Research article

Biodiversity, phenology and temporal niche differences between native- and novel exotic-dominated grasslands

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ABSTRACT

Many exotic species have been introduced or have escaped into grasslands where they form 'novel ecosystems' of species with no evolutionary history of interaction. Novel ecosystems are good model systems for understanding how diversity maintenance mechanisms might differ between species with a history of interaction (natives) and species without a history (exotics) in cases where exotics originated from several continents. We tested for lower species diversity and richness in exotic grasslands and found a negative correlation between species diversity measures and proportion of exotic species across 15 grasslands in an observational study in Texas. We then planted 9-species mixtures of all native or all exotics under ambient or elevated summer precipitation to compare dynamics of diversity and to test if exotic species respond more strongly to altered resource availability. Species diversity was lower in communities of exotic than native species by the second year. Reduced diversity in exotic communities resulted from lower complementarity and higher temporal niche overlap among species and occurred in both ambient and irrigated plots. In general, summer irrigation had additive positive effects and did not interact with native–exotic status. Exotic species and communities had much earlier green-up during spring than natives, and altered inter-correlations among phenology variables. There were no differences in flowering dates. Taken together, our results suggest that rapid and synchronous growth may increase niche overlap among exotic species and reduce local diversity in exotic-dominated grassland communities. Earlier green-up by exotics may complicate attempts to ascertain relationships between phenology and climate. An increase in exotic species may cause earlier green-up regardless of any climate change effects and our results suggest that phenology networks should take a species-based rather than an ecosystem approach to evaluate green-up if the abundance of exotics increases within the time-frame in question. These differences between native and exotic species and communities should be considered in future management and restoration projects.

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Introduction

Earth is now a human dominated planet, and anthropogenic influences are expected to increase in importance (Vitousek et al., 1997). Accompanying this human-mediated disturbance has been an unprecedented introduction and planting of exotic ('non-native' or 'alien') species. Although most research on exotic species has focused on case studies of single species, exotic species often are numerous (Vitousek, 1994; Hobbs et al., 2006; MacDougall and Turkington, 2005; Gurevitch and Padilla, 2004; Sax et al., 2002; Maron and Marler, 2008). For example, exotic plant species

increased from 150 to approximately 1000 in California, USA from 1900 to 1990 (Rejmánek and Randall, 1994). Most exotic plant species were intentionally introduced as ornamentals, for forage and erosion control, or as food plants (Mack and Lonsdale, 2001; Grace et al., 2001; Weber, 2003; Knapp et al., 2010). These introductions have impacted large portions of the modern landscape (Thompson et al., 2001; Mack and Lonsdale, 2001; Herrick et al., 2010), often resulting in diversity declines (Christian and Wilson, 1999; Wilsey et al., 2009) and changes in ecosystem functioning (Ehrenfeld, 2003; Liao et al., 2008; Hejda et al., 2009; Rout and Callaway, 2009; Wardle et al., 2011). However, it is not known if differences between invaded and non-invaded sites are caused solely by exotic species because they do not colonize randomly and are more common in areas with high levels of resources and disturbance (Stohlgren et al., 1999). This has led some to hypothesize that exotics are 'passengers' with diversity changes rather than 'drivers' of changes (MacDougall and Turkington, 2005; Sax et al.,

2002). It is important to conduct studies that compare native and exotic communities under common environments (as we do here) to help to tease apart the relative importance of the passenger and driver models (Agrawal and Kotanen, 2003).

Communities dominated by exotics are considered to be 'novel systems' (e.g. Hobbs et al., 2006) because they contain species from a variety of regions that do not have an evolutionary history of interaction. Novel ecosystems are common in agricultural areas and in suburban/urban areas where human impacts are high. Novel ecosystems are predicted to become more common in the future as (1) exotic species spread into or replace native systems and (2) species move at different rates due to climate change. Both of these scenarios will produce conditions where species interactions are between evolutionarily naïve species with no natural analog. Species interactions among evolutionarily naïve species may be fundamentally different from interactions among native species that have a longer history of interacting (Wilsey et al., 2009; Isbell and Wilsey, 2011).

Key traits that affect species interactions, such as growth rate, timing of growth and reproduction (phenology), and response to variable resource availability may differ between native and exotic species (e.g. Willis et al., 2010; Pan et al., 2010). This could result in functional differences between exotic- and native-dominated ecosystems that could influence how they respond to climate change. Daehler (2003) reviewed studies that found that exotic species showed a more plastic response to altered resource availability than natives, which suggests that they might respond differently to climate change. Willis et al. (2010) found that non-native species shifted their flowering phenology more to changes in climate than native species around Walden pond. A better understanding of if and when there are functional differences between natives and exotics will lead to improvements in global climate change models in situations where the proportion of the landscape that is exotic-dominated is increasing over time.

Global climate change has multiple aspects such as elevated atmospheric CO_2, increased temperature, N-deposition, land-use change and altered precipitation amounts and frequencies (Weltzin et al., 2003). Aspects such as elevated CO_2 have been studied much more intensively than other aspects such as altered precipitation regimes (Williams et al., 1998; Knapp et al., 2002; Weltzin et al., 2003; Miranda et al., 2009; Volder et al., 2010). Importantly, models vary in their predictions about precipitation regimes across regions. For example, the Hadley and Canadian models both predict that warming-induced evaporation in the summer will lead to drier soils in the central Great Plains but they predict much wetter (Hadley model) and slightly wetter (Canadian model) soils in the southern Great Plains (US National Assessment Synthesis Team of the US Global Research Program, 2000; Weltzin et al., 2003). In support of this prediction, precipitation increased by ~10% over the 20th century in the southern tallgrass prairie region (Karl and Knight, 1998). Summer increases in precipitation in the southern Plains are due to predicted increases in tropical storm activity (Allan and Soden, 2008). These changes in precipitation may have important impacts on grassland productivity and species diversity, and these impacts may differ between native- and exotic-dominated grasslands. Thus, we need to develop a general understanding of how precipitation affects biodiversity and ecosystem processes at both global and regional scales.

Species diversity can be maintained by equalizing or stabilizing interactions (Chesson, 2000). Equalizing forces maintain diversity by minimizing fitness differences among species (Chesson, 2000), and this is predicted to maintain diversity by reducing asymmetrical competition between species (Isbell et al., 2009). Stabilizing forces maximize negative intraspecific interactions relative to negative interspecific interactions (Chesson, 2000; Harpole

and Suding, 2007; Levine and HilleRisLambers, 2009; Isbell et al., 2009). Diversity can be stabilized by reducing negative interspecific interactions via reduced niche overlap while keeping intraspecific competition constant. For example, there are important differences between plant species with different modes of photosynthesis, with C_4 species being active at higher temperatures than C_3 species (Sage and Monson, 1998). These differences may reduce overlap in optimal growing periods within a growing season, leading to asynchrony in growth among species, lowered interspecific competition, a greater complementarity effect (Loreau and Hector, 2001), and higher species diversity. We predict that there will be reduced niche overlap in native communities than in comparable exotic communities (Wilsey et al., 2009). Furthermore, if interspecific competition is responsible for species loss, then summer irrigation should lead to more asymmetrical competitive exclusion by dominant exotic C_4 grasses, thus leading to an even greater drop in species diversity in exotic than native grassland plots. Our objective was to test hypotheses that (1) species diversity will be maintained at a higher level in native than exotic plant communities and (2) differences in diversity between exotic and native communities result from differences in species interactions and temporal niche overlap, and (3) exotic communities will have stronger responses to a summer irrigation treatment than native communities due to increased resource availability.

Methods

The work was conducted in the Blackland Prairie region of Texas where growing seasons are long and grasslands contain exotic species from multiple locations around the globe (Africa, Asia, South America, Europe, Table 1). Thus, theory can be tested within a realistic time-frame with a set of species that has a history of interaction (natives) and a set that does not (exotics). We tested hypotheses with data from: (1) observational data from surveys of 15 grassland sites and (2) a controlled experiment in which we compared dynamics of diversity in planted 9-species mixtures of all native or all exotic grassland species. Mixtures ($n = 64$) were established with equal functional group proportions using a paired species approach that controlled for phylogeny and growth form between pairs of native and exotic species. Origin (native vs. exotic) was crossed with summer irrigation treatments (Allan and Soden, 2008), and replication was achieved using multiple draws from a species pool of 36 species and with true replicates. All species were also grown in monoculture with and without summer irrigation. Note that all species used were 'invasive' based on the definition of Richardson et al. (2000) (reproductive populations > 100 m from parent); but we use the term 'exotic' rather than 'invasive' in this paper because some of the exotic species are economically beneficial (e.g. Cynodon dactylon).

Study sites

About 98% of the Blackland Prairie region was cultivated during the latter part of the 19th and early part of the 20th centuries. Now, roughly 50% of the area is used as cropland, with much of the rest returning to rangeland and oldfields dominated by a variety of mostly exotic species (Diggs et al., 1999; Polley et al., 2005). Approximately 2% of the area exists as unplowed remnants weakly dominated by Schizachyrium scoparium, Sorghastrum nutans, and a large number of other grasses and forbs (Polley et al., 2005). The site receives 878 mm of precipitation per year in a bimodal pattern with a large peak in the spring and a smaller peak in the fall (Temple weather station). Soils are Vertisol usterts.

Table 1
List of species used in the experiment. All species are already present in the Texas flora (Diggs et al., 1999). Nine-species plots were planted with random draws from the following list of C_4 grasses, C_3 grasses, C_3 forbs, and C_3 leguminous forbs, with all functional groups represented in each plot. Exotic and native species were paired based on phylogeny (Supplemental Fig. 3) and growth form. Only four C_3 grass species were used due to their paucity in the system.

Exotic species	Family	Origin	Native species pair
C_4 grasses			
1. *Bothriochloa ischaemum*[a,b,f]	Poacae	Asia	*Schizachyrium scoparium*[b,d,e]
2. *Cynodon dactylon*[a]	Poacae	Africa	*Buchloe dactyloides*[a]
3. *Eragrostis curvula*[f]	Poacae	Africa	*Sporobolus asper*[a,b]
4. *Panicum coloratum*[f]	Poacae	Africa	*Panicum virgatum* (short ecotype)[d]
5. *Paspalum dilatatum*[a]	Poacae	South America	*Eriochloa sericea*[d]
6. *Sorghum halapense*[a,b]	Poacae	Mediterranean	*Sorghastrum nutans*[a,b,d]
C_3 grasses			
7. *Dactylus glomerata*[f]	Poacae	Europe	*Nasella luecotricha*[a]
8. *Festuca arundinacea*[f]	Poacae	Europe	*Elymus canadensis*[d,e]
C_3 forbs			
9. *Leucanthemum vulgare*[f]	Asteraceae	Eurasia	*Ratibida columnifera*[d,e]
10. *Taraxacum officinale*[a]	Asteraceae	Europe	*Marshallia caespitosa*[g]
11. *Cichorium intybus*[f]	Asteraceae	Eurasia	*Vernonia baldwinii*[d,g]
12. *Nepata cataria*[f]	Lamiaceae	Eurasia	*Salvia azurea*[b,d]
13. *Ruellia brittoniana*[g]	Acanthaceae	Mexico	*Ruellia humilis*[f]
14. *Marrubium vulgare*[f,g]	Lamiaceae	Eurasia	*Monarda fistulosa*[d,g]
C_3 Leguminous forbs			
15. *Lotus corniculatus*[f]	Fabaceae	Eurasia	*Dalea purpurea*[c,d]
16. *Trifolium repens*[f]	Fabaceae	Europe	*Dalea candidum*[d]
17. *Medicago sativa*[f]	Fabaceae	Asia	*Desmanthus illinoensis*[d]
18. *Coronilla varia*[f]	Fabaceae	Mediterranean	*Astragalus canadensis*[f]

[a] Propagule source: field collected vegetative.
[b] Propagule source: field collected seed.
[c] Propagule source: 'Wildseed Farms' seed.
[d] Propagule source: 'Native American Seed Co.' seed.
[e] Propagule source: field collected seed from 'Sweet Briar Nursery'.
[f] Propagule source: other company seed.
[g] Propagule source: other company, vegetative.

Observational study

To test the hypothesis that species diversity and richness are greater in native than exotic communities, we sampled 15 sites (fields) in the region in July 2009. Sites were selected to include locations with a variety of past and current land uses, such as formerly plowed, formerly grazed and never plowed, and currently grazed or mowed with a similar climate and geological history (Supplement Table 1). We sampled diversity by dropping a pin vertically through the vegetation at 30–100 locations per site, with the number of points proportional to the size of the area and with all pin drops being at least 10 m apart. Locations were determined by walking systematically through the fields and tossing the pin to random locations. All hits were noted so that point intercept data would correspond strongly with biomass. Simpson's diversity ($1/\sum p_i^2$, where p_i is hits per species$_i$/total hits) was estimated at the site level. We used this diversity measure because it (1) takes into account species dominance, and a key question is whether exotics achieve higher dominance than natives and (2) saturates with sample size more quickly than other diversity measures. Species richness was estimated with rarefaction techniques (Ecosim; Gotelli and Entsminger, 2009) to compare sites at a common sample size.

Experimental study

The significant correlations that we found in the observational study (see "Results" section) could have been due to covarying factors unrelated to the exotic-native status of species present. We used data from a controlled experiment to test whether species themselves are important in explaining diversity differences between native and exotic grasslands. The study is the second MEND (Maintenance of Exotic vs. Native Diversity) experiment, and this new experiment differs from the experiment by

Wilsey et al. (2009) by including (1) irrigation treatments and two planting dates to assess effects over a wide range of environmental conditions and (2) measurements of several variables that directly address mechanisms. Our approach was to plant equal-mass transplants at a common density (72 individuals/m^2) of either all native or all exotic species, and then to compare responses over time. Plant locations for all species were randomized separately in each plot. There was no significant difference in biomass among species at planting ($n = 216$, 3 plants per species per block, origin, $P > 0.67$, grand mean 0.7 g plant^{-1}, SE = 0.07). Exotic and native species were planted in monocultures and in 9-species mixtures in a way that pairs species according to their phylogeny (Table 1) and growth form. We used a large pool of exotic and native species (Table 1), most of which are widely distributed in North America. This approach effectively compares native and exotic species and communities while keeping soil type, disturbance rate, and phylogeny controlled.

A two-way factorial treatment arrangement (irrigation × origin) was applied to plots with a randomized block design, using random draws to vary species composition. Plots were established in two blocks, one planted in October 2007 and one planted in March 2008. Blocks were planted at different times because the timing of planting was assumed to differentially affect relative biomass production of C_3 vs. C_4 species and hence, broader inferences can be made about treatment effects. Replication of mixtures within blocks was at both the species draw (composition) and true replicate levels. Draws were created by randomly sampling nine species from a pool of 18 native or 18 exotic species while keeping functional group relative abundance constant, with selection of a native species always being matched with its exotic pair (Table 1 and Supplemental Fig. 1). Four draws were included within each of the two blocks, and two replicates of each draw and treatment level were included for a total of 32 mixtures per block and 64 total (2 blocks × 4 draws [block] × 2 origin levels × 2 irrigation levels × 2

replicates). In each plot, we planted 10 plants of each of four C_4 grass species (each grass species equally abundant), 8 plants of one C_3 grass species, and 6 plants of each of four C_3 forb species (one legume, three non-legumes, all equally abundant). This gives a realistic proportion of each functional group based on previous work in the intact system (Wilsey and Polley, 2003; Polley et al., 2005). The plants for the study came from seed and vegetative propagules that were either hand-collected or purchased from local seed companies, with only local genotypes being used for the native species (Table 1). It is important to note that all the exotic species are already present in the region, and thus, no new exotics were introduced. Transplants established well during the establishment phase, with close to 100% survival observed by May 2008 (personal observations). Volunteer plants (i.e. weeds) were hand removed when necessary, usually once per month. Alley-ways between plots were seeded with the medium-statured grass *Bouteloua curtipendula* and were mowed two-three times per growing season to prevent alley-way plants from overtopping study plots.

Irrigated plots were hand watered from mid-July to mid-August at a rate of 128 mm per month in 8 increments of 16 mm beginning in 2008. Preliminary testing of our technique indicated no lateral water flow across our flat field. Soil cores (5-cm depth) from irrigated plots (mean of 21, 23 and 31% water content in 2008–2010, respectively) had consistently higher soil moisture than those from control plots (mean of 7, 12 and 26% water content in 2008–2010, respectively). Sampling to depth found that differences occurred to at least 45 cm deep. Irrigation was during the summer to match predictions from global change models that predict increased rainfall in summer months (Allan and Soden, 2008). By adding water only in summer, we also reduced the bimodal nature of rainfall, which makes our results from irrigated plots more typical of regions with unimodal precipitation patterns. In some studies, exotic species have responded more to resource pulses (Daehler, 2003) which has led to a general prediction that exotic species will respond more to global change than native species.

Rainfall was below average (878 mm) from October 2007 through September 2008 (631 mm), was average from October 2008 through September 2009 (786 mm), and was above average from October 2009 through September 2010 (1166 mm). Thus, the irrigation treatments eliminated the effects of drought in year 1 (631 and 759 mm in non-irrigated and irrigated plots, respectively), bracketed average values is year 2 (786 and 914 mm in non-irrigated and irrigated plots, respectively) and went well above average in year 3 (1166 and 1294 mm in non-irrigated and irrigated plots, respectively). Thus, sampling occurred over time periods that had both dry and wet conditions.

Biomass and species composition were determined twice per year (late June and October) in each plot with point intercept techniques. Point intercept was done by dropping pins vertically 25 times in a systematic fashion in the inner 90 cm × 90 cm portion of each plot, noting all plant hits. Pin drops were spaced 20 cm apart and were dropped in a 5 × 5 grid. All species were counted in each plot to determine species richness. Species that were present but not hit were given a value of 0.5 hits (Bowman et al., 2006; Yurkonis et al., 2010). This had a negligible effect on biomass or diversity when these very small relative abundance (p_i) and biomass values were summed with other species. Point intercept hits were converted to biomass (g/m^2) with regression equations based on concurrent point intercept sampling and biomass harvesting in October 2008. Relationships between number of hits and biomass were linear and were very strong across species (mean r^2 across 35 species was 0.89, range: 0.69–0.99, not including *Trifolium repens*, which went locally extinct during the first summer). We tested the accuracy of our technique by comparing estimates of whole-plot

biomass and Simpson's diversity to actual values from the concurrent harvests. In both cases, the relationship was strong between estimated and actual values, with correlation coefficients of 0.88 (biomass) and 0.89 (diversity), and similar means (biomass of 268 vs. 263, diversity of 2.99 vs. 2.90), and slopes close to one (1.05 for biomass and 1.03 for diversity).

To test for differential competitive exclusion between native–exotic treatments, we compared the species richness in the inner (3×3 grid of 9 pin drops with an area of 0.36 m²) and outer (16 pin drops along the perimeter of the plot with an area of 0.64 m²) portion of the plots during the 2009 growing season. The assumption behind this approach is that if plants are competing for resources (e.g. water and light), then the intensity of competition should be lower along the perimeter of the plots, and this should result in greater species richness. If other mechanisms such as pathogen or belowground herbivore attacks were solely responsible for differences, then we would not expect these factors to differentially impact the inner and outer portions of plots. The Menhinick's index of richness ($S/\sqrt{\text{area}}$) was used to compare inner and outer portions because it takes into account differences in area. The 2009 growing season was chosen because it encompassed the time period when diversity diverged significantly between treatments.

Green-up, frost damage, and temporal niche overlap (Cleland et al., 2006) were estimated in 2009 during the second year of the study. The date of first green-up was estimated by visiting all plots at least once per week and noting which species were dormant or emerging from dormancy. Green-up was noted only if the species remained green in subsequent weeks. Green-up data that were collected in 2008 in the first block had almost the exact same trends as 2009 (data not shown). Flowering (date of first flowering) and senescence (date when biomass was all brown) were assessed by visiting plots at least once per week. Length of growing season was calculated as senescence date – green-up date. Frost damage was determined by estimating the percent green and brown canopy cover before and after a major late frost on March 30, 2009, where frost damage = (green prefrost – green postfrost)/green prefrost. Temporal niche overlap was estimated by comparing relative species biomass (p = species biomass/total biomass) from point intercept sampling between June and October with the Bray–Curtis similarity measure: $BC = 1 - \left(\sum |p_{ij} - p_{io}/2| \right)$, where p_{ij} is a species relative abundance in June and p_{io} is a species relative abundance in October. Analyses used changes in diversity from June to October as a covariate to remove directional change due to increased rarity and local extinction. Thus, similarity values are indicative of temporal niche overlap that is statistically independent of directional changes in diversity.

We used a statistical approach to study species interactions in mixtures that involves comparing biomass production of each species in mixture to biomass of the species in monoculture. Intraspecific-interspecific competition ratios (stabilizing effects, Chesson, 2000) were calculated by comparing species performance in mixture to the expected performance values using monocultures, that is, the 'net biodiversity effect' (Loreau and Hector, 2001). Loreau and Hector (2001) developed a technique to partition the net biodiversity effect into a selection effect and a complementarity effect. We have found that this partition is useful in understanding diversity maintenance in earlier experiments (Wilsey et al., 2009; Isbell et al., 2009). The selection effect is the covariance between the relative yield of species in mixture and their biomass in monoculture ($S\,\text{cov}[\Delta RY, M]$), where S is the number of species, RY is relative yield, and M is monoculture biomass. Thus, when high biomass species overyield in mixture, the selection effect is positive. When low biomass species overyield in mixture, the

selection effect is negative. The complementarity effect addresses the mean relative yield ($S \times$ mean $\Delta RY \times$ mean M) by comparing species growth in mixture to expected values of the weighted average biomass of monocultures of component species (Loreau and Hector, 2001). We combined Fox's "trait independent" and "trait dependent" complementarity measures into one complementarity measure to standardize observed relative yields at one (Fox, 2005; Hector, 2006; Wacker et al., 2009). We call the "dominance" effect of Fox's tripartite partitioning the "selection" effect to remain consistent with other studies on this topic. The equalizing effect was approximated for each mixture by calculating the coefficient of variation (CV) of biomass across corresponding species monocultures for species in a particular plot (Isbell et al., 2009). Equal biomass among species would be expected to maintain high diversity by reducing asymmetrical competition (Keddy and Shipley, 1989). We conducted these analyses on end of years 1–2 data during the time period that diversity declined and when almost all monocultures had biomass >0. In the few instances where the monoculture had biomass of 0, we based calculations on the other species in the mixtures (Spehn et al., 2005).

Observational field data of diversity and proportion of natives/exotics were analyzed with Spearman's rank correlations. Experimental response variables were analyzed with mixed model ANOVA using PROC MIXED in SAS Version 9.2 (Littell et al., 2002). Species composition (draw [block]) and its interactions were random effects, and origin and irrigation treatments were fixed effects. Species diversity and richness were analyzed with repeated measures ANOVA using a first-order autoregressive AR(1) covariance structure, aboveground biomass used a first-order ante dependence covariance model ANTE(1). Green-up dates for mixtures were based on the mean across species in the plot; this value was ln-transformed to improve normality. Frost damage was not found in all plots and necessitated a non-parametric approach. Values were placed into 10% increments and analyzed to test whether origin or irrigation affected frost damage levels in separate contingency table analyses; significance was determined with Fisher's exact tests. Phenology measures of date of green-up, flowering, and senescence, and length of growing season were compared among treatments with the same ANOVA models as other variables above. Inter-correlations among these variables were compared between native and exotic species monocultures with PCA and factor analysis, interpreting principal components if eigenvalues >1.0. Irrigated and non-irrigated PCA's were very similar so that data were combined into two groups of natives vs. exotics.

Results

Observational study

Species diversity and richness decreased linearly with proportion of exotic species across grassland sites in the observational study (diversity $r_s = -0.89$, richness $r_s = -0.82$, $P < 0.001$, Fig. 1A and C). Sites that were plowed in the past contained communities that were 79–97% exotic with low diversity. Sites that were never plowed contained communities that were 74–99% native with high diversity. Two sites were formerly grazed by cattle, and contained a composite of exotic-invaded and non-invaded portions. When these sites were partitioned into invaded and non-invaded portions (resulting in four data points instead of two), invaded portions joined the low-diversity, exotic-dominated cluster and non-invaded portions joined the high diversity, native-dominated cluster (Fig. 1B). Thus, sites fell into two clusters, a group of
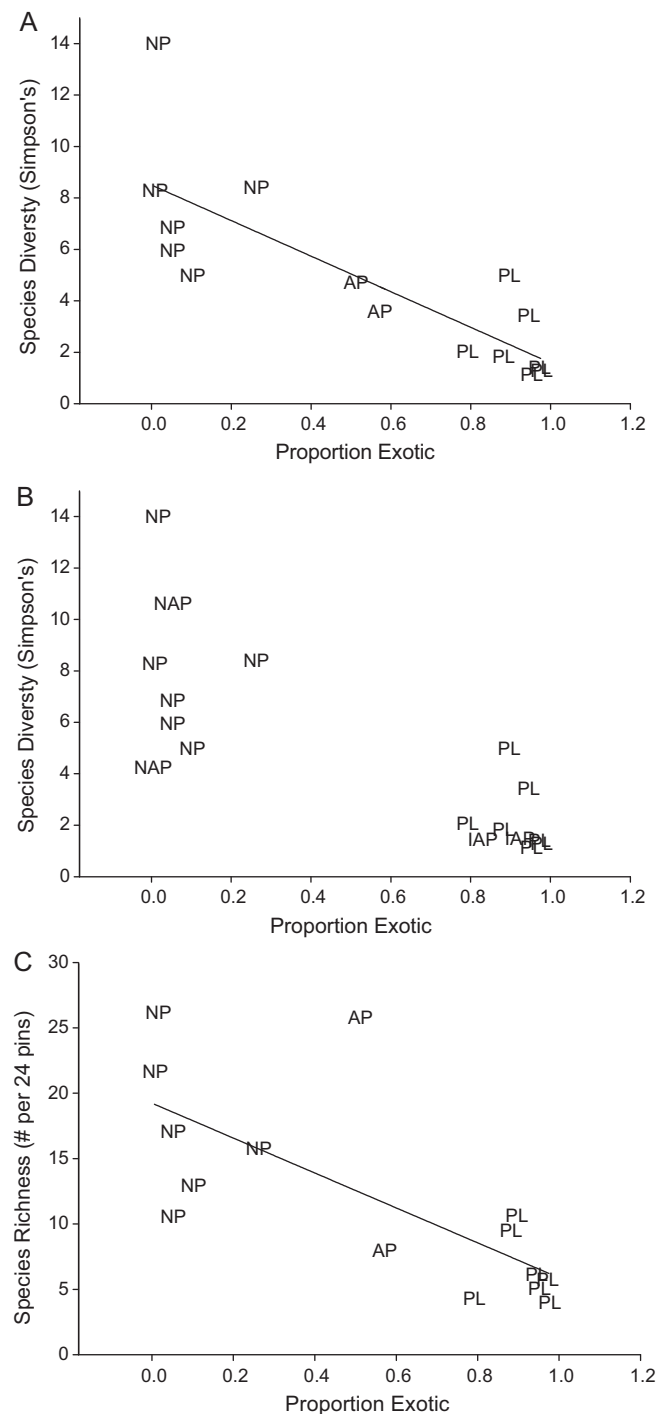

Fig. 1. Species diversity (A and B) and richness (C), and proportion of exotic species across grasslands in Central Texas that were never plowed (NP), formerly plowed (PL), abandoned pasture (AP), invaded abandoned pasture (IAP), and non-invaded abandoned pasture (NAP).

diverse native-dominated fields and a group of low diversity exotic-dominated fields.

Experimental study

Species diversity and richness

Exotic and native communities differed in species diversity measures by June of the second growing season (Fig. 2 and Table 2). Natives had a 32% greater species diversity and a 19% greater rich-
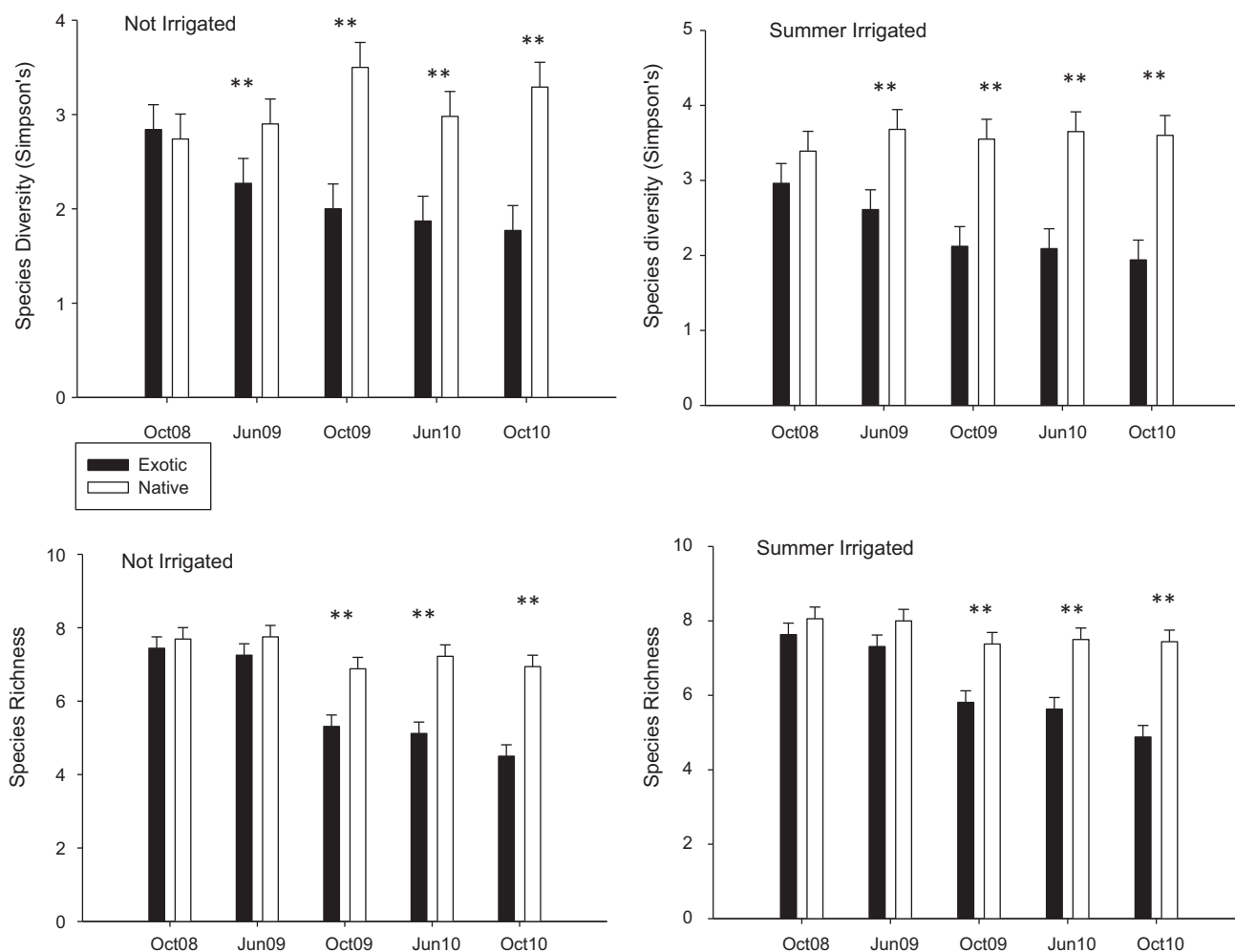
Fig. 2. Species diversity and richness (A–D, LS-means and SE) between native and exotic experimental communities with and without summer irrigation.

ness than exotic communities over the course of the experiment, and these differences grew in size as the study progressed, reaching 46% and 35% by the end of the study (i.e. after three full growing seasons). Summer irrigated plots had higher species diversity (mean of 2.96) and richness (mean of 6.96) than non-irrigated plots (diversity and richness means of 2.61 and 6.61, respectively), but irrigation did not alter differences between native and exotic communities (Table 2).

Native and exotic mixtures had different trends in species richness between the inner and outer portion of the plots. In native plots, richness was higher in the inner portion of the plots (ln difference measure of 0.167). In exotic plots, richness was higher in the outer perimeter of the plots (ln difference measure of −0.114). This difference between native and exotic plots was highly significant (origin $F_{1,7} = 11.0$, $P = 0.01$). No other terms in the ANOVA model were significant.

Aboveground biomass

Differences in diversity between native and exotic communities were not always associated with differences in aboveground biomass (Table 2 and Fig. 3A). Biomass was greater in exotic than native mixtures in late season sampling periods when C_4

Table 2

Mixed model ANOVA results (F-tests) from a field experiment that compared species diversity (Simpson's [1/D] and richness [S]), aboveground biomass, complementarity (Compl.) and selection (Sel.) effects and temporal niche measures (mean green-up date and temporal synchrony (Temp.) in biomass within the 2009 growing season) between exotic and native plots (Origin) that received summer irrigation or not (Irrig).

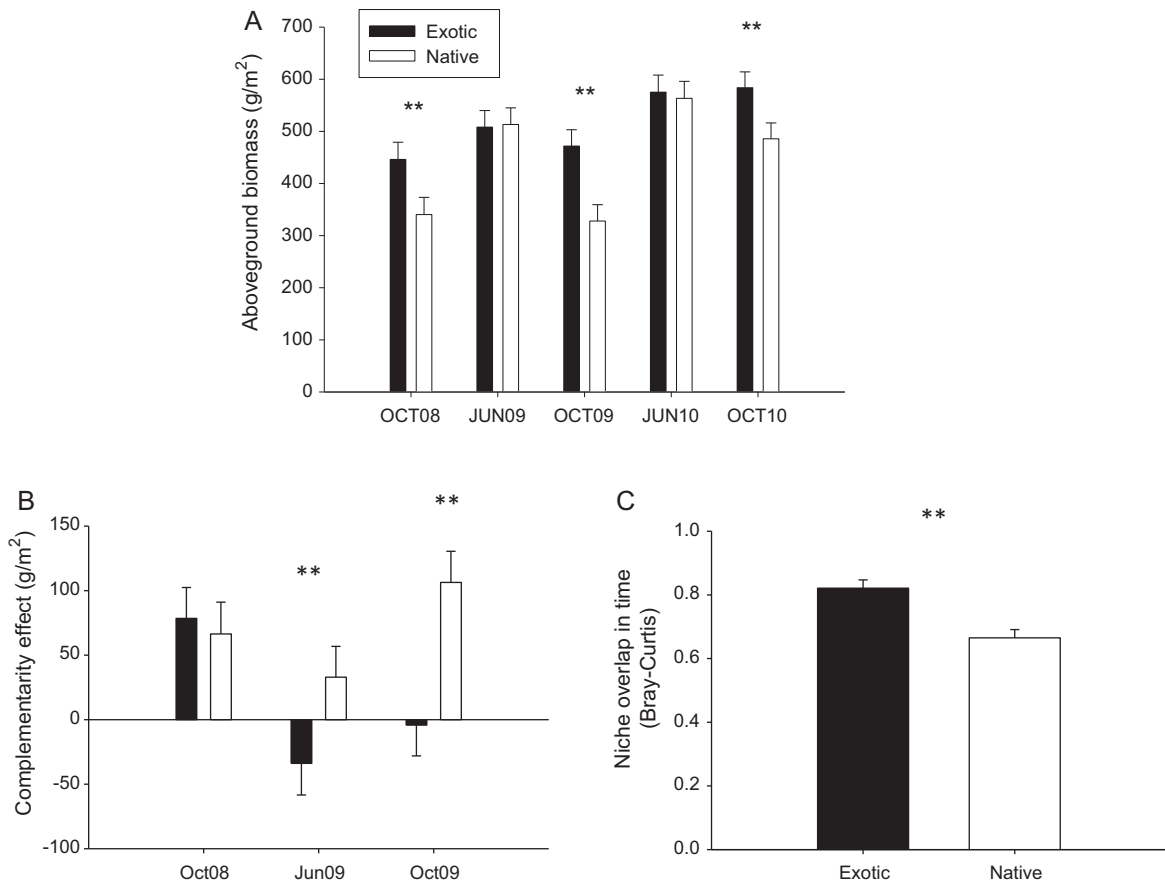| Source	df	1/D	S	Biomass	Compl.	Sel.	Green-up	Temp
Block								
Origin	1,7	21.8**	19.8**	7.6*	7.8**	1.3	87.3**	37.8**
Irrig	1,7	9.8*	8.4*	13.5*	0.5	0.1	0.4	1.4
O × I	1,7	1.9	0.1	1.5	1.2	0.6	0.1	0.6
Time	4,28	1.3	34.3**	20.6**	9.1**	4.3*		
Time × O	4,28	10.7**	22.6**	4.2**	5.1**	1.0		
Time × I	4,56	1.1	0.6	4.3*	2.6	2.2		
Time × O × I	4,56	0.5	0.3	1.1	1.5	1.5		

* <0.05.
** <0.01.

Fig. 3. Aboveground biomass (A) and complementarity effect (B) over time, and temporal niche overlap within the 2009 growing season (C, Bray–Curtis similarity between time periods) between native and exotic species and communities in experimental plots in central Texas (LS-means and SE).

grasses were prominent, but not during June of each year (Fig. 3A). Irrigation consistently increased aboveground biomass, and there was no interaction between origin and irrigation (Supplemental Fig. 2). Irrigated plots had 11% higher biomass on average (mean 482.5 g/m^2 over all time periods) than non-irrigated plots (mean 433.9 g/m^2).

Complementarity and selection effects

Higher diversity in native communities was associated with significantly higher complementarity (i.e. mean overyielding; Loreau and Hector, 2001, Fig. 3B and Table 2). Complementarity was greater by a factor of 69 in native than exotic communities (overall means of 32.6 g/m^2 for natives, 0.5 g/m^2 for exotics), and this difference between community types increased as the study progressed (Fig. 3B). Differences were consistent between irrigation regimes. The equalizing effect (CV_{mono}) and selection effect were not consistently different between natives and exotics (P values >0.37). Thus, higher diversity in native communities was most strongly associated with stabilizing effects that resulted because many species overyielded in mixture (i.e. had greater complementarity).

Temporal synchrony, phenological variables, and frost damage

Temporal synchrony, which is a measure of niche overlap, was 23% higher in exotic than native communities (Fig. 3C). Lower synchrony in native communities resulted from a seasonal shift in relative abundance of C_3 and C_4 species that was largely absent in exotic communities (functional group Bray–Curtis similarity: $F_{1,7} = 44.9$, $P < 0.001$). Irrigated (mean of

0.76) and non-irrigated plots (0.73) had similar synchrony rates.

Phenological patterns also differed between native and exotic plots (Fig. 4). Green-up occurred four weeks earlier in exotic than native mixtures ($P < 0.001$, Fig. 4A and Table 2), and three and a half weeks earlier in exotic monocultures ($F_{1,15} = 12.7$, $P < 0.001$, Fig. 4A). This trend was found in all draws (Fig. 4B), and in most species comparisons between natives and exotics (Fig. 4C). Differences in green-up between natives and exotics in 2008 were nearly identical to the differences in 2009 (data not shown). There was no significant interaction between irrigation and origin (native/exotic) for phenological variables (P values >0.4). Flowering data did not differ between natives and exotics.

Partly as a result of their earlier green-up, damage from a late-spring frost was greater for exotics than natives (Fig. 5, $P < 0.001$). The greater frost damage was found in both exotic monocultures and mixtures (Fig. 5).

Inter-relationships among phenology variables differed greatly between native and exotic communities (Fig. 6). In both cases, there were two principal components with eigenvalues >1.0. In native communities, flowering, green-up and senescence date were positively correlated and all three were negatively correlated with growing season length, which suggests that species that green-up early in the year also flowered and senesced early. The two components explained 51 and 33% of the total variance. These inter-correlations were altered in exotic communities (Fig. 6). The correlations were weak among variables in exotic species, and green-up date was largely uncorrelated with other variables. For example, the univariate correlation between green-up and flowering date, which was $r = 0.51$ in native species, was only $r = -0.11$
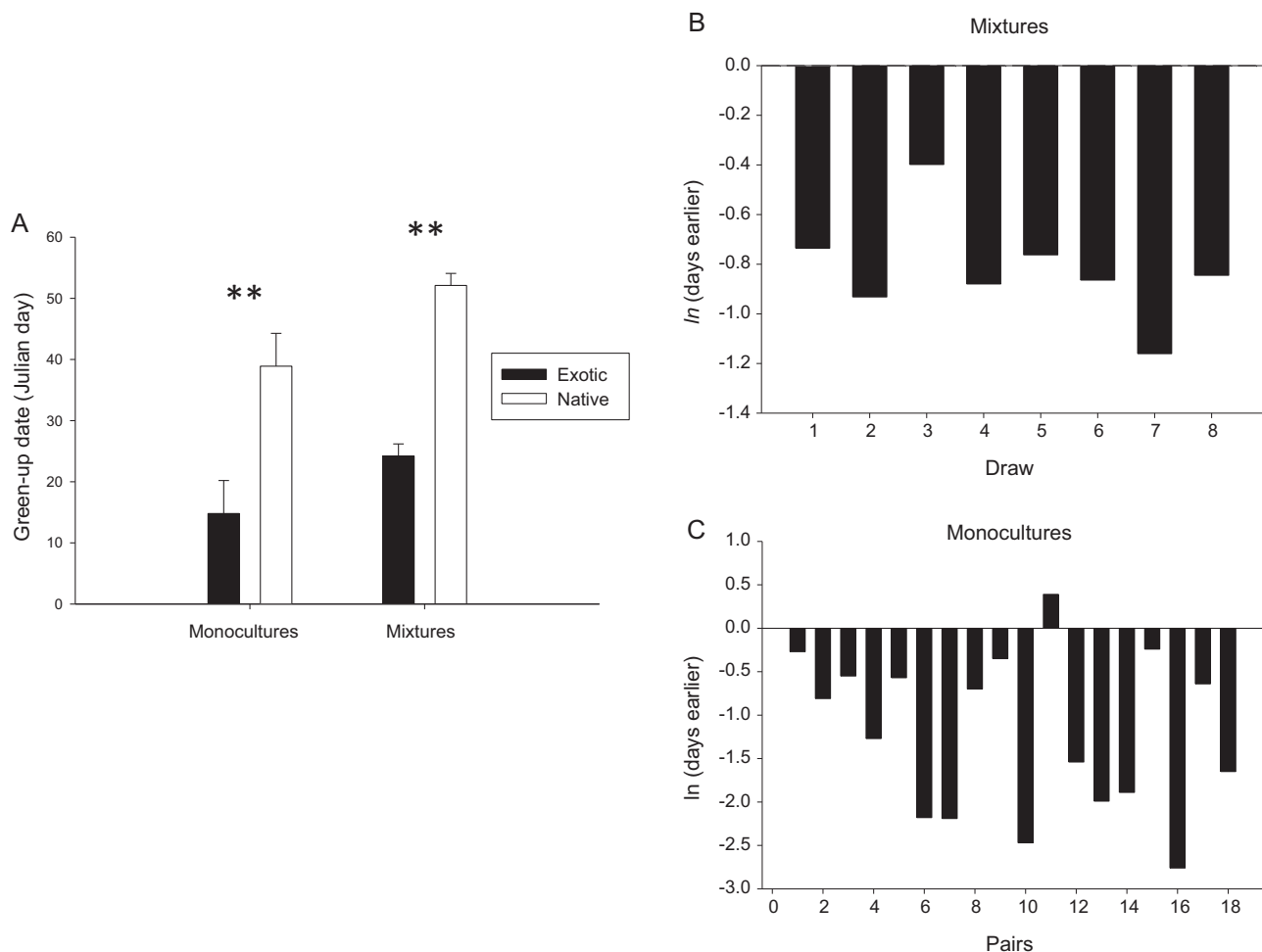
Fig. 4. Green-up date between native and exotic mixtures (A, LS-means and SEO, black bars are exotics and white are natives), and among mixture draws (differences between native and exotic pairs, B) and monocultures (C). See Table 1 for paired monoculture numbering.

in exotic species. The two principal components explained 48 and 26% of the total variance for exotics.

Discussion

We observed that species diversity was greater in native-dominated than exotic-dominated fields in central Texas, a trend similar to that reported elsewhere for invasions by *Agropyron crista-tum* (Christian and Wilson, 1999), *Imperata cylindrica* (Brewer, 2008), 13 invasive species in Europe (Hejda et al., 2009), *Melilotus officionale* (Dickson et al., 2010) and exotic C_3 grasses (Miles and Knops, 2010). Our observational data provide some support for the passenger model in that exotic species did not invade and drive down species diversity at all sites. Rather they had the greatest effects in formerly plowed (disturbed) areas. However, the difference that we observed between exotic and native communities in our experiment indicates that diversity decline was also due to the species themselves, which provides support for the driver model as well. Diversity was greater in native than exotic experimental communities grown under the same environmental conditions on a common soil type, and this result was consistent over two planting dates and two irrigation regimes. Thus, our results indicate that temporal niche overlap among exotic species can contribute to lower diversity when native systems are replaced by those dominated by exotic species. Community and species-level phenology

also differed between native and exotic species. Exotic communities greened up earlier in spring, suffered greater damage from a late spring frost, and had altered inter-correlations among phenology measures compared to natives. They also displayed greater dominance by C_4 grasses.

In an earlier study using separate plots, we found a similar difference in species diversity between native and exotic communities (Wilsey et al., 2009). Recent sampling has confirmed that differences persist through four field seasons (unpublished data). However, this earlier study did not include observational data, did not vary water availability, was initiated during a wetter than average year, and did not include measurements of temporal niches.

Here, we found that the native–exotic effect sizes were consistent across different water availability treatments and across years that differed in total precipitation. This suggests that the differences observed are likely to be robust. Rainfall amounts and patterns have been found to have significant effects on biomass and plant diversity of mesic grasslands (e.g. Grime et al., 2000; Knapp et al., 2002; Nippert and Knapp, 2007), and we also observed simple main effects from summer irrigation. Research on rainfall variability has found that subordinate species are more strongly affected by variability (Knapp et al., 2002) than dominant grass species (Williams et al., 1998; Fay et al., 2003). Irrigation during this especially dry part of the summer increased species richness primarily
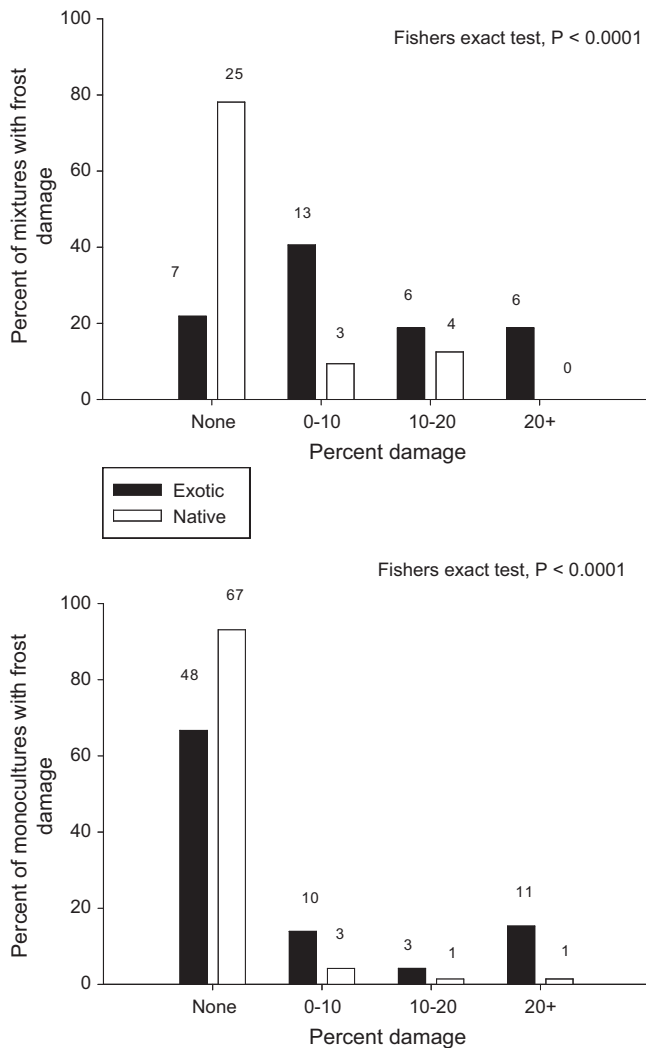
Fig. 5. Frost damage between native and exotic species and communities in experimental plots in central Texas (number of plots are denoted above histograms).

Fig. 6. Factor analysis loadings for phenology variables across exotic and native species monocultures.

by preventing the local extinction of subordinate species. However, our irrigation effects were smaller than native–exotic differences and irrigation and origin effects were additive.

Phenology

Scientists are attempting to estimate whether spring green-up and other phenological changes are occurring in response to global climate change (Betancourt et al., 2005; Cleland et al., 2007; Rich et al., 2008; Inouye, 2008; Miller-Rushing and Primack, 2008; Miranda et al., 2009; Morisette et al., 2009). Penuelas et al. (2002) and Von Holle et al. (2010) found that exotic and native species had similar flowering dates, a result that was consistent with our study. However, we found that exotics showed significant differences in green-up date compared to native species. The lack of interactions with irrigation suggests that differences are likely to be general. Exotics could have had earlier green-up because exotics that were preadapted to green up early were most successful during the establishment phase, they were human selected to green up early (e.g. during cultivar development), or they are still responding to cues from their native ranges. These mechanisms need to be tested in future studies. Regardless of the mechanisms involved, our results provide a warning to phenology researchers:
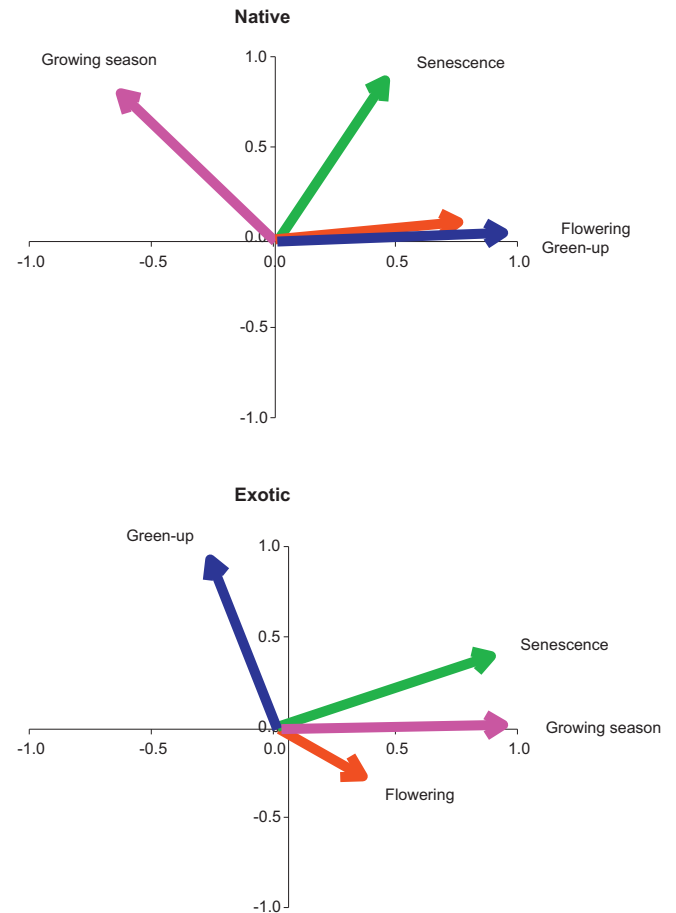
earlier green-up by exotics may complicate attempts to ascertain relationships between phenology and climate if the abundance of exotics increases within the time-frame in question. An increase in exotic species may cause earlier green-up regardless of any climate change effects. Our results suggest that phenology estimates should take a species-based approach rather than an ecosystem approach in areas where exotic species are increasing in abundance.

The altered inter-correlations in phenology variables between native and exotic species that we document are completely novel as far as we know and suggest that exotic communities are functioning differently than native communities. Native species had a very high correlation between green-up and flowering dates. This was not surprising as it means that species that green-up early tend to flower early and species that green-up late tend to flower late. What was surprising is that this correlation was missing across exotic species. Exotic species that greened-up early did not necessarily flower early, and species that greened-up late did not necessarily flower late. This difference among phenological variables between natives and exotics could be a result of human rather than natural selection on exotics. Most exotic species were intentionally introduced by humans (Mack and Lonsdale, 2001), and some of the forbs that we used were brought in as ornamentals (e.g. *Leucanthemum vulgare* and *Ruellia brittoniana*). Previously, we found that exotic C_4 grasses produce less root biomass at greater depths and had lower root allocation compared to native C_4 grasses under a common environment (Wilsey and Polley, 2006) suggesting that humans may have selected for lower root–shoot ratios in introduced grasses. This human selection hypothesis should be tested

with biogeographical comparisons of exotics in the introduced and ancestral range. Altered inter-correlations in exotic communities could be affecting pollinators and other animals (Godoy et al., 2009; Rafferty and Ives, 2011), and this should also be studied in the future.

The greater frost damage observed in exotic species suggests that there can be a cost associated with earlier green-up. This cost could be reduced in the future if late frosts become less frequent due to climate change. Nevertheless, it is important to point out that frost damage did not have lasting effects because biomass was greater for exotics than for natives by the end of each growing season (Fig. 3A).

Species diversity and richness

Species diversity and richness remained higher in native than exotic communities, and this difference was associated with higher complementarity and reduced temporal niche overlap (i.e. greater asynchrony in biomass production between time periods) among native plants. Species richness in year two was higher along the perimeter of the plots in exotic communities, suggesting that competition for light may have been responsible for richness declines (Grace, 1999; Hautier et al., 2009). Interestingly, this competitive effect was absent in native communities, and species richness was highest in the interior of the plots. This provides additional evidence that native and exotic species interactions differed in fundamental ways.

Our results also imply that species interactions, as indicated by yielding behavior and diversity maintenance mechanisms, differ fundamentally between presumably co-evolved natives and coevolutionarily naïve exotic species (Wilsey et al., 2009). Again, these differences were consistent across levels of summer water availability. Isbell and Wilsey (2011) found in an experiment in the northern Plains that native communities had a greater complementarity effect, a more negative selection effect, greater aboveground biomass, and different responses to grazing than comparable exotic communities. Here, we found that native–exotic diversity differences occurred both during periods when aboveground biomass was similar between community types and during time periods when biomass differed. These results suggest that observed native–exotic differences in diversity will not always be associated with concordant changes in biomass (Wilsey et al., 2009; Isbell and Wilsey, 2011).

Relationship to other studies

There are characteristics of our experimental study that are important to consider when making broader inferences about intact systems. In our experiment, we compared species diversity decline and ecosystem phenology under common environmental conditions in communities of all exotic to all native species in relatively small, weeded field plots (i.e. without outside invaders being allowed to persist). Our observational study (Fig. 1) and others (e.g. Tognetti et al., 2010) have found that intact communities vary from having all exotics to having various native/exotic proportions to having all natives, and our approach compared communities at the ends of the spectrum (i.e. all natives vs. all exotics). This made sense as a test of species interactions between native and novel communities. However, further work needs to be conducted on natives and exotics in various mixture combinations, and at key life stages (e.g. including seedling establishment, Yurkonis et al., 2005; Wardle et al., 2011) crossed with a variety of other predicted global climate changes (Marushia et al., 2010; Wolkovich and Cleland, 2011).

Studies of interactions in native–exotic mixtures have been done as well. A companion greenhouse study that varied tim-

ing of arrival, also using a paired species approach, found that three exotic species had stronger priority effects than three native species (Dickson, Hopwood and Wilsey, unpublished data). Schmidt et al. (2008) found that exotic *Bothriochloa* spp. outcompeted native grasses in a greenhouse experiment. A previous study with native–exotic mixtures in our study system found that a species-selection-effect driven decline in species diversity was associated ($r = 0.82$) with the proportion of exotic grass species in the mixture (Isbell et al., 2009). Finally, a seed addition experiment at our site with the additions of native and exotic species to exotic (*Bothriochloa ischaemum*) dominated fields found essentially no seedling establishment (unpublished data), results which were consistent with the low establishment seen in an earlier study by Wilsey and Polley (2003). Thus, differences between native and exotic communities appear to be fairly common whether exotics are mixed or kept separate from natives, and this suggests that we need research on the mechanisms behind these native–exotic differences, including more detailed study on how trait differences (Cadotte et al., 2008; Wardle et al., 2011) vary between native and exotic species.

Acknowledgements

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.ppees.2011.07.002.

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