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# Phenology differences between native and novel exotic-dominated grasslands rival the effects of climate change

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## Abstract

1. Novel ecosystems can differ from the native systems they replaced. We used phenology measures to compare ecosystem functioning between novel exotic-dominated and native-dominated grasslands in the central U.S.

2. Phenology, or timing of biological events, is affected by climate and land use changes. We assessed how phenology shifts are being altered by exotic species dominance by comparing remotely sensed Normalized Difference Vegetation Index within growing seasons at exotic- and native-dominated sites along a latitudinal gradient. Exotic species were dominated by the C3 species functional group in the north and the C4 species functional group in the south.

3. Date of senescence was an average of 36 days later in exotic than native-dominated grasslands, and this effect was consistent across latitudes.

4. Exotic-dominated grasslands greened-up an average of 10.7 days earlier than native-dominated grasslands, but this effect was highly dependent on latitude and the plant functional group that dominated at that latitude. Green-up differed between native and exotic sites the most in central and northern regions that had dominant C3 grasses.

5. We estimated the effects of an increase in global temperatures on green-up and senescence with a space-for-time substitution, and by comparing growing degree day differences between historical average temperatures and +2.5°C. Green-up was significantly earlier and senescence was significantly later with a 2.5°C increase in temperature. The native–exotic difference was significantly greater than the difference due to increased temperature for senescence, but not for green-up.

6. Synthesis and applications. Native to exotic plant conversions in central U.S. grasslands have led to highly altered phenology, especially in terms of senescence, and this effect should be considered along with global warming in models moving forward. This conversion will have to be considered in developing estimates of how global change will affect phenology in locations where exotics are present, especially in cases where their abundance is increasing concurrent with climate change. Global change models and policy should consider exotic species invasion as an additional widespread factor behind changes in phenology.

## Keywords

climate change, exotic-dominated, grasslands, invasive species, land use change, native ecosystems, novel ecosystems, phenology, senescence, tallgrass prairie

## Disciplines

Ecology and Evolutionary Biology | Environmental Sciences | Plant Sciences | Terrestrial and Aquatic Ecology

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# Phenology differences between native and novel exotic-dominated grasslands rival the effects of climate change

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## Abstract

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## KEYWORDS

climate change, exotic-dominated, grasslands, invasive species, land use change, native ecosystems, novel ecosystems, phenology, senescence, tallgrass prairie

## 1 | INTRODUCTION

Phenology is the timing of events within ecosystems such as spring green-up, flowering and late-season senescence. Plant canopies typically green-up, reach a peak and then decline (senesce) towards the end of the growing season. A dip in canopy activity is sometimes found during the peak of summer, especially in hot or dry climates. The timing of these events is important to higher trophic levels, and mismatches between timing of green-up/senescence and herbivore, pollinator and microbial activities can be detrimental. Green canopies have higher nutrient contents than dormant canopies, which attracts herbivores (Frank & McNaughton, 1992). Animals can track changes in phenology, and alter their activities and movements to match peak canopy growth and forage quality (Frank & McNaughton, 1992; Rivrud, Heurich, Krupczynski, Müller, & Mysterud, 2016). Senescence at the end of the growing season is as important as green-up, especially because it can affect migratory animals during migration. Nevertheless, it has been less studied compared to green-up (Fridley, 2012; Gallinat, Primack, & Wagner, 2015).

It is incompletely understood what controls the timing of phenological events. One well-established phenological pattern is that plant species with  $C_3$  photosynthesis ("cool-season" species) actively grow during spring and fall when temperatures are cool, whereas species with  $C_4$  photosynthesis ("warm-season" species) are active during summer when temperatures are warm (Sage & Monson, 1999; Tieszen, Reed, Bliss, Wylie, & Dejong, 1997). This difference can be linked to plant traits such as specific leaf area, which tends to be higher in  $C_3$  than  $C_4$  species (Polley, Fay, Gibson, & Wilsey, 2016). Phenology is also changing due to global temperature increases (Menzel et al., 2006; Wolkovich & Cleland, 2011), elevated atmospheric  $CO_2$  and nutrient deposition (Cleland, Chiariello, Loarie, Mooney, & Field, 2006), and altered rainfall patterns (Prevéy & Seastedt, 2014). Tieszen et al. (1997) found that land surface green-up occurred later in the spring as one moved from southern to northern latitudes in the U.S. Great Plains.

Current estimates are that green-up occurs 2.5–5 days earlier with each  $^{\circ}C$  increase in temperature (Wolkovich & Cleland, 2011). Warming experiments indicate that warming will induce green-up 1.9–3.3 days earlier for each  $^{\circ}C$  of warming (Wolkovich et al., 2012). This may increase the length of the growing season if middle and later stages are not impacted. However, earlier green-up can come at a cost if soil resources such as water are limiting (Steltzer & Post, 2009), and dips in canopy activity or reductions in peak Normalized Difference Vegetation Index (NDVI) can occur during mid-season. Mid-season dips in NDVI could lead to no changes in annual productivity even when green-up is earlier and senescence is later. Mid-season declines can be prominent in areas with higher temperatures (Sherry et al., 2007). Sherry et al. (2007) found that experimentally induced warming caused earlier flowering in early flowering species and later flowering

in later flowering species, which caused greater within-season bimodality in Oklahoma grasslands.

There have been other human impacts, however, that have occurred concurrently with climate change. Changing management regimes and invasion by exotic species have also been increasing over the last century. Exotic species are recent arrivals on most continents, and if their phenology differs from the native species present at the site (Polgar, Gallinat, & Primack, 2014; Wolkovich & Cleland, 2011), they could alter phenology of the sites as their abundance increases over time. Exotics are especially abundant in the former tallgrass prairie region of the central U.S., where an estimated 82%–99.9% of native prairie was converted to cropland and exotic-dominated pasture and rangeland (Samson & Knopf, 1994). Exotic species in grassland systems were found to green-up earlier than paired native species in a common garden experiment (Wilsey, Daneshgar, & Polley, 2011; Xu, Polley, Hofmocker, Daneshgar, & Wilsey, 2015), and fields that were exotic-dominated had earlier phenology than native-dominated fields (Martin, Harris, & Wilsey, 2015). In a forest shade garden experiment, exotic woody plant species stayed green longer into the fall than did natives (Fridley, 2012). If exotics green-up earlier and stay green later in the year than natives, they may have longer growing seasons and will fix more carbon compared to natives. Alternatively, a cost to the altered phenology might be present if exotics use up available soil moisture by mid-summer; mid-season drops in gross primary productivity (GPP) and lower peaks may lead to no overall difference in growing season GPP compared to native sites. A better understanding of how invasions alter green-up, senescence and mid-season dips in greenness is necessary for further understanding of how land surface phenology is expected to be altered by human activities.

The increased abundance of exotic species might complicate efforts to track phenological changes due to global change if invasion is happening concurrently with climate change over time (Fridley, 2012; Martin et al., 2015; Polgar et al., 2014; Wilsey et al., 2011; Wolkovich et al., 2013). The effects of exotic species will need to be teased apart from climate change for further progress on this topic. Exotics are predicted to have altered phenology compared to natives due to two processes: (1) human selection during introduction for earlier green-up and/or later flowering (Wilsey, Barber, & Martin, 2015), and (2) filtering during the invasion process that favours species that grow outside the normal growing period (Wolkovich & Cleland, 2011). Human introduction of species with early growth is more likely to occur in species that have a large native range, greater height and propagule size, and lower maximum latitude in their native range (Pyšek et al., 2014; Van Kleunen & Johnson, 2007; Van Kleunen, Johnson, & Fischer, 2007). The first process can also be associated with the development of cultivars, which are commonly selected for later flowering (Wilkins & Humphreys, 2003). Exotics have been found to differ from native species in multiple traits, including traits associated with establishment and growing

periods (Chrobock, Kempel, Fischer, & van Kleunen, 2011; Gravuer, Sullivan, Williams, & Duncan, 2008; Wilsey et al., 2015). Gravuer et al. (2008) found that human introduction factors were most important in explaining the spread of *Trifolium* species in New Zealand. The species that were introduced intentionally by humans were more problematic than species that escaped on their own (Gravuer et al., 2008).

Whatever the mechanism, exotic species could be affecting land surface phenology by invading formerly native-dominated sites in many human impacted regions. Here, we compare land surface phenology variables between native- and exotic-dominated grasslands in the former tallgrass prairie region of the U.S. to test whether exotic invasions are altering phenology on a large scale (Pettorelli et al., 2014). Our hypotheses were: (1) exotic-dominated fields will have earlier green-up and later senescence than natives, (2) fields will green-up earlier and senesce later in warmer southern latitudes than colder northern latitudes, (3) phenology differences between natives and exotics will be similar in magnitude to the changes expected with increased temperatures. We focus on the field scale because that is where many management decisions are made (e.g. seeding, animal stocking rate, prescribed fire applications). We tested these predictions with land surface measurements of phenology using NDVI data from Landsat ETM+ satellite measurements (Landsat 7) for green-up, peak NDVI, mid-season dips in activity, and senescence between native and exotic-dominated grasslands along a latitudinal gradient through the centre of the continental U.S. (Martin, Polley, Daneshgar, Harris, & Wilsey, 2014). Landsat data, which have small pixel sizes of 30 × 30 m, were used instead of MODIS data (250 m to 1 km pixel size) due to the small sizes of our native remnant sites (Reed, Schwartz, & Xiao, 2009). The native–exotic status of plant species and their functional types ( $C_3$  vs.  $C_4$ ) were determined within 42 fields using a point intercept field sampling technique described by Martin et al. (2014). On average, exotic fields were 89.6% exotic-dominated ( $SE = 1.8$ ), and native fields were 91.8% native-dominated ( $SE = 2.1$ )  $C_3$ – $C_4$  mixtures. The proportion of exotics did not change with latitude (Spearman's correlation  $r_s = .13$ ,  $p = .41$ ). Exotic fields in the north were strongly dominated by  $C_3$  species, whereas those in the south were dominated by  $C_4$  species (Martin et al., 2014). Native–exotic sites were paired so that they had similar soil characteristics and recent management (Martin et al., 2014), and sites were not hayed or grazed during the year of sampling. Here we find that these exotic fields had different phenology when compared to native fields, a difference that exceeds the impacts of global warming in the case of senescence.

## 2 | MATERIALS AND METHODS

### 2.1 | Location of sites

A total of 42 grassland sites, 21 exotic and 21 native-dominated, were sampled in the central U.S. for the study. Sites were located along a latitudinal gradient from northern Minnesota to central Texas, including sites in those states as well as South Dakota, Iowa, Missouri, Kansas, and Oklahoma (Figure 2). Previous work estimated net primary productivity,  $C_3$ – $C_4$  proportions, plant diversity, forage quality, and bee abundance and diversity at these sites (Martin et al., 2014).

Here, we used the same sites to look at spring green-up, late-season senescence, winter minimums and mid-season dips using NDVI from Landsat 7 ETM+ satellite data. Polley et al. (2016) found that NDVI provided a more sensitive measure of GPP in grassland plots than did Enhanced Vegetation Index (EVI) in a similar grassland situation, and Walker, de Beurs, and Wynne (2014) found that peak NDVI and EVI followed similar temporal trends in arid grasslands.

We used Landsat NDVI data for all our analyses using data from the year ground sampling occurred (Martin et al., 2014) and five of the previous years. By using years previous to the year of plant sampling by Martin et al. (2014), we are making the assumption that native–exotic dominant plant status is consistent across years. Visual monitoring of 12 of the sites over several years suggests that this is a reasonable assumption (B.J. Wilsey pers. observ.). Landsat satellite return interval is 16 days, which is longer than MODIS' return interval of 3 days. However, the advantage of Landsat is its small pixel size of 30 × 30 m. Many of our sites were too small for the larger pixel size of MODIS (250 × 250 m). The small pixel size is a great advantage of Landsat data, and Fisher, Mustard, and Vadeboncoeur (2006) and Fisher and Mustard (2007) found that very large changes in leaf onset can occur over very short distances (<500 m), which necessitates using the higher resolution datasets offered by Landsat. Fisher et al. (2006) found that Landsat provides more accurate estimates of green-up and senescence dates than MODIS due to this greater spatial resolution. Data were obtained from WELD (Web Enabled Landsat Data, Roy et al., 2010, 2011) using only pixels that completely fell within the boundaries of each site. The WELD produces data on day of year and NDVI, where  $NDVI = (NIR - VIS) / (NIR + VIS)$ , and NIR and VIS are reflectance in the near infrared (730–900 nm) and visible spectral ranges (550–680 nm), respectively. The year 2010 was not used due to well-known problems with satellite malfunction due to excessive spring cloudiness (Roy et al., 2011). This produced a dataset of NDVI and day of the year for each of the 42 sites for the years 2005, 2006, 2007, 2008, 2009 and 2011. The year 2011 was a historic drought year in Texas, so this year was excluded for all native and exotic Texas sites. This enabled us to estimate average (mean) phenology across years. Combining years could potentially have led to inter-annual variation around means, but variation from this appeared to be small, based on the variance explained by our models (i.e. the high  $r^2$  values, Tables 1 and 2; Figures S4 and S5) and the small amount of scatter in almost all sites. Looking at variation in NDVI across years within sites is important to do, but is beyond the scope of the current study. Cloudy days were excluded from analysis (i.e. Cloud <0.1). One site in central Texas was excluded for green-up because it was hayed during spring in some years of the study (USDA-Ex). A few negative NDVI values were converted to 0 before analysis. We averaged NDVI across pixels within each site for a total sample size of 41 (green-up and NDVI minimum) and 42 (senescence, peak NDVI and mid-season dips).

### 2.2 | Statistical analysis

Green-up date was estimated at each site with a logistic equation to estimate the date that the canopy reached 50% of its peak ( $X_0$ ):

**TABLE 1** List of exotic (E)- and native (N)-dominated sites, latitude, sum of squares,  $r^2$  and  $n$  for a logistic model, date of green-up ( $X_0$ , or NDVI that is 50% of peak values during early part of the growing seasons) and standard error (SE), minimum NDVI ( $y_0$ ) and standard error (SE)

Origin	Site	Dominant species	SS model	SS total	$r^2$	$n$	Green-up ( $X_0$ )	SE	$y_0$	SE
E	AndersonCoE	<i>Daucus carota</i> , <i>Setaria pumulis</i>	0.6856	0.9668	0.71	39	119.4	5.46	0.2661	0.028
E	Darr	<i>Poa pratensis</i>	1.3308	1.5114	0.89	42	114.2	4.13	0.2085	0.0264
E	Dilt	<i>Festuca arundinacea</i> , <i>Panicum anceps</i> , <i>Setaria pumulis</i> , <i>Poa pratensis</i>	0.8913	1.2389	0.72	51	101.4	6.88	0.2505	0.0413
E	KU	<i>Bromus inermis</i> , <i>Festuca arundinacea</i> , <i>Poa pratensis</i>	0.9549	1.1862	0.81	39	118.7	5.59	0.2759	0.0261
E	Boone	<i>Bromus inermis</i>	1.1556	1.3677	0.84	39	100.3	5.74	0.0754	0.0416
E	Christopherson	<i>Bromus inermis</i> , <i>Poa pratensis</i>	3.3499	3.6334	0.92	60	116.1	3.13	0.0403	0.0202
E	Dugout	<i>Bromus inermis</i> , <i>Poa pratensis</i>	1.2446	1.4548	0.86	35	119.9	6.82	0.0461	0.0551
E	Goodman	<i>Bromus inermis</i> , <i>Poa pratensis</i>	0.6864	0.8385	0.82	27	126.3	5.40	0.1284	0.0296
E	ISU	<i>Bromus inermis</i>	2.9223	3.0981	0.94	49	109.1	3.13	0.0762	0.0266
E	Kreger	<i>Bromus inermis</i> , <i>Poa pratensis</i>	2.816	2.9413	0.96	50	109.1	2.51	0.0608	0.0247
E	Montieth	<i>Bromus inermis</i>	1.0313	1.1898	0.87	36	108.2	5.95	0.1716	0.0303
E	Pankratz	<i>Bromus inermis</i> , <i>Poa pratensis</i>	2.8183	2.9066	0.97	51	137.7	3.05	0.0458	0.0129
E	Quall	<i>Poa pratensis</i> , <i>Bromus inermis</i> , <i>Phalaris arundinacea</i>	3.061	3.3009	0.93	57	135.3	4.11	0.0402	0.0231
E	CedarCreek	<i>Bothriochloa ischaemum</i>	0.3542	0.4228	0.84	35	95.5	5.02	0.1752	0.0139
E	Clymer36	<i>Festuca arundinacea</i>	0.8354	1.5728	0.53	50	76.3	9.71	0.2275	0.0485
E	ClymerExNorth	<i>Bothriochloa ischaemum</i>	0.6429	0.7304	0.88	55	113.1	3.57	0.2045	0.00985
E	ClymerExWest	<i>Festuca arundinacea</i>	0.8343	1.1653	0.72	54	87.8	6.34	0.2402	0.0236
E	OSUPerkins	<i>Cynodon dactylon</i>	2.0567	2.2844	0.90	44	124.2	17.99	0.2302	0.0661
E	TulsaE	<i>Sorghum halepense</i> , <i>Lespedeza cuneata</i>	1.3689	1.5199	0.90	49	122.5	2.97	0.1949	0.0138
E	USDAE	<i>Bothriochloa ischaemum</i> , <i>Cynodon dactylon</i> , <i>Sorghum halepense</i>	Hayed							
E	USDARiesel	<i>Panicum coloratum</i> , <i>Bothriochloa ischaemum</i>	0.8477	1.2047	0.70	64	75.0	7.41	0.225	0.0166
N	AndersonCoN	Mixed natives	2.2296	2.4244	0.92	47	128.7	2.86	0.1769	0.016
N	Comstock	Mixed natives	1.2982	1.4135	0.92	44	129.8	3.59	0.2088	0.0137
N	Risch	Mixed natives	1.7177	1.9388	0.89	49	127.3	0.95	0.234	0.0141
N	Rockefeller	Mixed natives	2.089	2.1685	0.96	39	127	2.02	0.2072	0.0137
N	Ames	Mixed natives	2.8085	3.0725	0.91	55	130	3.30	0.1567	0.0184
N	Anderson	Mixed natives	4.0927	4.3127	0.95	62	130.2	2.86	0.053	0.0167
N	Cayler	Mixed natives	1.8596	1.9863	0.94	35	135.9	2.71	0.1251	0.025
N	Florida	Mixed natives	2.1133	2.2481	0.94	36	144.5	3.62	0.0481	0.0232

(Continues)



**TABLE 1** (Continued)

Origin	Site	Dominant species	SS model	SS total	$r^2$	$n$	Green-up ( $X_0$ )	SE	$y_0$	SE
N	Hastad	Mixed natives	3.3011	3.5529	0.93	61	142.8	2.84	0.0589	0.0200
N	Liska	Mixed natives	1.9871	2.0842	0.95	34	138.4	2.69	0.1065	0.0196
N	PankratzPrairie	Mixed natives	4.6388	4.8598	0.95	67	149.6	2.88	0.0686	0.0133
N	SevenMile	Mixed natives	0.85	1.0392	0.91	19	132.7	5.57	0.0925	0.0426
N	Sheeder	Mixed natives	1.9972	2.0456	0.98	38	132.5	1.72	0.1873	0.0132
N	CountyLine	Mixed natives	1.4876	1.7607	0.84	50	86.8	4.00	0.2602	0.0184
N	Burleson	Mixed natives	1.1874	1.3049	0.91	33	90.4	3.32	0.2077	0.0159
N	ClymerNWest	Mixed natives	3.0811	3.4316	0.90	79	93.1	2.51	0.2353	0.0128
N	OSURange	Mixed natives	2.0127	2.2429	0.90	63	106.8	2.81	0.2179	0.0122
N	Parkhill	Mixed natives	1.779	2.0364	0.87	55	105.3	3.87	0.2493	0.0166
N	RieselPr	Mixed natives	1.0397	1.1591	0.90	52	84.4	1.96	0.2475	0.00745
N	TulsaN	Mixed natives	1.4972	1.6169	0.93	54	117.3	1.95	0.1997	0.0108
N	USDAN	Mixed natives	0.6149	0.8004	0.67	33	87.2	7.21	0.2104	0.0186

$y = y_0 + a/1 + e^{-(\text{day}-X_0)/b}$  using day of the year ( $X$ ) data from December to mid-summer (Figure S4). The winter minimum NDVI was estimated with the  $y$  intercepts ( $y_0$ , Figure S1). Senescence was based on day of the year ( $X$ ) data from mid-summer to the following January, and was estimated as the date that the canopy dropped to 50% of its peak ( $X_0$ ):  $y = a/1 + e^{-(\text{day}-X_0)/b}$ . The 50% value was used because of the difficulty involved with estimating the exact beginning and ending of the growing season (Fisher et al., 2006). These regressions produced a dataset of 41 green-up (Figure S4) and 42 senescence dates (Figure S5). Fit between NDVI and day of year was significant in all cases, with green-up  $r^2$  ranging from 0.53 to 0.98 (Table 1), and senescence  $r^2$  ranging from 0.94 to 0.99 (Table 2). Nonlinear regressions were conducted using SAS 9.4 with Proc NLIN.

Mid-season dips in NDVI were evaluated by comparing deviations from unimodal distributions for each site with the Dip test package using R software (Hartigan & Hartigan, 1985), and with peak NDVI. Departures from unimodality can denote drought and temperature stress during summer peaks. Xia et al. (2015) found that GPP can be calculated in grasslands with length of growing season multiplied by peak NDVI. We compared peak NDVI across sites to test for differences in maximum rates of GPP, which could run counter to any changes that are observed in growing season length across sites. Peak NDVI did not deviate significantly from a normal distribution and was not transformed (Wilk's Lambda tests,  $p = .89$  for native sites,  $p = .27$  for exotic sites).

Estimates of green-up, growing degree days, minimum NDVI ( $y_0$ ), departures from unimodality (i.e. dips) and senescence dates were then compared across latitudes and between native and exotic grassland sites with ANCOVA using Proc GLM of SAS. Latitude was a covariate, and origin (native vs. exotic) was a fixed effect. The interaction between latitude and origin was tested (common slope assumption), and then removed from the model if  $p > .05$ . If  $p < .05$ , the interaction was interpreted, separate slopes were estimated, and independent tests of significance for native vs. exotic sites were made for northern states

(MN, SD, IA), central states (KS, MO) and southern states (OK, TX). These categories were consistent with the commonly used "Northern," "Central" and "Southern Plains" designations. Soil data were included as covariates, which were primarily %clay (PRIN 1) and slope (PRIN 2), and were then dropped from the model if not significant as described by Martin et al. (2014). Sequential sum of squares (Type 1, Hector, Von Felten, & Schmid, 2010) were used with soil variables and latitude first, origin second and the interaction between latitude  $\times$  origin entered last in the model.

Comparisons of origin and temperature effect sizes were conducted to compare their relative importance with two approaches: a space-for-time approach using temperature changes along the latitudinal gradient, and with a comparison of degree day differences using the weather station nearest each site. Latitude and minimum temperature were highly negatively correlated ( $r = -.99$ , Figure S3), largely because longitude was similar among sites. Thus, we could model the effects of warming using a space-for-time substitution approach that assumed temperature changes associated with latitude mimicked the effects of temperature increases over time (Phillimore, Stalhandske, Smithers, & Bernard, 2012; Piao et al., 2011). Minimum temperature was used instead of maximum or average temperature because of its importance to frosts, which can affect phenology measures (e.g. Augsberger, 2013), but results were similar when using maximum or average temperatures, and all temperatures were very highly correlated (all  $r > .99$ ). Analyses used average green-up and senescence between native and exotic grasslands across the latitudinal gradient (i.e. using a common slope). Growing degree days were used to compare differences between native and exotic sites using pairs of sites, at ambient and  $+2.5^\circ\text{C}$ . Green-up growing degree days used the formula  $\sum (\text{mean}_i - 5)$  accumulated across days after means reached  $5^\circ\text{C}$ , where  $\text{mean}_i$  is the average temperature from 1981 to 2010 for that site (Arguez et al., 2010, www.ncdc.noaa.gov). This was calculated for the  $+2.5^\circ\text{C}$  treatment by adding  $2.5^\circ\text{C}$  to the average temperature of each day. Senescence used a similar formula  $\sum (\text{mean}_i - 25)$



**TABLE 2** List of exotic- (E) and native-dominated sites (N), latitude, region (Central, Northern, Southern Plains), Sum of squares,  $r^2$  and  $n$  for a logistic model, date of Senescence (X0, or NDVI that dropped to 50% of peak values during the latter part of the growing seasons) and Standard Error (SE).

Native	Region	Site	Latitude	SS model	SS total	$r^2$	$n$	Senesce x0	SE
E	C	AndersonCoE	38.18	8.7628	8.9089	0.98	31	317.3	12.66
E	C	Darr	37.61	12.4991	12.8359	0.97	39	354.6	11.96
E	C	Dilt	37.64	11.8627	12.4533	0.95	41	347.5	13.51
E	C	KU	39.05	9.0827	9.2737	0.98	31	352.8	11.2
E	N	ISU	42.05	18.4778	18.7053	0.99	53	306.7	3.33
E	N	Boone	42.32	9.1199	9.2771	0.98	42	311	4.8
E	N	Christopherson	43.45	11.9047	12.1732	0.98	57	306.5	4.78
E	N	Dugout	43.41	10.4794	10.7093	0.98	39	295.8	12.75
E	N	Goodman	44.92	4.2852	4.4511	0.96	32	317	8.18
E	N	Kreger	44.76	20.952	21.2589	0.99	66	312.4	3.54
E	N	Montieth	41.63	8.5218	8.7088	0.98	33	322.2	8.13
E	N	Quall	45.05	16.3939	16.6088	0.99	62	308.7	3.58
E	N	Pankratz	47.72	9.3759	9.4784	0.99	41	300.8	3.55
E	S	OSUPerkins	35.99	15.5036	16.2225	0.96	63	344.9	17.4
E	S	TulsaE	36.12	9.1338	9.3337	0.98	50	275.3	37.2
E	S	CedarCreek	31.17	2.4481	2.5252	0.97	30	370.2	14.2
E	S	USDAE	31.05	4.4932	4.8188	0.93	28	372.2	13.5
E	S	USDARiesel	31.46	7.0874	7.3198	0.97	59	369.2	21.16
E	S	Clymer36	33.3	13.0884	14.0591	0.93	64	369.9	18.73
E	S	ClymerExNorth	33.32	6.1798	6.3516	0.97	53	320.7	21.15
E	S	ClymerExWest	33.31	9.9383	10.8641	0.91	66	321.5	68.16
N	C	AndersonCoN	38.18	11.1813	11.5056	0.97	44	252.7	40.92
N	C	Risch	37.64	10.2164	10.5047	0.97	47	234.4	58.05
N	C	Comstock	37.64	9.8142	10.1728	0.96	43	287.9	35.49
N	C	Rockefeller	39.05	10.3693	10.5486	0.98	34	310.8	9.45
N	C	Ames	42.04	12.4029	12.6486	0.98	59	296.2	4.97
N	N	Liska	42.41	9.7853	9.9828	0.98	37	282.4	5.03
N	N	Anderson	43.44	14.6884	14.8359	0.99	57	290	3.36
N	N	Cayler	43.4	10.9807	11.0992	0.99	36	295	5.33
N	N	Florida	44.86	8.292	8.391	0.99	34	295.1	3.38
N	N	SevenMile	44.75	5.8945	5.9698	0.99	24	287.1	8.04
N	N	Sheeder	41.69	11.7881	11.9019	0.99	35	295.4	3.95
N	N	Hastad	45.15	15.9869	16.24	0.98	62	301.2	3.5
N	N	PankratzPrairie	47.73	13.6315	13.7551	0.99	45	284.8	3.12
N	S	OSURange	36.06	14.0232	14.3708	0.98	75	295.5	15.17
N	S	TulsaN	36.12	9.7716	9.9468	0.98	51	297.2	21.25
N	S	Burleson	31.1	8.7244	9.1483	0.95	50	291	57.26
N	S	USDAN	31.04	3.6044	3.716	0.97	28	344.7	21.33
N	S	RieselPr	31.46	7.0269	7.3222	0.96	50	315.9	54.76
N	S	CountyLine	33.26	9.6704	10.211	0.95	50	352.5	50.68
N	S	ClymerNWest	33.31	13.8245	14.11	0.98	73	242.4	32.66
N	S	Parkhill	33.27	9.9561	10.4787	0.95	54	286.2	78.02

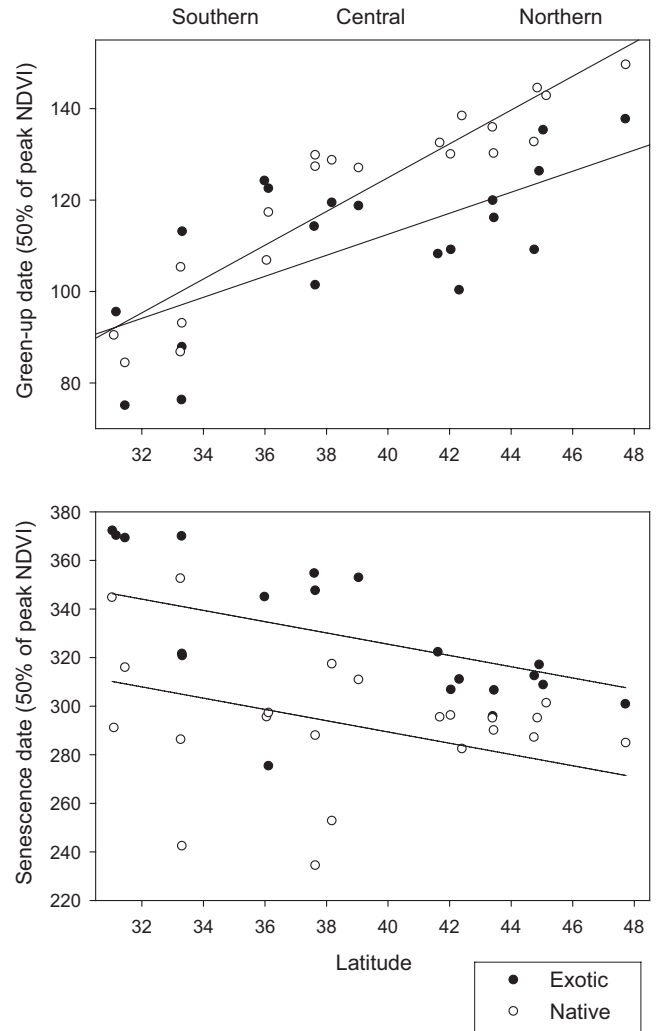
summed across days after means dropped below 25°C after 1 August. Differences between native and exotic sites were computed for each pair of sites, were averaged across ambient and +2.5°C values, and this difference was then compared with the difference between ambient and +2.5°C with *t* tests with unequal variances. Our objective with this analysis was not to study the effects of temperature per se, but to compare the effects of native vs. exotics compared to the predicted effects of temperature change with a comparable approach and dataset.

### 3 | RESULTS

Exotic-dominated sites had substantially different phenology compared to native-dominated sites, especially in date of senescence. Exotic-dominated grasslands greened-up an average of 10.7 days earlier than native-dominated grasslands, but this effect was dependent on latitude (origin main effect  $F_{1,35} = 10.0$ ,  $p = .003$ , model  $r^2 = 0.75$ , Figure 1 top panel). Exotic sites greened-up on average on day 110.0 ( $SE = 2.37$ ), whereas native sites greened-up on day 120.7 ( $SE = 2.31$ ). These differences between native and exotic grasslands were strongest and significantly different in northern and central latitudes with diminished to no difference in southernmost latitudes (origin  $\times$  Latitude interaction,  $F_{1,35} = 5.2$ ,  $p = .029$ ). Green-up differences between native and exotic fields ranged from 19 days in northern states (137.4 vs. 118.0 for natives and exotics,  $SEs = 3.4$ ,  $F_{1,16} = 15.8$ ,  $p = .001$ ), to 15 days in the central states (128.2 vs. 113.4 for natives and exotics,  $SEs = 3.0$ ,  $F_{1,6} = 12.3$ ,  $p = .001$ ), to non-significant differences in the south (96.4 vs. 99.0 for natives and exotics,  $SEs = 5.9$ , 6.5, respectively,  $F_{1,13} = 0.1$ ,  $p = .75$ ). Both soil measures affected green-up date as well ( $p < .01$ ). These native-exotic green-up differences in day of the year equated to a 87.6 growing degree day difference (i.e. 378.7 in native sites [ $SE = 24.9$ ], 291.1 in exotic sites [ $SE = 25.5$ ]), which was significant at  $p < .02$  without a significant latitude  $\times$  origin interaction.

Southern latitudinal exotic grasslands are dominated by  $C_4$  grasses (Martin et al., 2014), and  $C_4$  grasses green-up later than  $C_3$  grasses on average. Shifts in  $C_3$ - $C_4$  proportions could have explained the green-up differences along the latitudinal gradient. To test this, we looked at the difference between native- and exotic-dominated grasslands after taking into account the proportion of biomass produced by  $C_3$  and  $C_4$  species using proportion  $C_3$  as a covariate in an ANCOVA. After taking into account  $C_3$  proportions, the earlier green-up effect was non-significant (ANCOVA with  $C_3$  as a covariate:  $F_{1,36} = 1.0$ ,  $p = .319$ ), which supports the hypothesis that the  $C_3$ - $C_4$  proportions were responsible for a lack of effect in the south compared to the central and north. Taking into account  $C_3$  proportions also resulted in non-significant differences in growing degree days between native and exotic species (ANCOVA with  $C_3$  as a covariate:  $F_{1,37} = 0.2$ ,  $p = .64$ ).

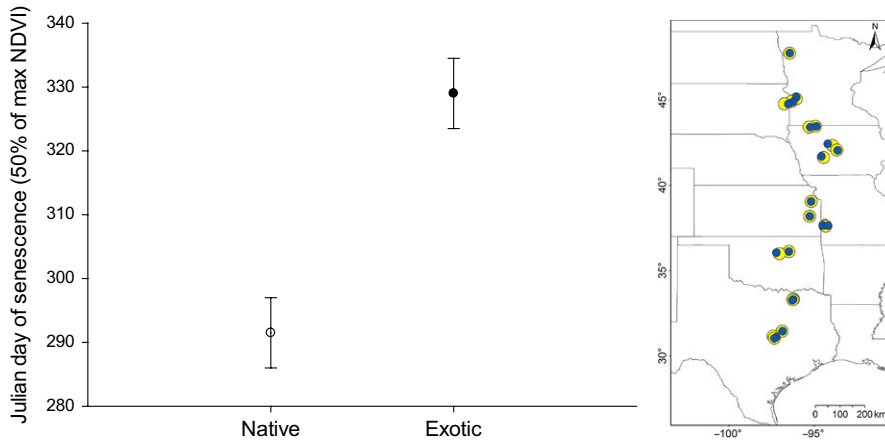
Date of senescence, or the day that declining canopies hit 50% NDVI of their maximum was, on average, 36 days later in exotic- than native-dominated grasslands (Figure 1 bottom panel, Figure 2, origin main effect  $F_{1,38} = 21.3$ ,  $p < .001$ ). This effect was consistent across latitudes (i.e. non-significant origin  $\times$  latitude interaction). The means



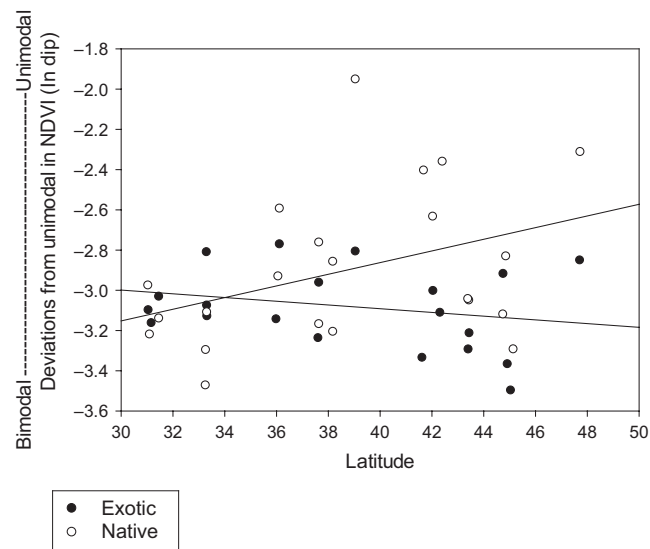
**FIGURE 1** Green-up (top panel, date that canopies reached 50% of peak during the early part of the growing season) and senescence date (bottom panel, date that canopies drop to 50% of peak at the end of the growing season) averaged across years in native (N)- and exotic (E)-dominated grassland sites along a latitudinal gradient in the tallgrass prairie region of the central U.S.

correspond to native canopies reaching 50% on 18 October (day 291.5,  $SE = 5.5$ ) and exotic canopies on 23 November (day 329.0,  $SE = 5.5$ ) of a given year. This difference in senescence date was also highly significant after accounting for soil differences with latitude (origin main effect  $F_{1,38} = 23.2$ ,  $p < .001$ ). Senescence date was significantly related to latitude ( $F_{1,39} = 9.14$ ,  $p = .004$ ). The covariate soil clay content (principle component 1) was positively correlated with senescence date ( $F_{1,38} = 4.46$ ,  $p = .04$ ). Accounting for this soil variable shifted the native-exotic difference to 37.6 days later for exotic sites (37.6,  $SE = 7.82$ ). The model that included soil characteristics, latitude and origin accounted for 47% of the variance in senescence. These differences equated with a 545.2 degree day difference between native and exotic sites ( $SE = 97.08$ , origin main effect,  $p < .001$ , non-significant latitude  $\times$  origin interaction).

Exotic sites had more dips from peak NDVI during summer than did native sites according to the dip test, but only in the north



**FIGURE 2** Average date of senescence (50% of maximum NDVI  $\pm$  SE) across years between native- and exotic-dominated grasslands across 42 sites along a latitudinal gradient (left panel) from Minnesota to central Texas (map in right panel) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 3** Dips in NDVI across native (N)- and exotic (E)-dominated grassland sites (ln transformed). Higher (less negative) values denote smaller deviations from unimodality, and lower values (more negative) denote bimodality due to dips in NDVI during summer. Native and exotic sites responded differently to latitude (origin  $\times$  latitude interaction,  $p = .04$ ). Peak NDVI was consistently higher in native sites than exotic sites (see text for details)

(Origin  $\times$  Latitude,  $F_{1,38} = 4.49$ ,  $p = .04$ ). Native and exotic sites were related differently to latitude, with native sites becoming more unimodal (less heat and drought stress during summer), and exotic sites becoming less unimodal as one moved north (Figure 3). As a result, there was no main effect of latitude in the model ( $F_{1,38} = 1.21$ ,  $p = .28$ ). Peak (maximum) NDVI was consistently higher in native sites ( $M = 0.4630$ ,  $SE = 0.0146$ ) than in exotic sites ( $M = 0.4197$ ,  $SE = 0.01496$ ) along the latitudinal gradient (origin main effect,  $F_{1,38} = 4.3$ ,  $p = .045$ , no significant interaction).

The y intercept was used to compare minimum NDVI during the winter (dormant season) across the latitudinal gradient and between native and exotic grasslands. Minimum NDVI was not affected by the native–exotic status of sites (origin  $F_{1,36} = 0.21$ ,  $p = .69$ , Figure S1). Latitude was the only significant predictor of minimum NDVI ( $F_{1,36} = 61.3$ ,  $p < .001$ ), accounting for 67% of the variation. Minimum

NDVI remained at a high level as one moved north until about 38°; it then declined linearly as latitude increased above that point (Figures S1 and S2).

By substituting minimum temperature for latitude in a model regressing phenological variables against temperature, we were able to develop an estimate for how green-up and senescence dates may be affected by temperature increases expected from global warming. Regression equations were used to estimate how much a general climate change prediction of 2.5°C increase in temperature would affect phenology variables, and these values were compared to the phenology changes due to native–exotic differences with  $t$  tests with unequal variances. A 2.5°C value was used because it is the 50th percentile estimate of 42 global change models for June–August for the central U.S. under the RCP 4.5 scenario by the end of the 21st century (Christensen et al., 2013). A 2.5°C increase in temperature led to a 7.6 day earlier green-up date. The average native–exotic difference in green-up of 10.7 days was significantly greater than the 7.6 day expected difference due to global warming ( $t = 4.05$ ,  $p = .001$ ). A 2.5°C increase in temperature also affected senescence, with a 5.6 later senescence date. The native–exotic difference in senescence of 36.1 days was significantly greater than the 5.6 day expected difference due to global warming ( $t = 26.2$ ,  $p < .001$ ). Similar results would be found with maximum or average temperatures due to very high correlations among temperature variables (all  $r > .99$ ).

When growing degree days were used in comparisons, we found a greater effect of exotics vs. natives than for a 2.5°C increase for senescence, but not for green-up. The 487.77 degree day difference between native and exotic sites in senescence was greater than the 182.1 degree day difference between ambient and +2.5°C ( $t = 96.8$ ,  $p < .01$ ). For green-up, the 97.2 degree day difference between native and exotic sites was smaller than the 163.6 degree day difference between ambient and +2.5°C ( $t = -28.4$ ,  $p < .01$ ).

## 4 | DISCUSSION

Our results from 42 grassland sites indicate that a major factor affecting land surface phenology in the former tallgrass prairie region of the U.S. is conversion of native tallgrass prairie to exotic-dominated

grassland. Based on our analyses, phenology differences between native- and exotic-dominated grassland fields exceeded phenology shifts one may expect from typical increases in temperature due to climate change in the case of senescence. Green-up date differences between native and exotic sites were found in central and northern sites where dominant exotic species had  $C_3$  photosynthesis, but was not found in southern sites where dominant exotic species were  $C_4$ . This last effect was not initially predicted, and indicates that functional types will be important to consider in understanding exotic effects on green-up.

Many exotics were introduced to prevent erosion after the 1930s dustbowl and as forage species. Other species are escaped annual weeds or ornamentals. Most exotic species were intentionally introduced by humans (Mack & Lonsdale, 2001; Van Kleunen et al., 2007; Wilsey & Polley, 2006), and current research focuses on how multiple species affect ecosystem processes in novel ecosystems (Hobbs et al., 2006; Kuebbing, Nuñez, & Simberloff, 2013). In our study, 12 species dominated at least one of the exotic sites, and six grass species were dominant in two or more sites (*Bromus inermis*, *Poa pratensis*, *Bothriochloa ischaemum*, *Festuca arundinacea* [also called *Schedonorus arundinaceus*], *Cynodon dactylon* and *Sorghum halepense*). In a common environment experiment in central Texas, Xu et al. (2015) found that exotic plant mixtures green-up 18 days earlier than native species mixtures using the same metric as we have used here (50% of peak canopy). A greenhouse experiment with 28 perennial grassland species found that exotic species seedlings emerged earlier than native species, had higher germination rates and suppressed establishment of later arriving species to a greater extent than native species (Wilsey et al., 2015). Here, we found that exotic-dominated fields across a large geographic region had an average of a 10.7 day earlier green-up, and a 36 day later senescence than native-dominated fields. The senescence difference was much larger than the green-up date, which was similar to what Fridley (2012) found for forest understorey woody plant species. Invasion during winter (minimum NDVI) appeared to have similar effects on phenology of native and exotic fields, which suggests that it is growing season phenology alone that is affected.

Mid-summer dips in greenness (NDVI) indicate that higher temperatures and associated water limitations might limit gains in annual productivity one might expect from earlier green-up and later senescence. For instance, earlier green-up in exotic sites could have resulted in the canopy drying the soil to low levels at an earlier date than native-dominated areas as seen for annuals invading perennial systems (Polley, Wilsey, Derner, Johnson, & Sanabria, 2006). This might have led to exotic fields in the north, which were dominated by  $C_3$  species, to have more mid-season dips than native fields in the north (Figure 3). (Native fields in the north were dominated by a mixture of  $C_3$  and  $C_4$  species; Martin et al., 2014.) Furthermore, the shorter growing season in native sites was countered by having higher peaks in NDVI during summer, with peak NDVI being consistently higher in native than exotic sites. Taken together, our results indicate that exotic invasions may be leading to a shift in phenology without a concomitant change in annual productivity. What appears to be a longer growing season in exotic sites may not translate into increased GPP. Based on this, we recommend that mid-season dips in NDVI and peak

NDVI be considered in future phenology studies before concluding that growing season length and GPP have increased in cases where green-up is earlier and/or senescence is later.

We sampled 42 sites along the entire tallgrass prairie region of the U.S., and work will have to be conducted in other systems before broad generalizations can be made. In grasslands with few or no exotic species, phenology will be regulated purely by native species. In many systems, effects will depend on the  $C_3$ - $C_4$  photosynthetic status of the species involved, as we found for green-up. Species with  $C_3$  photosynthesis green-up earlier and senesce later than  $C_4$  species, on average.  $C_4$  grass species are major invaders in subtropical and tropical regions of the world (Hughes, Vitousek, & Tunison, 1991; Sage & Monson, 1999; Tognetti & Chaneton, 2015). Invasion by exotic  $C_4$  species into a mixed native grassland will lead to earlier green-up compared to the native  $C_4$  species present (Wilsey et al., 2011), but the native-exotic difference may be smaller than if the invader had been a  $C_3$  species. In a common garden study comparing grassland species within a functional group in monoculture (i.e.  $C_4$  exotic grass vs.  $C_4$  native grass, exotic  $C_3$  forb vs. native  $C_3$  forb, and so on), Wilsey et al. (2011) found that exotics had leaf break 28 days earlier than natives independently of functional group. Studies of invasion should consider both the native-exotic status of the species concerned, their mode of photosynthesis ( $C_3$  vs.  $C_4$ ), and the community shifts that have occurred between  $C_3$  and  $C_4$  species. However, our results also indicate that photosynthetic mode is expected to have a much smaller effect on late-season phenology (senescence), which was consistently different between native and exotic grasslands across the latitudinal gradient. Forested systems are being altered by exotics growing further into the fall than native species (Fridley, 2012), consistent with our work. Finally, our work was at the field scale, and important small-scale variation can occur within fields, and this variation should be further studied in the future with non-satellite, site-based measurements.

The grasslands that we sampled were dominated primarily by perennial species (Table 1), and annuals are more prominent in arid and Mediterranean grasslands. Proportion annual species averaged about 2% in our study across sites, with no significant difference between native and exotic sites (means 3.1% [1.4 SE] and 1.2% [0.6 SD] in exotic and native sites, respectively,  $F_{1,38} = 1.4$ ,  $p = .25$ ). Proportion of annual species did not change with latitude ( $r_s = -.22$ ,  $p = .45$ ). In more arid grassland systems, it is well known that the annual species cheatgrass (*Bromus tectorum*) alters phenology, and this difference has been used to map invaded and non-invaded areas (Peterson, 2008). Preve and Seastedt (2014) found that irrigation in the winter favoured cheatgrass over native species, thus altering phenology. Green-up by this annual exotic species might alter spring green-up, and mid-season activities in a manner similar to what we found for tallgrass prairie. Further research is needed on how climate change may be interacting with exotic-native proportions, and the traits (e.g. the mode of photosynthesis and annual vs. perennial status) of the species involved across sites.

Our results have important ramifications for studies of climate change in areas where exotic abundances are high and rising, as the effects of exotic species were greater than that expected from

climate change in the case of senescence. Taking into account shifts in species composition from native species towards exotics will be necessary for better estimates of how temperature increases will alter land surface phenology. These two factors have the potential to interact as well (Dukes & Mooney, 1999). Estimates of how plant species composition is changing, both in terms of native to exotic and  $C_3$ - $C_4$  shifts should accompany studies of how phenology is changing over time. Shifts in community composition is an issue in all studies that use remote sensing for estimates of land surface phenology, which is likely to be the major method used in future studies (Pettorelli et al., 2014). We recommend that phenology studies should use single species approaches, or take into account species shifts towards exotic species dominance in future phenology studies. Differences in phenology between native- and exotic-dominated sites should be taken into account in management plans for grazing mammals (Frank & McNaughton, 1992) and pollinators (Delaney, Jokela, & Debinski, 2015). Differences in phenology between native and exotic sites could be useful in guiding restoration plans for native species in exotic-dominated regions (Wainwright, Wolkovich, & Cleland, 2010).

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## AUTHORS' CONTRIBUTIONS

B.W. conceived of the idea to look at phenology with satellite data, L.M. and B.W. developed the gradient of sites, A.K. collected data and conducted dip tests, B.W. analysed data and wrote the paper with input from all authors.

## DATA ACCESSIBILITY

Data are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.g4437> (Wilsey, Martin, & Kaul, 2017).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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