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REPORT

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Long-term drought promotes invasive species by reducing wildfire severity

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Abstract

Anthropogenic climate change has increased the frequency of drought, wildfire, and invasions of non-native species. Although high-severity fires linked to drought can inhibit recovery of native vegetation in forested ecosystems, it remains unclear how drought impacts the recovery of other plant communities following wildfire. We leveraged an existing rainfall manipulation experiment to test the hypothesis that reduced precipitation, fuel load, and fire severity convert plant community composition from native shrubs to invasive grasses in a Southern California coastal sage scrub system. We measured community composition before and after the 2020 Silverado wildfire in plots with three rainfall treatments. Drought reduced fuel load and vegetation cover, which reduced fire severity. Native shrubs had greater prefire cover in added water plots compared to reduced water plots. Native cover was lower and invasive cover was higher in postfire reduced water plots compared to postfire added and ambient water plots. Our results demonstrate the importance of fuel load on fire severity and plant community composition on an ecosystem scale. Management should focus on reducing fire frequency and removing invasive species to maintain the resilience of coastal sage scrub communities facing drought. In these communities, controlled burns are not recommended as they promote invasive plants.

KEYWORDS

coastal sage scrub, drought legacy, *Eriogonum fasciculatum*, feedbacks, global climate change, invasive species, *Malosma laurina*, multiple global change stressors, plant community composition, *Salvia mellifera*, wildfire frequency

INTRODUCTION

Understanding the synergistic impacts of multiple anthropogenic global change stressors on natural systems is a key challenge facing the field of ecology (Van Moorsel et al., 2023). Climate change is driving more frequent and intense drought and wildfires, and these drivers may interact with species invasions to dramatically alter ecosystems. While experimental studies have evaluated the effects of drought, wildfire, and invasion of non-native species on natural systems, the complexity of multiple interacting effects is less understood and is typically studied through large-scale modeling efforts (De Kort et al., 2018; Franklin et al., 2016). Studies of these three stressors demonstrate varying interactions from positive to negative (Erskine-Ogden et al., 2016; Stevens et al., 2018; Wigginton et al., 2020). Experimental studies of multiple global change stressors are needed to anticipate interacting impacts.

Periods of drought lead to a reduction in fuel load, which is generally thought to decrease fire severity (Batllori et al., 2013; Garcia-Llamas et al., 2020). Here, fire severity is defined as the impact of fire on organic matter, as opposed to fire intensity, which is the energy released by fire (Keeley, 2009). Drought can also increase fire severity through increased evaporative demand and decreased fuel moisture (Huang et al., 2020; McEvoy et al., 2020). In forested systems, fire severity influences postfire vegetation recovery, such that more severe burns cause higher mortality of trees and a greater likelihood of vegetation-type conversion to non-native dominated systems (Coop et al., 2020; Landesmann et al., 2021). Invasive plants establish in areas disturbed by wildfire because they are typically ruderals that quickly colonize bare ground (Hess et al., 2019; Jauni et al., 2015).

Our study was conducted in coastal sage scrub (CSS), a shrub-dominated community of Southern California that is a biodiversity hotspot and a vulnerable system important to preserve and restore (Myers et al., 2000). CSS has been heavily impacted by urbanization and fragmentation, is home to many threatened and endangered species, and provides important recreational opportunities for millions of people in the region (Riordan & Rundel, 2009). While severe fires are harmful to forest systems, in fire-adapted systems of Southern California, severe wildfire can limit the spread of invasive species and promote native plants with adaptations to crown-sprout or germinate from seed after fires (Schlau, 2022). Invasives are less impacted by low-intensity fires (Keeley et al., 2008), and the cover of native shrubs that germinate from seed following fire is positively correlated with fire severity (Keeley, Fotheringham, & Baer-Keeley, 2005).

Some invasive species are generalists that can thrive in a range of weather conditions (LaForgia et al., 2020; Qian & Ricklefs, 2006). Non-native species may outcompete natives under drought if their traits enable them to grow faster than natives in dry conditions (Duell et al., 2021; Kimball, Gremer, et al., 2014). Extreme drought may lead to invasion by suppressing native cover and opening up bare ground for non-natives to invade (Diez et al., 2012). In Southern California shrublands, drought-induced shrub mortality can lead to the invasion of herbaceous non-natives (Jacobsen & Pratt, 2018). However, the influence of drought on invasion is uncertain, as natives in arid and semiarid regions have adaptations to tolerate or avoid drought, such as deep roots and drought-deciduous habits for shrubs or long-lived seed banks for annuals, that can give them an advantage over some herbaceous non-native species during occasional dry periods (Kimball et al., 2018; Puritty et al., 2019). Drought occurring in the years immediately following wildfire can limit native regrowth and promote invasion due to increased bare ground (Keeley, Baer-Keeley, & Fotheringham, 2005; Oleary & Westman, 1988).

We tested for interactions between rainfall history and wildfire in Southern California at the Loma Ridge Global Change Experiment (hereafter: Loma Ridge), a whole-ecosystem precipitation manipulation that was established in 2007. That same year, the entire experiment burned in the wind-driven Santiago Fire. In the first 4 years after the fire, reduced water plots exhibited greater non-native herbaceous cover and lower native shrub cover than added water and ambient plots (Kimball, Goulden, et al., 2014). Other studies have tested how altered precipitation affects community composition and ecosystem processes at Loma Ridge (Allison et al., 2013; Finks et al., 2021; Kimball et al., 2016; Malik et al., 2020; Martiny et al., 2017; Matulich et al., 2015; Matulich & Martiny, 2015; Potts et al., 2012). On 26 October 2020, Loma Ridge burned again in the 5419-ha Silverado Fire, a wind-driven conflagration similar in behavior to the 2007 Santiago Fire.

In this study, we leveraged ongoing rainfall manipulations, vegetation data sets, and the Silverado Fire at Loma Ridge to test the impact of prefire drought on postfire recovery. While greater fire severity damages native forested ecosystems, shrub-dominated systems such as chaparral and CSS can recover following low-frequency, high-severity fire but are threatened by conversion to non-native systems with increasing fire frequency and drought (Pratt, 2022). We addressed the following hypothesis: Fuel load and burn severity decrease with drought, leading to higher invasion after a fire (Batllori et al., 2013; Keeley et al., 2008; Malanson & Westman, 1991) (Figure 1A). Our study provides a rare opportunity to test the influence of pre-fire precipitation, fuel load, and fire severity on postfire community composition at the ecosystem scale.

METHODS

The Loma Ridge experiment consists of eight replicate experimental blocks established in CSS and grassland communities. Each experimental block includes six plots, with each plot randomly assigned to a unique water (reduced water, ambient, and added water) and nitrogen (ambient or added nitrogen) manipulation treatment.

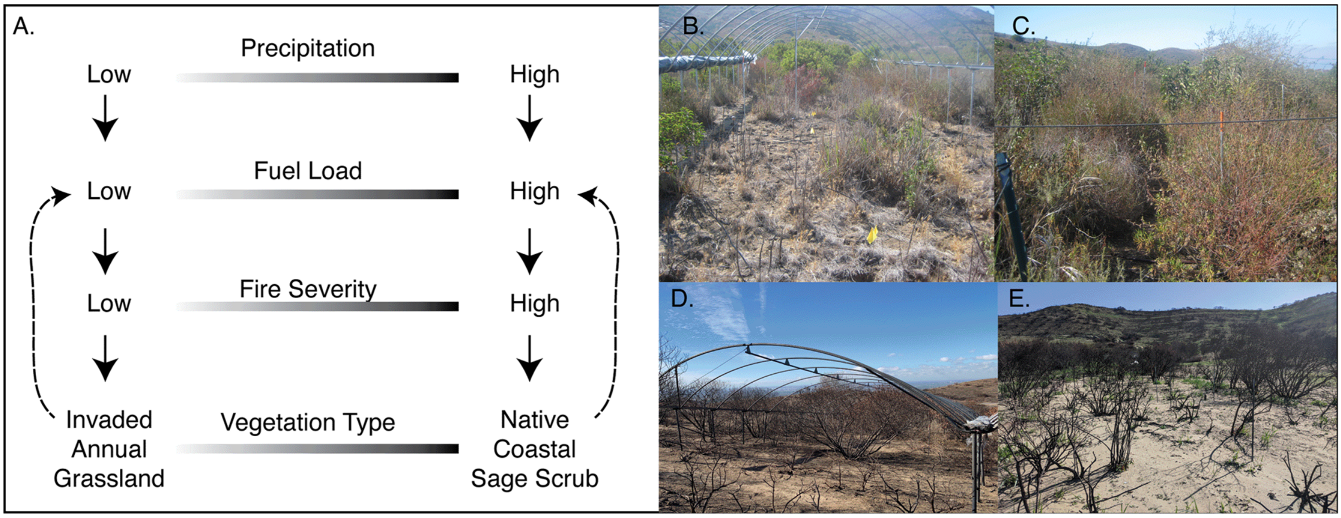

FIGURE 1 (A) Hypothesized relationships between prefire precipitation, fuel load, fire severity, and vegetation type in coastal sage scrub. Dotted lines indicate feedbacks. Actual precipitation values are provided in Appendix S1: Figure S1. (B) Photograph of one of the reduced water plots before the Silverado Fire. (C) Photograph of an added water plot before the fire with many shrubs. (D) Photograph of a reduced water plot after the fire, in which some of the shrub skeletons have small branches and even some leaves remaining. (E) Photograph of an added water plot 1 month after the fire showing shrubs with only a few large branches remaining. Illustration and photographs by Sarah Kimball.

The climate is Mediterranean (dry summers and wet winters) with a mean annual temperature of 17°C, mean annual precipitation of 325 mm, and mean relative humidity of 58% (Barbour et al., 2023). Mean annual precipitation at the site during the rainfall manipulation (2007–2022) was 268 mm (Appendix S1: Figure S1). The drought involved an approximately 40% reduction in precipitation, achieved by covering plots with plastic during large storms, reducing mean annual precipitation to 153 mm. Water was funneled into storage tanks and later pumped on water addition plots via irrigation lines, resulting in an ~25% increase in water received (mean annual precipitation increased to 336 mm). In this study, we focused on the precipitation manipulations in CSS and only collected data on ambient nitrogen plots from the reduced water, ambient, and added water treatments within that community (Figure 1B–E).

Here, we use plant community composition data collected in April of 2020 (the spring immediately before the Silverado wildfire) and April 2021 (after the wildfire but before the rainfall manipulation had been reestablished) to determine how prefire water manipulations influenced plant biomass (Appendix S1: Section S1: Biomass: Methods and results), fire severity (Appendix S1: Section S2: Fire severity: Methods and results), and resulting plant community composition. To measure plant community composition, each plot was divided into three 4 × 4-m quadrats, within which all species were identified and percentage cover was visually estimated. For all shrubs, separate cover values were recorded for crown sprouting individuals, dead shrubs, and seedlings. Overlapping plants meant that plant cover could total >100%. Ground cover values (bare ground, thatch, litter, cryptobiotic crust, rock, or moss) were separately estimated so that they totaled 100%.

Data were analyzed by mixed model ANOVAs using the nlme package in R (Pinheiro et al., 2021). If necessary, variables were ln-transformed so that residuals were approximately normally distributed. Cover of vegetation was analyzed with two-way ANOVAs to test the effects of water treatment (reduced, ambient, or added), fire (before or after fire), and the treatment-by-fire interaction on total plant cover, native shrub cover, native forb cover, non-native grass cover, non-native forb cover, and litter and thatch cover. Plot was included as a random factor in the analyses.

RESULTS

Experimental drought led to reduced prefire biomass (Appendix S1: Section S1: Biomass: Methods and results) and lower fire severity (Appendix S1: Section S2: Fire severity: Methods and results). Shrubs were taller, had more terminal branches that tended to have a smaller diameter, and had a greater proportion of branches with singed leaves in the reduced water plots compared to ambient and added water plots, consistent with decreased fire severity (Appendix S1: Section S2: Fire severity: Methods and results). The cover of vegetation in experimental plots varied before versus after fires and with water manipulation treatment (reduced, ambient, or added water), such that native and non-native plants responded to fire and water treatment differently (Figure 2A,B,

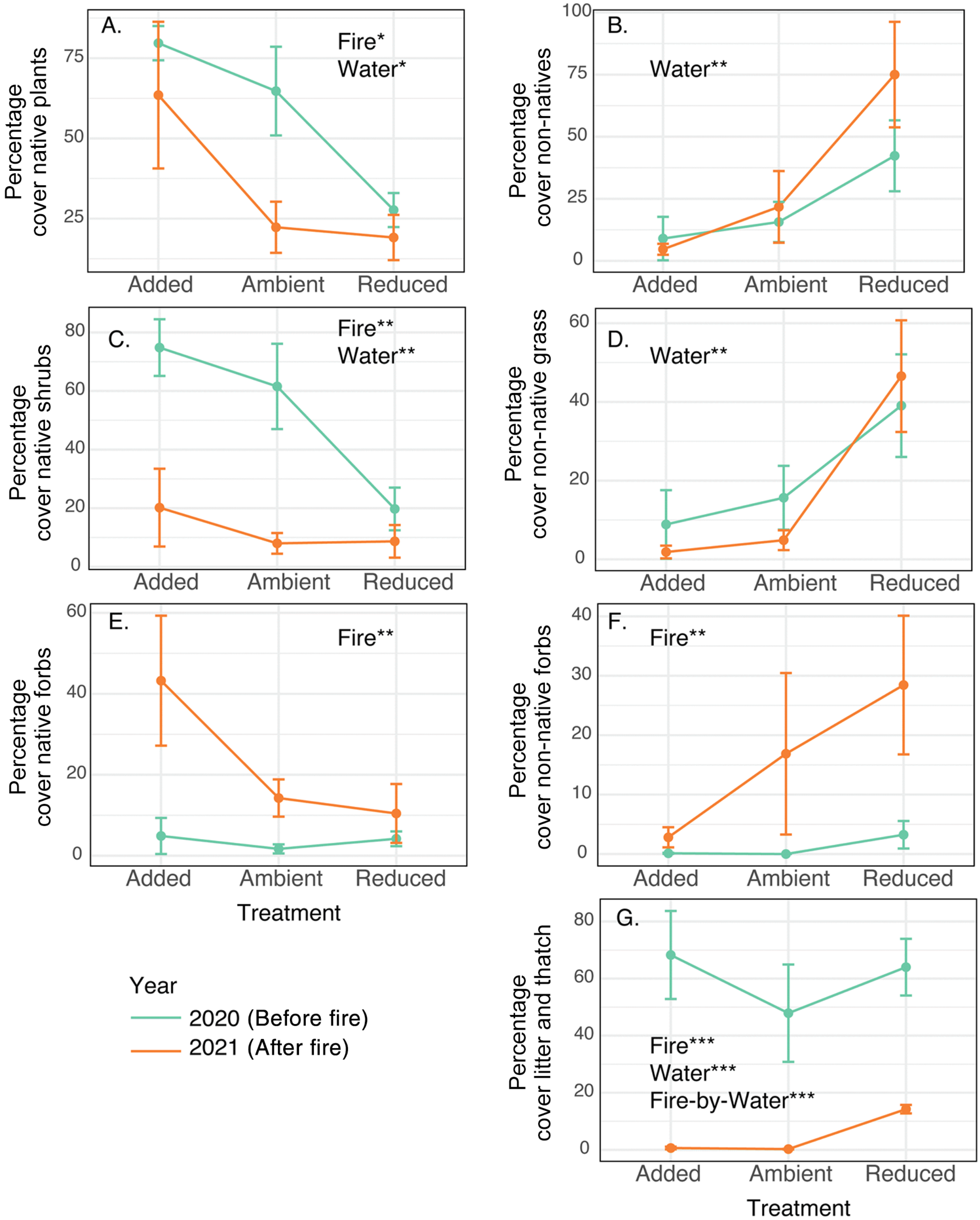

FIGURE 2 Interaction plots demonstrating influence of fire (before and after fire, shown in turquoise and orange) and water treatment on (A) total native plant cover, (B) total non-native plant cover, (C) native shrub cover, (D) non-native grass cover, (E) native forb cover, (F) non-native forb cover, and (G) litter and thatch cover. Results from mixed-model two-way ANOVAs testing the effects of water treatment (reduced, ambient, or added), fire (before or after fire) and the treatment-by-fire interaction are included such that factors with low *p*-values are listed: ***$p < 0.0001$, **$p < 0.01$, *$p < 0.05$, and no * indicates $p < 0.07$. Plot was included as a random factor in the analyses. Native and non-native forb cover, non-native grass cover, and cover of litter and thatch were ln-transformed prior to analysis so that residuals were approximately normally distributed.

Appendix S1: Table S1). Native shrubs, which make up the majority of biomass in CSS due to their large stature, had prefire absolute cover values averaging 75% in added water plots compared to 20% reduced water plots (Figure 2C). Postfire shrub cover was very low in all plots. Fire caused shrub cover to drop from 75% to 20% in added water plots, from 60% to 10% in ambient plots, and from 20% to 10% in reduced water plots (Figure 2C). Native forbs had a combined cover of only ~5% before fire that jumped after the fire to an average of 42% in the added water plots, 15% in ambient plots, and 10% in reduced water plots (Figure 2E).

The response of non-native plants was in the opposite direction, such that non-natives had the highest cover in postfire, reduced water plots (Figure 2B). Non-native grasses had the highest cover in reduced water plots (40%) compared to added and ambient water plots (from 2% to 15%), both before and after wildfire (Figure 2D). Non-native forbs were more influenced by fire than water treatment and had the highest cover in postfire plots (Figure 2F). Ground cover of litter and thatch was between 40% and 80% in all water treatments before the fire (Figure 2G). After fire, there was almost no litter and thatch in added and reduced water plots but around 15% ground cover of litter and thatch that remained in reduced water plots, consistent with lower fire severity and a thicker pre-fire thatch layer (Figure 2G).

DISCUSSION

In our rainfall manipulation experiment, CSS plots receiving less water prior to the 2020 Silverado wildfire had lower native shrub cover and lower biomass, which in turn led to lower fire severity that maintained high non-native cover and low native herbaceous cover (Figure 1). Before fire, reduced water plots contained less fuel and burned at a lower severity, providing important ecosystem-scale confirmation of modeling efforts to relate precipitation and fuel load to fire severity (Kane et al., 2015; Parks et al., 2018). Lower fire severity associated with drought also maintained high cover of invasive annual species, which could lead to vegetation-type conversion (Cox & Allen, 2008b; Keeley et al., 2008).

In Southern California, increased fire severity has been linked to decreased cover of invasive species and increased cover of herbaceous natives that germinate from seed after the fire (Keeley et al., 2008), something that we also found in our experimental plots. The native forbs have seeds that withstand high-severity fires, while the non-native forbs are negatively impacted by high-severity wildfire (Cox & Allen, 2008a; Schlau, 2022). In our study, the only plots that contained litter and thatch on the ground after fire were the reduced water plots, consistent with lower-severity fire and lower temperatures experienced by the seed bank. Non-native forb cover was greatest in the postfire plots that were under drought before the fire and that burned at lower severity. The cover of non-native grasses was also greater in the reduced water plots after a fire. These plots had higher non-native grass cover before the 2020 Silverado fire, so the higher cover of non-natives in reduced water plots was likely due to water treatment altering succession after the 2007 Santiago wildfire (Kimball, Goulden, et al., 2014) in addition to lower-severity burning during the 2020 Silverado wildfire. Feedbacks between invasive species and fire severity have been documented in other systems as well (Blackhall et al., 2017; Tiribelli et al., 2018).

From a management perspective, these data indicate the importance of reducing fire frequency to promote the growth of native shrubs and increase fuel load. High fuel loads were linked to high native shrub cover and higher-severity fires, which in turn promoted higher native forb diversity and lower non-native cover. Less frequent fires that allow fuels to build up will improve the long-term persistence of the CSS community (Eliason & Allen, 1997). Prescribed burning is recommended to reduce fuel load and fire severity in forest systems (Knapp et al., 2005) but should not be used in CSS systems (Keeley, 2002). Our results support other studies indicating that controlled burns in CSS reduce fuel load, lead to lower-severity fires, and increase non-native, invasive species (Keeley, 2002; Keeley, Baer-Keeley, & Fotheringham, 2005).

Postfire control of invasive plant species may be the optimal management strategy to thwart continued invasion. In CSS systems, including at our study site, fires are occurring at a higher frequency than they have historically (Talluto & Suding, 2008; Wells et al., 2004) due to increases in anthropogenic ignitions. With this higher fire frequency, native plants are unable to build up a seed bank or biomass in between fires (Syphard et al., 2007; Wells et al., 2004). Local land stewards cannot prevent drought and high winds, so the increased ignition sources result in more frequent fires. Postfire invasion control is likely the only possible option to mitigate the effects of drought combined with high fire frequency (Schlau, 2022). On a national and global scale, a reduction of anthropogenic CO_2 emissions and related temperature increases would reduce the frequency and severity of drought (Dong et al., 2019; Williams et al., 2019).

In conclusion, three global change stressors (extreme drought, high-frequency wildfire, and invasive species) had a compounding influence on plant community composition. Experimental drought shifted plant community composition toward non-native annual dominance while reducing plant biomass and fire severity. In contrast, increased precipitation led to more native shrubs and fewer invasive grasses. More water also led to more fuel build-up because more native shrub cover means more biomass (Figure 1). The higher biomass of native shrubs led to greater fire severity. After a fire, native shrubs continued to dominate with water addition, whereas non-native dominance was maintained with drought. Our results demonstrate the importance of fuel load and fire severity to plant community composition on an ecosystem scale. To maintain resilient CSS communities, management strategies should focus on reducing fire frequency and controlling non-native species after fires occur.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Kimball, 2024) are available in Dryad at https://doi.org/10.7280/D10M6S.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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