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Beyond the Hydro-Regime: Differential Regulation of Plant Functional Groups in Seasonal Ponds

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Abstract: Plant community assembly can be influenced by many environmental factors. In seasonal wetlands, most studies focus on the considerable variation that occurs from the hydro-regime (patterns of inundation and desiccation). Other factors and their interactions also influence plants but are seldom studied, including nutrient and thatch levels. Furthermore, the responses of aquatic and terrestrial functional groups can provide important insights into patterns of cover and richness. The aim of this study was to evaluate how algae and plant functional groups (aquatic and terrestrial plants) respond to variation in hydro-regime (stable and unstable), nutrient addition (none and added), and thatch (none, native plants, and exotic plants) addition. We measured algal cover, total species richness, and the cover of the functional groups over two years. Algal cover increased with unstable hydroperiods and the addition of nutrients. Algae were also negatively associated with aquatic plant cover and positively associated with terrestrial plant cover. Aquatic plant cover increased with a stable hydro-regime and decreased with increased thatch. Terrestrial plant cover increased with an unstable hydro-regime and decreased with thatch addition. Thatch accumulation and excess nutrients can be linked to human activities, which directly and indirectly alter plant community composition. The interactions of these factors with the hydro-regime should be considered when evaluating a plant community's response to changing environmental conditions. Overall, these results are necessary for the conservation and management of essential wetland functions and services.

Keywords: algae; California vernal pools; functional groups; macrophytes; mesocosms; seasonality; species richness

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1. Introduction

Plant recruitment and community assembly are commonly influenced by changes in environmental conditions [1–3]. These effects can include direct or indirect abiotic (e.g., soil moisture, light) and biotic (e.g., competition and herbivory) interactions that can vary in space and time [4]. Different environmental effects on individual species can also lead to changes in plant species composition, richness, and cover [5,6]. These differences in responses can stem from differences in life history traits (e.g., timing of germination and growth) that interact with the environment to facilitate species coexistence [7]. Therefore, plant functional groups may respond differently to the environment, which results in observed patterns of cover and richness [5–8]. The presence of extreme conditions (natural and human-mediated) provides an opportunity to examine questions related to species traits that can affect species distributions [4,8]. This situation is found in many habitats worldwide, including deserts, high-elevation locations, and wetlands.

In wetland habitats, the hydro-regime (inundation timing, duration, and frequency) is the principal factor determining plant community structure [9–12]. Species traits (e.g., life history, growth structure, and phenology of germination, growth, and flowering) all affect how plants respond to the hydro-regime [4,8,11–16]. For example, individual species from many taxonomic groups exhibited variation in germination and growth under different hydroperiod timings and lengths in greenhouse studies [8,17]. The variation in response to the environment, combined with species interactions, results in what is observed in the community composition [2,4,11,17]. These patterns also hold for seasonal wetland habitats, including vernal pools found in California.

Seasonal wetland habitats, including California vernal pools, consist of species adapted to wet and dry cycles [18–21]. Inundation timing and length affect plant germination and growth [8,17] and result in the distribution of plants within a vernal pool basin along an inundation gradient [4,18,22]. Further, long hydroperiods have been found to prevent the establishment of competitively dominant introduced species, which are invasive in California vernal pools [17]. Vernal pool plant communities exhibit patterns that include annual flood-tolerant species near flood zones and competitive species along edge zones of the vernal pool-grassland ecotone [20]. Changes in hydro-period can create a year-to-year variation that can carry across aquatic and terrestrial phases and determine plant community composition, richness, and cover [16,20,23,24].

Shifts in plant community composition can alter above-ground biomass and lead to thatch deposition [25–27]. Plant thatch affects the germination of native forbs and grasses by affecting light availability and soil temperature in vernal pools [25,27]. This results in overall declines in species richness and diversity. Changes in nutrient cycling (e.g., decomposition rates) and decreased inundation periods and pool depths have also been linked to increased thatch, making vernal pool habitats more susceptible to plant invasions, drastically affecting existing communities [27,28].

Nutrient levels in vernal pools can greatly vary and depend on different factors, including soil properties and human activities [24,29–31]. California vernal pools tend to be oligotrophic (i.e., have low nutrient levels) but are commonly surrounded by human-modified habitats, primarily urban and agricultural development. The modified habitats export excessive nutrients into surrounding ecosystems [31], which are known to be detrimental to vernal pools [24,29,30]. For example, it can lead to algal blooms and decreased richness of plants and invertebrates [24,29–31]

Many studies have investigated the individual effects of hydroperiod, thatch, and nutrient concentrations but have not looked at the potential for additive or interactive effects on plant community composition. Specifically, we conducted a two-year mesocosm experiment that measured the cover and richness of aquatic and terrestrial plants in response to different treatments of hydro-regime (stable and unstable), thatch (control, native, or exotic plant addition), and nutrient (control or nitrogen and phosphorus addition), for a total of 12 experimental treatments. We hypothesized that aquatic plants will respond more to hydroperiod and nutrients [27,28,32] because they directly interact with these treatments, while terrestrial plants will be more negatively affected by thatch and its shading effects during desiccation [25,27,33,34].

2. Materials and Methods

2.1. Experimental Design

Soil from vernal pool complexes in the Elder Creek Watershed and Gill Ranch in Sacramento County was used for the mesocosm experiment [20,24,29,30]. The top 6 cm of soil was collected to ensure the presence of a viable seed bank [34]. Dry soil was homogenized with a cement mixer to intersperse the seed bank.

The study occurred from December 2014 to May 2016. In December 2014, 48 mesocosms (plastic containers with volume = 151 L; mesocosm dimensions: diameter = 1.03 × 0.36 m, height = 0.72 m, area = 0.37 m^2) were established outdoors at the California State University, Sacramento Arboretum. Approximately 7 kg of the homogenized soil was added, leaving an approximately 2 cm depth of soil. Mesocosms were left uncovered over the course of the study. Well water was used to supplement natural rainfall to fill the entire mesocosm. This water was used because it is easily accessible at the site and lacked any chlorinated treatment. Nutrient levels were not measured but all treatments received approximately the same amount of supplemented water. Previous mesocosm studies using this water have found negligible nutrient increases in control treatments [30]. The timing of the treatments and sampling was the same in both years.

Twelve treatments were randomly assigned to four blocks of mesocosms in a randomized block design. The experimental design was a full factorial 2 × 2 × 3 that consisted of hydroperiod (stable and unstable), nutrient addition (control and addition), and thatch (control, native plant thatch, and exotic plant thatch). A stable hydroperiod treatment was inundated for 20 weeks (December–May) and the unstable treatment was 2 short hydroperiods that consisted of a 9-week inundation (December–March), which was desiccated and kept dry for 2 weeks and then refilled for another 9 weeks (March–May). Desiccation at the end of the experiment occurred naturally, but approximately 20 L was removed twice weekly over the last 2 weeks. Removed water was poured through a net (0.2 mm mesh) and all filtered individuals (e.g., seed and eggs) were returned to the mesocosm because we only wanted to remove water to simulate the natural desiccation of vernal pools. To ensure the water removal did not create an added disturbance, the long hydroperiod treatments had the same procedure applied to them, but water was added to refill the mesocosm.

Nutrient addition treatments included nitrogen and phosphorus addition via an aqueous solution of $NaNO_3$ and KH_2PO_4. A 0.5 mg/L concentration was used for both N and P and added every two weeks. Plant thatch treatments included control, exotic plant thatch, and native plant thatch. Aboveground plant vegetation from vernal pools and adjacent upland habitat was collected from Mather Field (Sacramento County, CA, USA). Plants were haphazardly collected and included typical native and exotic plants from vernal pools. Native species included *Eleocharis macrostachya*, *Eryngium castrense*, and *Plagiobothrys stipitatus*, and exotics included *Erodium botys*, *Avena* spp., and *Hordeum* spp. [35]. Fifty grams of dried vegetation (thatch) were added to the appropriate treatment replicates prior to inundation.

2.2. Plant Sampling

Plant cover and richness were sampled at the end of the experiment. Percent cover was measured as the percent of mesocosm area covered. The algal cover was measured two weeks prior to the complete desiccation of mesocosms, while plant cover and richness were measured following desiccation. This allowed plants to complete growth, flower, and fruit. Nine macroalgae and two algal (multicellular) species were present (Table 1). Most of the macroalgae were vernal pool endemic species. Species were categorized into their hydro-phase affiliation (aquatic or terrestrial) based on when most of their growth and flowering occurred (Table 1).

Table 1. Species list with each characteristic of habitat affiliation, growth form, and phase affiliation.

Species	Habitat Distribution	Hydro-Phase Affiliation
Cladophora sp. [1]	Widespread	Aquatic
Nitella sp. [1]	Widespread	Aquatic
Eleocharis macrostachya	Endemic	Aquatic
Callitriche marginata	Endemic	Aquatic
Ranunculus aquatilis	Widespread	Aquatic
Marsilea vestita	Widespread	Aquatic
Plagiobothrys stipitatus	Endemic	Terrestrial
Downwingia bicornuta	Endemic	Terrestrial
Gratiola ebracteata	Endemic	Terrestrial
Navarretia leucocephala	Endemic	Terrestrial
Psilocarphus brevissimus	Endemic	Terrestrial

[1] Macroalgae.

2.3. Statistical Analysis

To assess the effects of treatments on the richness and cover (total) and functional group cover (aquatic and terrestrial affiliated plants) of each of the species, the General Linearized Model (GLMM) (gamma distribution with log link) was used with the year (random factor), hydro-regime, thatch addition, and nutrient addition as independent variables in a fully factorial model. All richness and densities were ln-transformed. Correlations among algal cover, total cover and richness, and functional group cover were assessed using partial correlations, which controlled for the year. These analyses were conducted using IBM SPSS, version 24 (IBM Corp., Armonk, NY, USA).

3. Results

3.1. Macroalgae

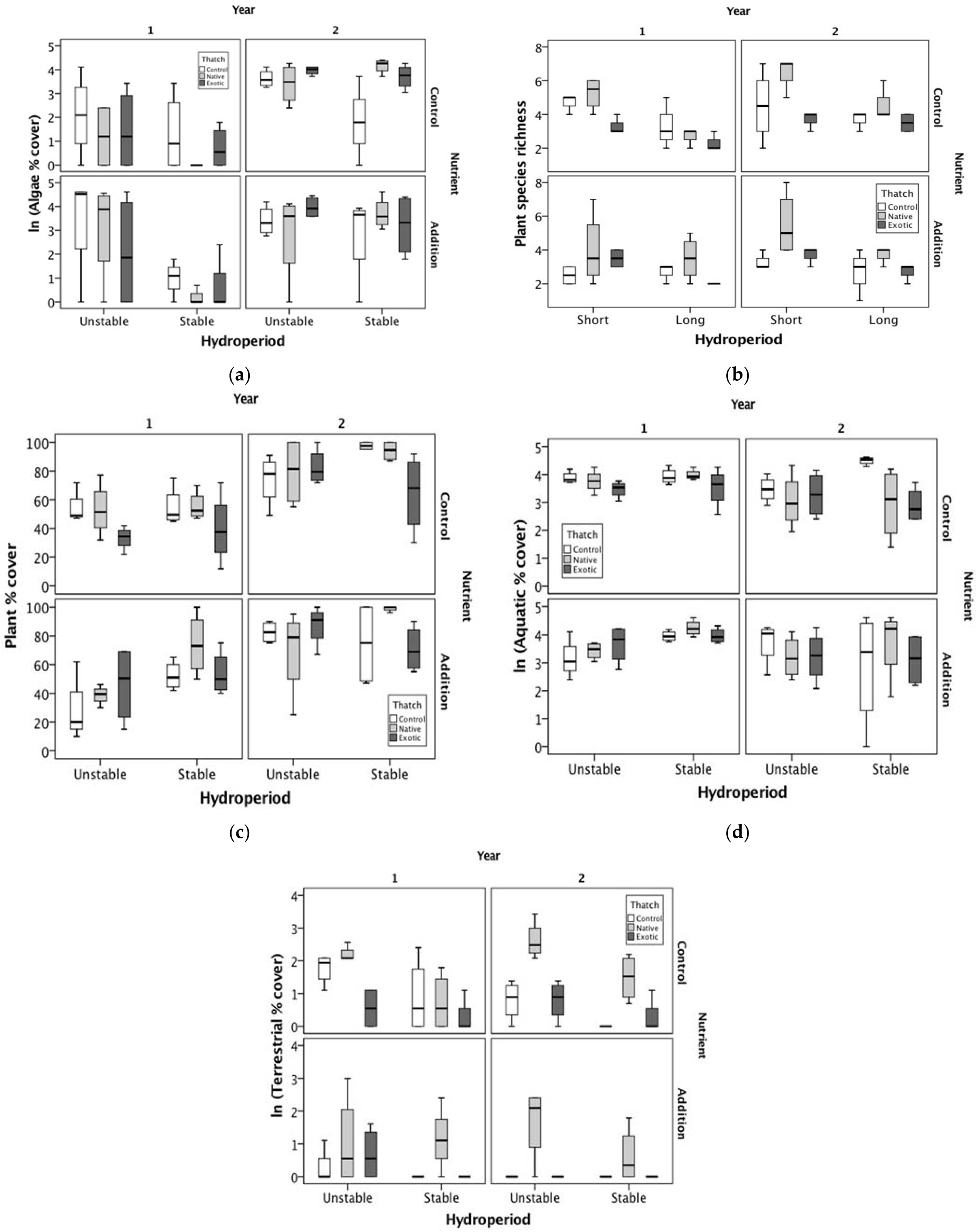
Cladophora sp. dominated the first year, but *Nitella* sp. invaded during the second year and dominated many of the treatments. Year, hydro-regime, and nutrients were all significant main effects on the algal cover (Figure 1a, Table 2). On average, algal cover in unstable hydroperiods increased by over 69% compared with stable hydroperiods, and nutrients increased algae by 38% on average. Several interactions were also found, including year–hydroperiod, year–thatch, and hydroperiod–nutrient. In the first year, unstable hydro-regime and nutrient addition increased algae, and their coupling resulted in the highest levels of algae. Significant year–hydroperiod–nutrient interactions resulted in nutrient addition increasing algae in unstable hydro-regime treatments in the first year.

Table 2. Generalized linear models for each of the dependent variables.

Dependent Variable	Independent Variable	Wald Chi-Square	df	*p*
Algae				
	Year	54.313	1	<0.001
	Hydroperiod	52.147	1	<0.001
	Thatch	3.170	2	0.205
	Nutrient	5.925	1	0.015
	Year * Hydroperiod	40.840	1	<0.001
	Year * Thatch	12.052	2	0.002
	Year * Nutrient	2.023	1	0.155
	Hydroperiod * Thatch	0.158	2	0.924
	Hydroperiod * Nutrient	5.163	1	0.023
	Thatch * Nutrient	1.985	2	0.371
	Year * Hydroperiod * Thatch	3.295	2	0.193
	Year * Hydroperiod * Nutrient	9.122	1	0.003
	Year * Thatch * Nutrient	6.624	2	0.036
	Hydroperiod * Thatch * Nutrient	3.089	2	0.213
	Year * Hydroperiod * Thatch * Nutrient	8.485	1	0.004
Species richness				
	Year	17.856	1	<0.001
	Hydroperiod	36.815	1	<0.001
	Thatch	39.877	2	<0.001
	Nutrient	13.598	1	<0.001
	Year * Hydroperiod	0.802	1	0.370
	Year * Thatch	2.906	2	0.234
	Year * Nutrient	0.359	1	0.549
	Hydroperiod * Thatch	3.998	2	0.135
	Hydroperiod * Nutrient	0.941	1	0.332
	Thatch * Nutrient	7.599	2	0.022
	Year * Hydroperiod * Thatch	1.999	2	0.368
	Year * Hydroperiod * Nutrient	3.287	1	0.070
	Year * Thatch * Nutrient	1.205	2	0.548
	Hydroperiod * Thatch * Nutrient	5.252	2	0.072
	Year * Hydroperiod * Thatch * Nutrient	1.230	2	0.541

Table 2. *Cont.*

Dependent Variable	Independent Variable	Wald Chi-Square	df	*p*
Total percent cover				
	Year	78.223	1	<0.001
	Hydroperiod	8.152	1	0.004
	Thatch	5.888	2	0.050
	Nutrient	0.010	1	0.922
	Year * Hydroperiod	1.893	1	0.169
	Year * Thatch	0.729	2	0.694
	Year * Nutrient	0.021	1	0.886
	Hydroperiod * Thatch	6.671	2	0.036
	Hydroperiod * Nutrient	2.629	1	0.105
	Thatch * Nutrient	5.555	2	0.062
	Year * Hydroperiod * Thatch	1.825	2	0.401
	Year * Hydroperiod * Nutrient	2.014	1	0.156
	Year * Thatch * Nutrient	3.353	2	0.187
	Hydroperiod * Thatch * Nutrient	1.800	2	0.407
	Year * Hydroperiod * Thatch * Nutrient	2.375	2	0.305
Aquatic plants				
	Year	1.300	1	0.254
	Hydroperiod	5.561	1	0.018
	Thatch	7.684	2	0.021
	Nutrient	0.412	1	0.521
	Year * Hydroperiod	0.192	1	0.661
	Year * Thatch	6.134	2	0.047
	Year * Nutrient	0.753	1	0.386
	Hydroperiod * Thatch	4.378	2	0.112
	Hydroperiod * Nutrient	2.008	1	0.156
	Thatch * Nutrient	1.583	2	0.453
	Year * Hydroperiod * Thatch	2.324	2	0.313
	Year * Hydroperiod * Nutrient	0.228	1	0.633
	Year * Thatch * Nutrient	1.004	2	0.605
	Hydroperiod * Thatch * Nutrient	1.916	2	0.384
	Year * Hydroperiod * Thatch * Nutrient	1.931	2	0.381
Terrestrial plants				
	Year	163.145	1	<0.001
	Hydroperiod	0.446	1	0.504
	Thatch	10.387	2	0.006
	Nutrient	0.087	1	0.768
	Year * Hydroperiod	0.016	1	0.898
	Year * Thatch	8.300	2	0.016
	Year * Nutrient	0.087	1	0.768
	Hydroperiod * Thatch	4.703	2	0.095
	Hydroperiod * Nutrient	0.042	1	0.837
	Thatch * Nutrient	0.887	2	0.642
	Year * Hydroperiod * Thatch	6.902	2	0.032
	Year * Hydroperiod * Nutrient	0.111	1	0.739
	Year * Thatch * Nutrient	1.930	2	0.381
	Hydroperiod * Thatch * Nutrient	1.715	2	0.424
	Year * Hydroperiod * Thatch * Nutrient	1.035	2	0.596



(**a**) (**b**)

(**c**) (**d**)

(**e**)

Figure 1. Box plots of dependent variables ((**a**) algal cover, (**b**) plant species richness, (**c**) total plant cover, (**d**) aquatic plant cover, and (**e**) terrestrial plant cover) in response to hydro-regime, nutrient addition, and thatch addition over the two years of the study.

3.2. Plants

All main effects of year, hydro-regime, thatch, and nutrients affected total species richness. Unstable hydro-regime increased, and nutrients decreased plant species richness, but thatch treatments had variable effects. Species richness increased with native thatch addition and decreased or was neutral with exotic thatch addition (Figure 1b, Table 2). Thatch–nutrient was the only significant interaction with thatch having variable effects depending on nutrient addition. In contrast, year and hydro-regime and a hydro-regime–thatch interaction affected total cover. Stable hydro-regimes alone increased total percent cover, and native thatch increased cover while exotic thatch decreased cover (Figure 1c, Table 2).

Aquatic plant cover was significantly affected by the main effects of hydroperiod and thatch. Thatch effects also changed over the two years (Figure 1d, Table 2). In general, aquatic plant cover increased with hydroperiod stability and decreased with thatch addition. Furthermore, aquatic plant cover was negatively associated with algal cover ($r = -0.59$, $p < 0.001$). Terrestrial plant cover changed across years and responded to the main effects of thatch and the year–hydroperiod–thatch interaction (Figure 1e, Table 2). Thatch effects varied based on type; native thatch increased cover while exotic thatch did not affect cover compared with the control treatment. The interaction resulted from increased terrestrial cover with an unstable hydroperiod. This effect occurred in both years but was more pronounced in the second year. Terrestrial plant cover and algal cover were positively correlated ($r = 0.48$, $p < 0.001$).

4. Discussion

The California vernal pool plant community is a seasonal habitat that experiences considerable environmental variation, including those influenced by human activities. Climate change affects both temperature and precipitation patterns [36], which determine the hydro-regime of seasonal wetlands. Nutrient inputs can indirectly increase following regional fertilizer application [30,31], and thatch can increase following the introduction of exotic plant species, all resulting in decreased plant productivity and diversity [37,38]. The present experiment examined how algae and plant species responded to manipulated hydro-regime, thatch, and nutrients. Each of the functional groups (algae, aquatic plants, and terrestrial plants) responded differently to the treatments and their interactions. Therefore, these are important regulation factors of richness and cover that create the patterns of species coexistence, species composition, and community structure.

As expected, algal cover increased with unstable hydroperiods and with nutrient addition, patterns commonly found in freshwater ecosystems [24,39–41]. Results were observed after the first year and carried over into the second year. Furthermore, the increase in algae was negatively associated with aquatic plant cover and positively with terrestrial plant cover. Filamentous algae, *Cladophora* spp. and *Nitella* spp., became dominant across many of the treatments after two years, likely reducing aquatic plant cover via competitive exclusion for resources (e.g., light and space) [24,27,42–44]. This is often a result of the formation of algal mats, which are associated with P retention and reduction in light attenuation [24,44–47]. During unstable hydroperiods, algae can increase in growth [40,48], which can also stabilize the spatial distribution of nutrients and water fluctuations, promoting plant establishment during the terrestrial hydro-phase [24,47]. Excess nutrients released from algal mats during the terrestrial hydro-phase are directly associated with an increase in exotic plants, facilitating increases in exotic thatch [24,25,27,29,47].

The aquatic plant functional group increased with increased hydroperiod and decreased with increased thatch. Hydro-regime is well-known for affecting plant germination and growth, as the native plant community is specially adapted to environmental cues from inundation and desiccation cycles [8–13]. The presence of a stable hydroperiod also ensures the completion of the plant life cycle. Decreased cover in response to thatch, like increased algae, was likely the result of light attenuation or creating a barrier to emerging seedlings [24,42]. Many wetland plant seeds rely on light availability for germination and are unable to germinate in unfavorable conditions (e.g., shaded, limited space), so they remain dormant in the soil until those conditions are met [34,49–51]. Increased exotic thatch in vernal pools has further been shown to inhibit native plant richness and cover in both hydro-phases by altering vernal pool inundation periods and depths (e.g., shortens hydroperiod and lowers depth of water in pools) [27]. This also creates divergent plant communities that favor invasive plant species [27]. The presence of exotic thatch, which decomposes more slowly than native thatch, and its accumulation can further promote invasive plants by adding to invasive seed banks, which readily germinate compared with native seed banks [27,34]. Our seed bank did not support invasive plants and therefore we could not assess a shift to an invasive-dominated community.

Terrestrial plants have a later phenology of germination, growth, and flowering during the hydroperiod. They exhibited complex responses to the hydro-regime and thatch that differed compared with the aquatic plants. Terrestrial plant cover increased with an unstable hydro-regime, because of a direct effect on their phenology (e.g., an environmental cue from desiccation) [8], or indirectly by decreasing the competitive advantage of aquatic plant cover. Thatch addition effects differed among the types (native or exotic) and these effects increased over the two years. Native plant thatch effects on plant cover were similar or greater than controls, which was likely due to the contributed seeds to the mesocosms. This has been shown to be effective for restoration in California vernal pools [2,51]. In contrast, exotic plants decreased the cover of the plant functional groups. Exotic plants in California are composed of mostly grasses and some forbs from the Mediterranean region and are known to have high phenotypic plasticity that aids in their ability to colonize various ecosystems [36,52,53]. Exotic plants have slower decomposition rates compared with natives [28] and, as a result, can have many influences on hydrology, soil chemistry, and plant species composition by altering inundation patterns, retaining more nutrients such as phosphorus, and further promoting plant invasions [27,28,54–57]. Our findings corroborate previous research that exotic plant thatch inhibits the growth of vernal pool natives by reducing light, creating a structural barrier, and overall, not meeting favorable environmental conditions needed for germination and growth [27,55].

Exotic thatch impacts the availability of nutrients and moisture in the soil, which impedes native plants and decreases species richness [25,27,34,56,58,59]. Environmental variation caused by the addition of exotic thatch combined with unstable hydro-regimes disrupts ecosystem functions, further preventing the establishment of native plants [27,59,60]. Our findings highlight the need for appropriate management of exotic species in vernal pool habits to mitigate the impacts of exotic thatch. The effects of exotic thatch during the terrestrial phase were shown to carry over into the aquatic phase and reduce cover and richness. Previous research has found that exotic plants can be managed using grazing and fire, which are commonly used in California vernal pool habitats [61,62]. Targeted, low-intensity grazing and fire have been found to reduce the above-ground biomass of exotic thatch and promote the recruitment of native forbs and grasses while facilitating stable hydroperiods [51,63–65]. Further investigations are needed to determine other appropriate management approaches in addition to grazing and fire to keep up with projected climate change.

The current study was conducted in mesocosms with homogenized soil, which has many advantages to understand environmental effects on biodiversity [66]. However, there are disadvantages to this approach, including simplified treatment variation, limited species pool, and smaller scales [66]. The treatment effects were largely consistent over the two years with a couple of exceptions, which may have been the result of temperature and precipitation differences or legacy effects of the first year [24]. Long-term effects of prolonged environmental variation, in conjunction with spatial dynamics (i.e., dispersal), should be further explored to better understand community changes in natural vernal pools over different spatiotemporal scales.

Another limitation of this study was that we could not distinguish the treatment effects on emergence, species interactions, and fitness. For example, we could not decipher whether algal cover and exotic thatch prevented species emergence from the seed bank or prevented growth once they germinated. All of the species present had an annual lifecycle with considerable seed banks that can remain dormant in the soil for decades [20,34,48–50]. Distinguishing how life history stages are affected by the relative effects of the treatments and species interactions (i.e., competition) is important for understanding community dynamics. Nevertheless, our results and those of previous studies [7,34] point to the storage effect being an important mechanism of species coexistence under environmental variation.

While our study showed that the hydro-regime played a dominant role, other factors (nutrients and thatch) and their interactions also affected species composition in significant ways. These results contribute to the knowledge gap regarding the high unexplained variation commonly found in wetland communities beyond the hydro-regime [67]. Climate change, habitat loss, invasive species, and pollution are the primary stressors threatening wetland function globally [36], including California vernal pools. Understanding how wetlands respond to interconnected environmental conditions [68] is critical for their conservation. The effects of abiotic and biotic factors on functional groups and overall biodiversity can provide insight for prioritization of management practices to mitigate impacts from human activity and climate change [36].

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