured by homogenizing green biomass from each plot, grinding 2 g of a random subsample from each plot using a model 2601 Pica Blender Mill (Cianflone Scientific Instruments, Pittsburgh, PA), weighing 15–20 mg of each ground sample using an Orion Cahn C-33 microbalance (Thermo Electron, Beverly, MA), and analyzing the subsample of ground material using a Flash EA 1112 Elemental Analyzer (Thermo Finnigan Italia, Rodano, Italy) with

atropine as standards. Digestibility was assessed by measuring acid detergent fiber (ADF), which measures relative cellulose and lignin content of plant material (Sensenig et al. 2010) and neutral detergent fiber (NDF), which measures ADF plus hemicellulose. Subsamples from two randomly selected biomass plots from each site were sent to AgSource Laboratories, Bonduel, Wisconsin, for digestibility analyses. All digestibility estimates are expressed on a 100 % dry matter basis. Proportion of C₃ biomass per site was assessed by dividing the number of C₃ hits by the total number of hits. Species were designated as C₃ or C₄ using Waller and Lewis (1979) and Sage and Monson (1999).

Bees were sampled at each site using a pan trapping technique, where eight each of blue, white, and yellow 3.25-oz. Solo brand cups (24 total) were randomly placed in an opening in the canopy 5 m apart in a 120-m-long straight transect in the middle of each site and filled with a mixture of water and Dawn dish soap (Westphal et al. 2008). Blue and yellow pan traps were painted with a mixture of blue or yellow fluorescent paint and Silica Flat Paint (Guerra Paint and Pigment, New York). Average and total number of hours pan traps were deployed in native and exotic sites were comparable (mean 6.5 h in native and 6.7 h in exotic, total 136 h in native and 140 h in exotic). Bees were sampled at one native and one exotic site during each day to eliminate biases associated with weather conditions. All specimens were stored in 70 % ethanol, and were then dried, pinned, and identified to the lowest taxonomic level possible using the Discover Life key (Ascher and Pickering 2012) or to morphospecies if species identification was not possible. Some species from the genus *Lasioglossum* were potentially combined within sites if morphospecies could not be identified. All bees captured at a site were combined to generate one site-level estimate. Bee abundances were the number of total bees captured at a site, taxonomic richness was the number of taxa identified at a site, and taxonomic diversity was estimated using $1/D$ at each site.

Soil and topography covariates

Although there were variables such as historical grazing intensity that we were unable to take into account statistically, we did test whether results changed after taking into account soil variables. Soil variables included percent sand, silt, and clay, soil pH, percent slope, and cation exchange capacity (CEC), estimated using the SSURGO Soils Database (SSURGO 2012). Each soil variable in our analysis represents an area-weighted average for the site calculated by multiplying values for each soil type (i.e., SSURGO Soil Map Unit, data extracted using Soil Data Viewer 6.0 in ArcGIS 10) by the proportion of the site area occupied by the soil type. These values were then averaged to obtain

one site value per soil variable. Data were missing for one site, so 10-cm soil cores were taken in each biomass plot, homogenized, and analyzed for soil texture instead. Because values of some soil variables were correlated, we conducted a principal components analysis on all soil variables and used the principal component scores from the first two axes, which explained 74 % of the variation in soils, as covariates in analyses. Percent clay and CEC were highly correlated with each other and negatively correlated with percent sand on the first axis, and percent slope and percent silt loaded heavily on the second axis. We tested whether soil variables differed between native and exotic sites by using the first and second principal component axes as covariates in all analyses of covariance (ANCOVA) and multivariate ANCOVA (MANCOVA).

Statistical analyses

We used MANCOVA and ANCOVA to assess whether exotic sites differed from native sites ($n = 21$). Response variables in the MANCOVA included plant diversity, plant species richness, net primary productivity, ADF, NDF, crude protein, and C:N ratios. Explanatory variables included the first and second soil principal component scores as covariates, as well as latitude, origin and latitude by origin interactions. Multivariate data did not deviate from multivariate normal ($W = 0.98$, $P = 0.59$). We then tested for management tradeoffs by comparing the signs of percent change for measured variables between native and exotic grasslands (Tallis et al. 2008). Site area was added as an additional covariate to the univariate test of differences in plant species richness between exotic and native sites. Data were \ln transformed when necessary to improve normality (C:N ratios) in both multivariate and univariate analysis. All analyses were conducted in SAS 9.2 using the Proc GLM procedure and type I SS, and significance was assigned at the $\alpha = 0.05$ level (Littell et al. 2004). Untransformed least-squared means are reported, and percentage change was measured between native and exotic grassland means. Since plant material with higher values of ADF is less digestible, and plant material with higher values of NDF occupies more space in the rumen, thus lowering dry matter intake of cattle, we calculated percent change in digestibility and dry matter intake as percent change in ADF and NDF, respectively, multiplied by -1 in order to represent an increase in those variables in exotic-dominated sites. We fit a linear regression and a logistic, four-parameter regression to the relationship between latitude and proportion of C₃ biomass for native- and exotic-dominated sites, respectively.

Bee variables were analyzed separately due to higher numbers of zero and singleton values and high variability relative to means. Bee variables can exhibit high variability

among sampling dates, with lower numbers of bees found early and late in the growing season due to lower floral resources. To account for variability associated with sampling date of pollinators, we included linear and quadratic Julian day (sampling day) terms as additional covariates in pollinator analyses. We used PROC GENMOD in SAS 9.2 to analyze the bee abundance and richness data with a generalized linear model using a negative binomial error distribution and log-link function (Winfrey and Kremen 2009), and the same explanatory variables as the other tests. Simpson's diversity could not be calculated for sites with zero values, which reduced the number of sites by 12 (exotic $n = 18$, native $n = 12$) for analysis of bee diversity. Bee diversity was then analyzed using a generalized linear model in PROC GENMOD with a Poisson distribution and the log-link function. Untransformed least-squared means are reported.

Experiment

Any differences in species and functional diversity or ecosystem services between native and exotic grasslands along the latitudinal gradient could result from variation in environmental factors not accounted for by covariates in analysis, or from variation among species themselves (species identity or interactions). We tested for the potential contributions of species identities/interactions to native–exotic differences in functional diversity ($C_3:C_4$ proportions) using data from an ongoing experiment with all native and all exotic communities grown under a common environment in Temple, Texas (Maintenance of Exotic vs. Native Diversity experiment) (Wilsey et al. 2011). We interpret data of no difference in $C_3:C_4$ proportion between experimental communities of native vs. exotic species as evidence that native/exotic differences in functional diversity along the latitudinal gradient resulted from environmental differences alone. Alternatively, we interpret differences in $C_3:C_4$ proportion between experimental communities of exotic and native species as evidence that native/exotic differences in functional diversity along the latitudinal gradient resulted partly from species themselves.

For the experiment, we established 64 mixtures using equal-sized transplants (biomass $P > 0.1$ g at planting) planted into 1×1 -m plots in two blocks in October 2007 or March 2008. Plots were assigned to have either all native or all exotic (origin) species crossed with summer irrigation (128 mm from 15 July to 15 August of each year vs. no irrigation; ambient precipitation was not excluded from any of the plots) treatments using a factorial treatment arrangement. Each mixture was planted with 72 equal-sized plants of nine species with identical functional group proportions (i.e., ten plants of each of four C_4 grass species, eight of one C_3 grass, and six of three C_3 forbs and

one C_3 legume), and species diversity (Online Resource 2; see Wilsey et al. 2011 for more details). Functional group proportions were designed to match native dominated sites in the area. Native–exotic plots were established so that species were paired phylogenetically and by growth form using a species pool of 18 native and 18 exotic species (Online Resource 2, all species were perennials). Thus, for every native plot, a plot of phylogenetically paired exotic species was established that was initially equivalent in species richness, diversity and proportion of C_3 biomass. This allowed us to test whether native and exotic communities diverged over time under equivalent environmental conditions, which would be consistent with the hypothesis that species can drive differences. Species composition within each treatment was replicated by using random draws of species (four draws within each of the two temporal blocks) to increase generality. There were two replicates of each draw per treatment, for a total of 2 origin \times 2 irrigation \times 4 draws \times 2 blocks \times 2 replicates = 64 in total. Irrigation treatments were designed to add 10–15 % extra precipitation in the summer to mimic predictions of global climate models (Wilsey et al. 2011). Proportion of C_3 biomass was estimated in June (except 2011) and October of each year using a point-intercept method and abundance values were converted to biomass estimates with regression equations. Species diversity was previously found to decline in exotic-dominated experimental communities (Wilsey et al. 2009, 2011). See Wilsey et al. (2011) for further details.

Statistical analysis

We analyzed the proportion of C_3 biomass with mixed model repeated measures ANOVA (PROC MIXED in SAS) and type III SS (Littell et al. 2004). Origin and irrigation were fixed effects, and draw was considered a random term nested within block. Repeated measures used an AR(1) covariance structure. Proportion C_3 biomass was logit [$\log(y/1-y)$] transformed before analysis, with the minimum value added to the numerator and denominator.

Results

We found management tradeoffs between plant species diversity and ecosystem services (Tallis et al. 2008), wherein exotic-dominated grasslands had much lower levels of diversity but higher or similar levels of ecosystem services (Fig. 1a; Table 1). Point-intercept sampling confirmed the native–exotic status of grasslands: native sites ranged from 0 to 30 % exotic biomass and exotic sites ranged from 68 to 100 % exotic biomass. We found that exotic- and native-dominated grasslands differed in diversity and multiple ecosystem services [MANCOVA, origin,

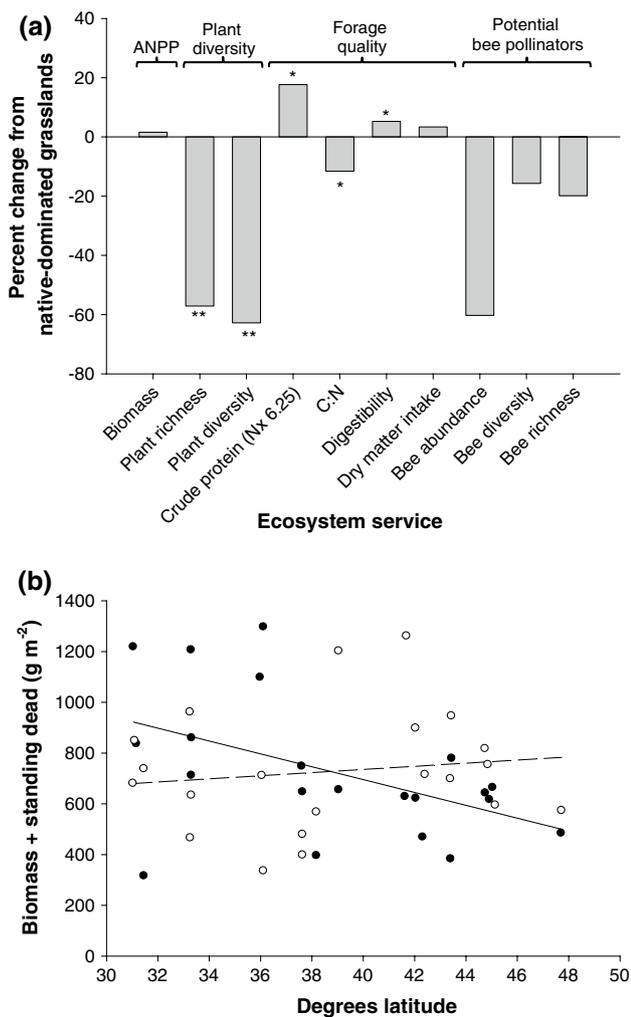


Fig. 1 Diversity and ecosystem services in exotic- and native-dominated grasslands. **a** Percent change in means of diversity and multiple ecosystem services from native-dominated to exotic-dominated grassland across a latitudinal gradient in the tallgrass prairie region, USA ($n = 21$). The line at zero represents no difference; bars above zero represent an increase and bars below zero represent a decrease in a particular service in exotic- compared to native-dominated grasslands. Significant differences between native and exotic conditions are denoted by asterisks (** $P < 0.001$, * $P < 0.05$). **b** Aboveground net primary productivity (ANPP; biomass + standing dead) was higher in exotic grasslands at lower latitudes and lower in exotic sites at higher latitudes [exotic (closed circles, solid line); native (open circles, dashed line)] (origin \times latitude interaction, $F_{1,36} = 4.06$, $P = 0.05$, $n = 21$)

Wilk's lambda (W) = 0.16, $F_{7,30} = 22.05$, $P < 0.001$; origin \times latitude, $W = 0.69$, $F_{7,30} = 1.91$, $P = 0.1$). Tests for soil differences between exotic and native grasslands confirmed that soil and topography did not differ between grassland types [MANCOVA, origin, Wilk's lambda (W) = 0.95, $F_{2,37} = 0.89$, $P = 0.42$; origin \times latitude, $W = 0.99$, $F_{2,37} = 0.20$, $P = 0.82$]. Thus, the differences between native and exotic sites were highly

significant whether or not soil variables were included as covariates. Overall, a slightly higher level of tissue N concentration and forage quality was countered by drastically lower levels of plant species richness and diversity in exotic grasslands (exotic vs. native means ± 1 SEM, plant richness 13.2 ± 1.4 vs. 30.8 ± 1.4 species; plant diversity 2.5 ± 0.4 vs. 6.8 ± 0.4 ; crude protein 7.3 ± 0.3 vs. 6.2 ± 0.3 %; C:N 39.6 ± 2.2 vs. 44.8 ± 2.2 ; ADF 38.1 ± 0.7 vs. 40.2 ± 0.7 %; NDF 60.7 ± 1.0 vs. 62.8 ± 1.0 %) (Fig. 1a). Richness significantly increased with grassland area (Table 1). ANPP differences between native- and exotic-dominated systems changed with latitude despite no difference overall (means, NPP exotic 733.1 ± 54.9 , native 721.7 ± 54.9 g m⁻² year⁻¹) (Fig. 1a, b; Table 1). No significant differences in potential pollinator variables were detected despite higher averages in native sites (exotic vs. native means ± 1 SEM, bee abundance 4.3 ± 4.1 vs. 10.9 ± 4.1 bees; richness 1.9 ± 0.6 vs. 2.4 species ± 0.6 ; diversity 1.9 ± 0.3 vs. 2.2 ± 0.3) (Fig. 1a; Table 2).

We found profoundly different proportions of C₃ and C₄ biomass between native and exotic grasslands across the latitudinal gradient and in the experiment. Although species diversity was related to proportion of C₃ biomass (Online Resource 1), native/exotic differences in proportion C₃ biomass across the gradient were significant regardless of whether or not linear and quadratic species diversity terms were included as covariates in ANCOVA (latitude \times origin $F_{1,35} = 12.6$, $P = 0.001$ with diversity; $F_{1,36} = 12.4$, $P = 0.001$ without diversity as covariates). The proportion of C₃ biomass increased linearly with latitude across native sites as expected [$r^2 = 0.29$, $P = 0.01$, $y = -0.20 + 0.02(\text{latitude})$] (Fig. 2). However, exotic sites were better modeled with a logistic rather than linear regression, with strong dominance by C₄ species biomass at southern latitudes, and C₃ species biomass at northern latitudes with a sharp transition at 36–38° (logistic regression, $P < 0.001$, $y = 0.06 + \{0.91/[1 + (\text{latitude}/37.3)^{-78.8}]\}$) when two C₃-dominated sites at ~33° latitude were removed ($P < 0.001$, $y = 0.26 + \{0.69/[1 + (\text{latitude}/37.5)^{-108.6}]\}$ when those points were not removed) (Fig. 2). The fit (r^2 -values) for exotic sites went from 0.77 with linear regression to 0.95 with logistic regression (0.59 to 0.68 when outliers were not removed).

Proportion of biomass from C₃ species dropped to much lower levels in experimental communities established as all exotic compared to all native species (Fig. 3). The lower proportion of C₃ species biomass in experimental exotic communities is consistent with field results at this latitude (Fig. 2). Native communities had significantly higher proportions of C₃ biomass than exotic communities on all sampling dates (origin, $F_{1,7} = 68.5$, $P < 0.001$, $n = 32$), and differences were larger during the June

Table 1 Analysis of covariance results (*F/P*-values) for tests of differences between native and exotic sites and interactions with latitude for each ecosystem service

Source	<i>df</i>	NPP	Plant diversity		Forage quality			
		ANPP	Simpson's diversity	Richness	C:N	Crude protein	ADF	NDF
PC1	1	2.0/0.17	1.5/0.23	2.3/0.14	1.1/0.31	1.1/0.30	1.8/0.19	0.8/0.38
PC2	1	0.1/0.82	4.9/0.03	15.9/<0.01	1.1/0.29	1.7/0.20	2.6/0.11	0.8/0.38
(Area)	(1)			12.7/<0.01				
Latitude	1	0.8/0.39	0.5/0.47	0.17/0.69	0.7/0.42	0.0/0.84	0.3/0.60	8.7/<0.01
Origin	1	0.0/0.9	52.5/<0.01	67.5/<0.01	5.2/0.03	6.1/0.02	4.9/0.03	2.0/0.16
Latitude × origin	1	4.1/0.05	0.01/0.92	3.1/0.09	2.7/0.11	2.2/0.15	0.3/0.59	4.7/0.04
Error	36 (35 ^a)							

Principal component 1 (*PC1*) and *PC2* covariates are the first and second PC axes explaining 74 % of the variation in soil and topography across sites. Area (*in parenthesis*) was used as a covariate only for plant species richness; all other analyses did not include area as a covariate. Values significant at the $\alpha \leq 0.05$ level are in *italic*

NPP Net primary productivity, *ANPP* aboveground NPP, *ADF* acid detergent fiber, *NDF* neutral detergent fiber

^a Plant richness error *df* = 35; all other error *df* = 36

Table 2 Generalized linear model results (χ^2/P -values) for tests of differences between native and exotic sites and interactions with latitude for potential pollinator (bee) variables

Source	<i>df</i>	Abundance	Simpson's diversity	Richness
PC1	1	3.1/0.08	3.3/0.07	3.3/0.07
PC2	1	0.5/0.48	5.8/0.02	5.1/0.02
Julian day	1	0.0/0.98	0.1/0.81	1.2/0.27
Julian day quadratic	1	7.6/0.01	0.0/0.95	2.7/0.10
Latitude	1	6.1/0.01	0.1/0.82	0.2/0.65
Origin	1	0.1/0.72	0.5/0.49	0.0/0.84
Latitude × Origin	1	2.1/0.15	0.7/0.41	2.4/0.11
Error	34 (22 ^a)			

PC1 and *PC2* covariates represent the first and second PC axes explaining 74 % of the variation in soil and topography across sites. Julian day represents sampling day of the year. Values significant at the $\alpha \leq 0.05$ level are in *italic*

^a Diversity error *df* = 22; all other error *df* = 34

sampling periods (time × origin, $F_{7,450} = 18.8, P < 0.001$). Thus, the difference between exotic and native communities was greatest during sampling dates early in the growing season when *C*₃ species were most prominent. In native communities, there was a seasonal shift between *C*₃ and *C*₄ species dominance, indicative of temporal niche partitioning (Fig. 3; also see Wilsey et al. 2011). This seasonal *C*₃–*C*₄ shift was missing in exotic communities, which showed a decline and then a relatively flat level of *C*₃ biomass. Irrigation did not significantly alter *C*₃ proportions (irrigation $F_{1,7} = 1.0, P = 0.34$, irrigation × time, $F_{7,450} = 0.7, P = 0.64$), nor did it interact with origin

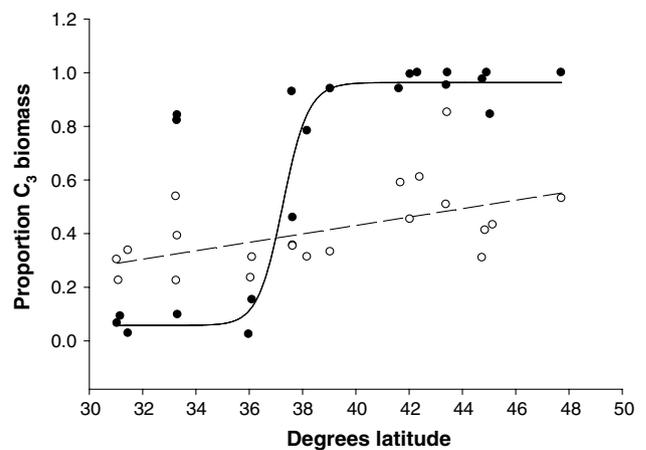


Fig. 2 Proportion of aboveground biomass from plants with the *C*₃ mode of photosynthesis (1–*C*₄ biomass) in exotic- (*closed circles*, *solid line*) and native-dominated (*open circles*, *dashed line*) grasslands across a latitudinal gradient in the tallgrass prairie region, USA. Proportion of *C*₃ biomass increased linearly across native-dominated sites [$r^2 = 0.29, P = 0.01, y = -0.20 + 0.02(\text{latitude})$]. Exotic sites exhibited very strong *C*₄ dominance at southern latitudes, and very strong *C*₃ dominance at northern latitudes (logistic regression, $r^2 = 0.95, P < 0.001, y = 0.06 + \{0.91/[1 + (\text{latitude}/37.3)^{-78.8}]\}$ when two *C*₃-dominated sites at ~33° latitude were removed; $r^2 = 0.68, P < 0.001$ when those points were not removed)

(irrigation × origin, $F_{1,7} = 3.4, P = 0.11$, irrigation × origin × time, $F_{7,450} = 0.85, P = 0.55$).

Discussion

Ecosystem-level impacts of novel ecosystems have rarely been assessed at broad scales (but see Mascaro et al. 2012). Our results indicate that replacement of native- by

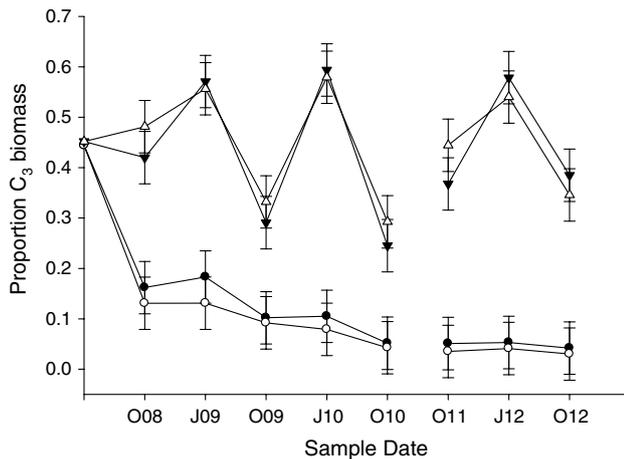


Fig. 3 Proportion of aboveground biomass from plants with the C₃ mode of photosynthesis in experimental plots in central Texas over five growing seasons. Sampling was conducted in June (J) and October (O) of each year, but not in June 2011. Plots were planted with equal-sized transplants with either all native or all exotic perennial species using a paired-species approach, and plots were irrigated in the summer (128 mm) to mimic altered climate or were exposed to ambient precipitation [exotic irrigated (*closed circles*), exotic non-irrigated (*open circles*), native irrigated (*closed triangles*), native non-irrigated (*open triangles*)]

exotic-dominated systems in the tallgrass prairie region of the U.S. is associated with a tradeoff in the relationship between species diversity and ecosystem services, with lower diversity but enhanced or similar ecosystem services in exotic sites. The altered latitudinal gradient in C₃/C₄ proportions in exotic grasslands also implies a shift in functional diversity. Although sites had varying legacy effects that are not fully controlled in an observational study, results imply that exotic grasslands did not have consistently lower productivities and had enhanced tissue N and forage quality, presumably qualities for which many exotic species were selected on introduction (Mack and Lonsdale 2001). This occurred despite lower species and functional diversity in exotic grasslands. We were unable to test for differences in attributes of all ecosystem services in the experiment due to small plot sizes [but see Wilsey et al. (2011) for diversity-productivity relationships], but when environmental effects were controlled in the experiment, exotic communities exhibited vastly altered C₃/C₄ proportions (this study) and reduced complementarity and temporal niche partitioning (Wilsey et al. 2009, 2011). Strong dominance by species with a single photosynthetic type greatly reduced the amount of species turnover observed within the growing season in exotic communities. Thus, our experimental results are consistent with the view that the differences in C₃:C₄ proportions observed between native and exotic grasslands are at least partially caused by species themselves (see also Isbell and Wilsey 2011b; Wilsey et al. 2011).

Plant species richness and diversity were consistently lower in exotic-dominated sites across the latitudinal gradient, but productivity was not. These results emphasize two important points. First, previous analyses found that adding exotic species increased species diversity at broad scales (e.g., Ellis et al. 2012), but even with an additional 40 exotic species, site-level grassland richness and diversity were 57 and 63 % lower, respectively, in exotic than native sites. Diversity and richness also were 46 and 35 % lower in exotic than native experimental communities at low latitude (Wilsey et al. 2011) and richness was 15 % lower in exotic communities at high latitudes (Isbell and Wilsey 2011a), consistent with the trend observed along the latitudinal gradient. Highly diverse native grasslands therefore have been replaced by exotic grasslands dominated by fewer species and, hence, with lower species evenness (Wilsey et al. 2005). Second, reduced richness in exotic grasslands did not consistently lead to reductions in primary productivity at the spatial scale of measurements (but see Chalcraft et al. 2004), contrary to the prediction from biodiversity-ecosystem functioning theory (Hooper et al. 2005; Isbell et al. 2011; Mascaro et al. 2012). If dominant exotic species that are especially productive overyield in species mixtures, then diversity declines due to exotics may not be associated with productivity declines (Wilsey et al. 2009).

Our results contrast those from a study of tropical forests in Hawaii, and may be dependent on the types and number of ecosystem services that we measured. Mascaro et al. (2012) found that both local diversity and primary productivity were higher in exotic-dominated forests. The consistent trend between our study and that of Mascaro et al. (2012) is that diversity differed between native and novel systems, albeit in a different direction. Zavaleta et al. (2010) and Isbell et al. (2011) found that including a greater number of ecosystem measures and environmental contexts increased the proportion of species that were deemed to be significant, so we may have found a greater number of trade-offs had we utilized a larger number of ecosystem services. There are also several ecosystem services that remain to be fully explored. Insect herbivores and predators (Tallamy et al. 2010) as well as other animals in addition to bees should be compared between native and exotic grasslands in future studies.

We expected that native-dominated grasslands would have higher abundances and diversity of bee pollinators, but this trend was not significant. We hypothesize that either (1) perennial grasslands in general are important habitats to bees (Morandin et al. 2007); (2) bee species turnover is great during a season, which limited our ability to detect differences; (3) soils (i.e., covariates) are better predictors of bees than exotic-native status (Table 2); or (4) overwhelming trends in pollinator declines across broad scales in highly fragmented landscapes such as the tallgrass

prairie (Samson and Knopf 1994) have limited detectability of differences between native and exotic sites.

Perhaps the most significant finding from this study is that the replacement of native- by exotic-dominated grasslands strongly impacted an important measure of functional diversity—the proportion of C_3 and C_4 species biomass. Our experimental results imply that differences in C_3 : C_4 proportions seen in the latitudinal study could at least partially be caused by exotic species themselves rather than by unaccounted for co-varying factors (e.g., disturbances or fertility levels). Thus, our results imply that native–exotic status can contribute to differences in C_3 : C_4 proportions beyond environmental and topographic differences found in other studies (e.g., Barnes et al. 1983). The large decrease in contribution of C_3 species to experimental exotic communities resulted from strong dominance by C_4 grass species. The strong dominance by either C_3 or C_4 species in exotic grasslands in the latitudinal study implies that, like the experimental communities, exotic communities may lack functional diversity and complementary resource use that underlies diversity–productivity and diversity–stability relationships (Wilsey et al. 2009; Isbell et al. 2011; Martin et al., unpublished data). The extremely strong dominance by a single photosynthetic type and the sharp transition in dominant photosynthetic mode that we observed in exotic communities has not been previously documented along a latitudinal gradient [but see Rundel (1978) for a shift along an elevational gradient]. One explanation for the transition could be that there were large differences in C_3 / C_4 status of species that were introduced at lower versus higher latitudes. Past introductions could have targeted C_3 species in the north, and C_4 species in the south. Consistent with this, Isbell and Wilsey (2011a) found that C_3 species and not C_4 grasses were overyielders in a common garden study in the Northern Plains. Establishing exotic versus native common garden experiments at multiple sites along latitudinal gradients would help to address mechanisms associated with shifts to a dominant photosynthetic mode.

Biodiversity loss is sometimes considered a component of global change (Isbell et al. 2011; Reich et al. 2012). Our results imply that loss of natives and additions of exotics to landscapes have fundamentally altered grassland attributes at regional scales (Wardle et al. 2011; Barnosky et al. 2012). In particular, additions of multiple exotic species into grassland systems in the Great Plains have resulted in greatly decreased site-level diversity, and altered latitudinal trends in C_3 : C_4 proportions and productivity. Models of C_3 / C_4 distribution (e.g., Epstein et al. 1997; Tieszen et al. 1997; von Fischer et al. 2008; Edwards et al. 2010) should be revisited to account for effects associated with exotic species dominance. This will be important when predicting responses of vegetation to climate change, feedbacks to element cycles and climate (e.g., Collatz et al. 1998; Sala

et al. 2000), anthropogenic alteration of $^{13}\text{C}/^{12}\text{C}$ ratios in plant and animal remains (Edwards et al. 2010; Ellis 2011), and phenology (Wilsey et al. 2011; Fridley 2012). Based on this, we maintain that native–exotic status of grasslands should figure prominently in future projections.

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