Water primrose invasion changes successional pathways in an estuarine ecosystem

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Abstract. Invasive species fundamentally change the bio-physical and ecological characteristics of the ecosystems they invade. Rapidly expanding invasive species may facilitate the spread of other invasive species, and successive invasion events may lead to novel species interactions that may push the system beyond its equilibrium state and change successional pathways. Knowing the direction of the invasion front may be useful to predict impacts of invasive species. Water primrose (*Ludwigia* spp.), one of the invasive floating macrophytes in the Sacramento-San Joaquin River Delta (hereafter, Delta), has increased in cover rapidly over the past three decades likely outcompeting native and non-native species, changing their functional relationships, with cascading effects in the macrophyte communities of the aquatic ecosystem. In this study, we analyze the directionality of water primrose invasion and assess which spaces it occupies, whether it has overcrowded or outcompeted other vegetation communities, and its implications for succession in the Delta. We used imaging spectroscopy data acquired in June of 2004, June of 2008, November of 2014, and October of 2016 for the 2500 km^2 of the Delta to map the communities of submerged macrophytes, floating macrophytes, and emergent marsh. We found that water primrose cover increased fourfold in the Delta over the past 13 yr, changing significantly in the central Delta and Liberty Island region from 122 ha in 2004 to 471 ha in 2016. Water primrose expanded first by spreading over open water and submerged macrophytes and, when that habitat was exhausted, primrose invasion switched direction and encroached into emergent marsh. This bilateral expansion to both open water and the marsh is likely to change rates of succession and affect the restoration of the native Delta marshes. Understanding the mechanisms behind the expansion dynamics of this invasive will allow managers to counter its impact on newly established vulnerable marshes.

Key words: biological invasions; California Delta; community turnover; hyperspectral; *Ludwigia;* remote sensing; succession; wetlands.

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Introduction

Invasive aquatic species (hereafter "invasives") have a tremendous impact on fragile wetland ecosystems by modifying ecosystem processes such as nutrient availability, nutrient cycling, soil chemistry, water tables, hydrology, food webs, and habitat (Gordon 1998, Scheffer et al. 2003, Dukes and Mooney 2004, O'Farrell et al. 2009, Pejchar and Mooney 2009). Invasives have been

exceptionally good at occupying wetland habitats, with increasing rates of invasion as global connectivity rises (Cohen and Carlton 1998). Additionally, anthropogenic intervention upstream and in wetlands has shifted hydrologic regimes and altered sediment supplies due to dams, levees, landuse, and climate change, promoting changes in spatial and temporal community assembly and distribution in aquatic ecosystems making them vulnerable to invasion (Johnson et al. 1985, Day et al. 2000, Reed 2002).

Invasives in wetlands have many negative effects within and across trophic levels and greatly reduce biodiversity (Bax et al. 2003, Malik 2007, Molnar et al. 2008, Clavero et al. 2009, Thouvenot et al. 2013a). Many invasives may directly compete with other species by secreting allelopathic chemicals that reduce germination and seedling survival (Gopal and Goel 1993, Bais et al. 2003, Rudrappa et al. 2007, Dandelot et al. 2008), or by changing light accessibility (Penfound and Earle 1948, Malik 2007, Stiers et al. 2011). Invasives may also significantly impact invertebrate distribution, diversity, and abundance (Meerhoff et al. 2003, Toft et al. 2003, Stiers et al. 2011); induce anoxic conditions detrimental to fish and other aquatic life (Penfound and Earle 1948, Dandelot et al. 2005, 2008, Nehring and Kolthoff 2011); and act as barriers for fish movement (Penfound and Earle 1948, Stiers et al. 2011, Thouvenot et al. 2013a). They also reduce open water habitat for water birds and other wildlife (Thouvenot et al. 2013a). Removal of invasives may facilitate the establishment or expansion of either native or non-native species into the niche that was created and modified by the invasive (Klötzli and Grootjans 2001, Lugo 2004, Khanna et al. 2012). Gaertner et al. (2014) highlighted the risk of regime shifts in ecosystems invaded by aggressive non-native species due to feedback mechanisms and ecosystem engineering characteristics of such invasives (Crooks 2002).

Because of these negative effects of invasives in wetlands, their presence may alter wetland functioning and the ecosystem services they provide. Wetlands are unique, supporting multiple successional communities that are in dynamic equilibrium with the hydrologic regime (Ward et al. 2002, Mitsch and Gosselink 2007). From river floodplains to freshwater, brackish, and tidal marshes, wetland vegetation communities are consistently organized along hydrologic and bathymetric gradients in space and time (Johnson et al. 1985, Junk et al. 1989, Mitsch and Gosselink 2007). Submerged, emergent, and floating communities in wetlands are characterized by pulse stability, that is, pulse perturbations resulting in lateral movements of successional communities along these gradients (Odum 1969, Greco et al. 2007, Ives and Carpenter 2007, Mitsch and Gosselink 2007, Viers et al. 2012). Alterations to sediment supply, flow regimes, and species composition as those brought about by invasive species (Crooks 2002) may change the distribution of plant communities along these gradients and change wetland functioning.

Invasives can induce pulse perturbations and either speed up successional processes or slow them down. The fast growth and large dense mats of invasive submerged vegetation decrease water velocity and accelerate sedimentation (Penfound and Earle 1948, Fonseca and Fisher 1986, Fonseca and Cahalan 1992, Champion and Tanner 2000, Dandelot et al. 2005, Nehring and Kolthoff 2011) eventually leading to hyper-sedimentation, silting, and decreased water transport within waterways (Thouvenot et al. 2013a). This can facilitate deposition leading to vertical accretion and thus providing new habitat for submerged, emergent, and riparian species (Dukes and Mooney 2004). Alternatively, invasive species may modify habitat to slow down succession or even reverse it. Studies describing this disruptive phenomenon come from examples of mammalian ecosystem engineers such as nutria, beavers, or muskrats and how they have engineered wetlands and modified them from lotic to lentic systems and reversed sedimentation and succession processes (Shaffer et al. 1992, Jones et al. 1996). Thus, it is important to know the direction of invasion both in terms of what communities get invaded and whether it changes over time. This will provide insight into how biotic communities establish and if they are resilient to invasion in the short and the long run.

This study focuses on understanding the impacts of the rapid expansion in recent decades of the floating invasive, water primrose (*Ludwigia* spp.) in the Sacramento-San Joaquin River Delta (henceforth, the Delta) in California. Globally, deltas are prone to invasion and this delta is no

exception (Cohen and Carlton 1998, Light et al. 2005). It is one of the most modified estuaries in the world maintained via an extensive network of dams upstream, with canals and levees downstream constraining the flows of rivers, tributaries, and the Delta canal complex itself (Nichols et al. 1986). Water primrose was reported in California as early as 1916 and in the Delta by 1949 (public communication: Light et al. 2005). The extent of water primrose in the Delta has increased almost fourfold from 2004 to 2016, and it now occupies 3% of the waterways (personal observation). The objective of this study is to determine whether invasion by water primrose changes expected successional pathways and rates in aquatic plant communities.

DATA AND METHODS

Study system

The Sacramento-San Joaquin River Delta spans approximately 2220 km^2 in Northern and Central California. It is a diverse network of 1800 km of channels and freshwater tidal marsh at the confluence of two major rivers, the Sacramento and the San Joaquin (Fig. 1). Here, we will focus on two areas, highlighted in yellow in the figure. These two sections correspond to two-thirds of all waterways in the Delta.

The first section is Liberty Island in the northwest Delta, a naturally restored freshwater tidal wetland of ~21 km^2 that was created by flooding a reclaimed agricultural tract following a levee breach in 1998 (Lehman et al. 2010). Flooding has produced a shallow wetland with spatially variable tides and flow, and temporally variable seasonal and yearly fluctuations in water levels, depending on the upstream freshwater supplies (Whitley and Bollens 2014). Over the past couple of decades, tule (*Schoenoplectus* spp.) has dominated the emergent marsh and has been expanding in the shallow northern end of Liberty Island (Ustin et al. 2015). Water primrose (*Ludwigia* spp.) has been documented in Liberty Island at least since 2004 but has increased in area since then (Khanna et al. 2012). The emergent marsh forms triangular shapes into the water that are separated by the original agricultural access roads between fields, with deposition starting along this edge and filling outward. These recovered wetlands now support a year-

round habitat for the critically endangered Delta Smelt, (*Hypomesus transpacificus*; Sommer et al. 2011).

The second area is the Central Delta, which is characterized by tidally active dynamic marshes. This area is composed of meandering channels and inundated islands, all created by land reclamation and building of levees in the early 1900s. Inundated islands arise from levee failure over time. This has created a diverse system of channels and large expanses of water with varying bathymetry and water velocity. Over recent years, the Central Delta has experienced major changes in its vegetation communities, with variable extents of invaded submerged plant communities (Santos et al. 2012), and dynamic floating communities (Khanna et al. 2012). Water primrose has been mapped in this area since the 2000s and surged after the population crash of pennywort (*Hydrocotyle umbellata*) in the past decade (personal observation). Until 2016, water hyacinth (*Eichhornia crassipes*) was chemically controlled by California State Park's division of Boating and Waterways, but the state did not have permission to spray water primrose (Division of Boating and Waterways, personal communication). Hence, each year, water hyacinth cover was removed by management but water primrose was not.

The submerged vegetation community consists of five native and four non-native species (Table 1), with the invasive Brazilian waterweed (*Egeria densa*) being the dominant species (Santos et al. 2012). The floating vegetation community is dominated by two invasive species, water hyacinth and water primrose (*Ludwigia grandiflora* ssp. *hexapetala* and *Ludwigia peploides*; Santos et al. 2009, Khanna et al. 2011) and also native species like pennywort (Table 1). The emergent vegetation community in the Delta is dominated by two cattail species (*Typha latifolia* and *Typha angustifolia*) and their hybrids, two tule species (*Schoenoplectus acutus* and *Schoenoplectus californicus*) and their hybrids, and the invasive common reed (*Phragmites australis*; Khanna et al. 2012).

There are two non-native water primrose species in the Delta, *L. peploides* ssp. *peploides* and *L. grandiflora* ssp. *hexapetala* (Zardini et al. 1991, Rejmánková 1992, Okada et al. 2009, Armitage et al. 2013). Water primrose, although nominally rooted, develops adventitious roots that can
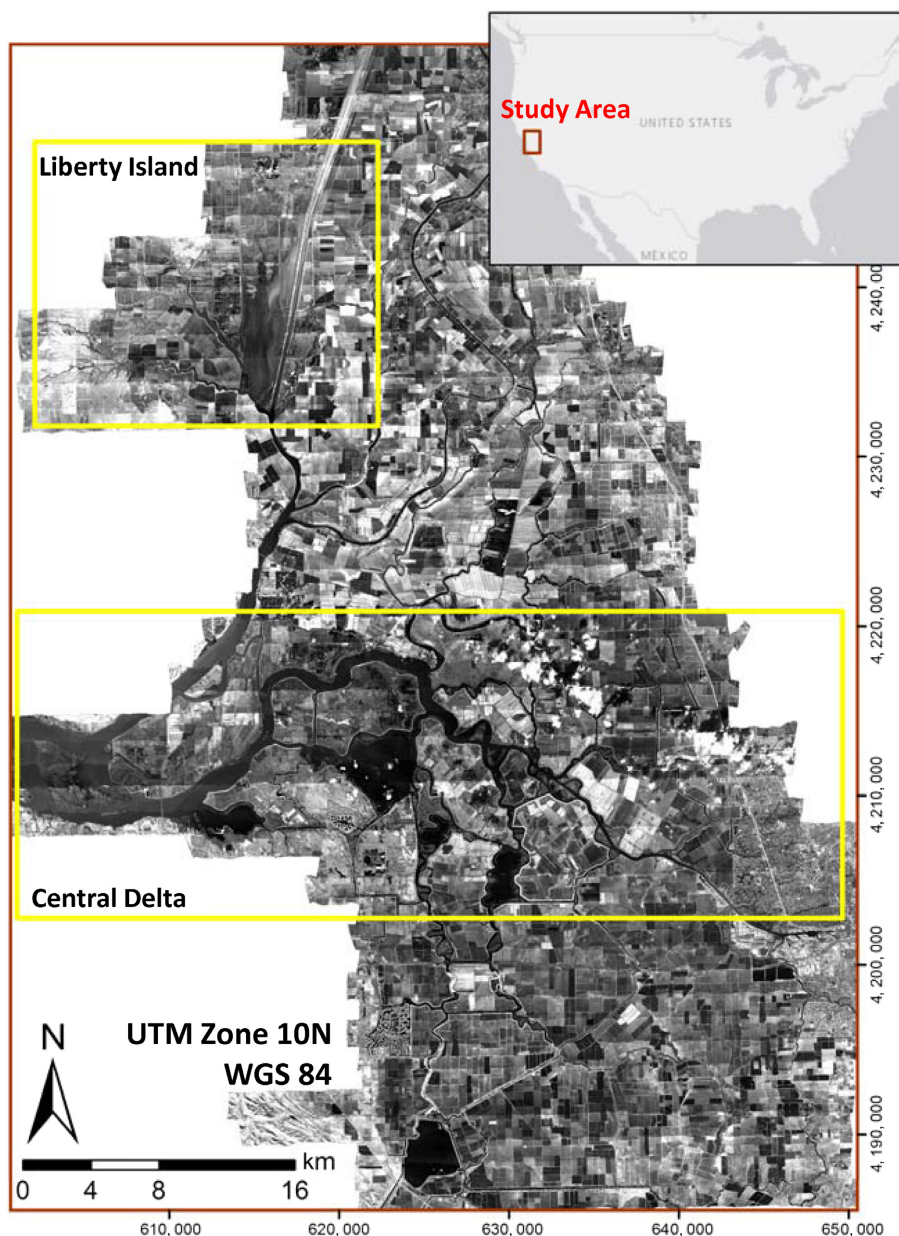
Fig. 1. Imagery extent of the Delta (2014 dataset, AVIRIS NIR band), acquired in 2004, 2008, and 2014. 2016 image extent is shown in yellow. Inset US map shows location of study site in red box.

draw nutrients directly from the water, which allow them to form floating canopies that extend several meters into the channel from the shore (Cook 1990, Rejmánková 1992). Hence, we refer to these two species as Floating Aquatic Vegetation; however, they are amphibious tolerating both aquatic and seasonally wet environments (Thouvenot et al. 2013a). Non-native water primrose species are native to South America and among the most invasive plants in the world (Cronk and Fuller 1995, Thouvenot et al. 2013a). While their distribution is limited to small patches in their native range, they can grow aggressively and rapidly in their new environment (Lambert et al. 2010, Nehring and Kolthoff 2011, Haury et al. 2014). A competitive life

Table 1. Vegetation communities and respective species composition (common and scientific names), and native and invasive aquatic species status of species in the Delta.

Vegetation community	Common name (Scientific name)	Status
Submerged aquatic vegetation (SAV)	Brazilian waterweed (*Egeria densa*)	Invasive
	Watermilfoil (*Myriophyllum spicatum*)	Invasive
	American pondweed (*Potamogeton nodosus*)	Native
	Curly leaf pondweed (*Potamogeton crispus*)	Invasive
	Sago pondweed (*Stuckenia pectinata*)	Native
	Fanwort (*Cabomba caroliniana*)	Invasive
	Coontail (*Ceratophyllum demersum*)	Native
	Waterweed (*Elodea canadensis*)	Native
Floating Aquatic Vegetation (FAV)	Water hyacinth (*Eichhornia crassipes*)	Invasive
	Water primrose (*Ludwigia* spp.)	Invasive
	Pennywort (*Hydrocotyle umbellata*)	Native
	Mosquito fern (*Azolla* spp.)	Native
	Duckweed (*Lemna* spp.)	Native
Emergent aquatic vegetation (EAV)	Cattail (*Typha* spp.)	Native
	Tule (*Schoenoplectus* spp.)	Native
	Common reed (*Phragmites australis*)	Invasive

history strategy with fast growth rates, both vegetative and sexual reproduction, high seed production and successful germination, plasticity of morphology and breeding systems due to polyploidy, allelopathy, and C4 photosynthetic mechanisms (Dandelot et al. 2005), all serve to make water primrose an ideal invasive species capable of engineering ecosystems to benefit its own growth (Dandelot et al. 2005, 2008, Thouvenot et al. 2013*a*, *b*). In addition to its effects on ecosystem equilibrium and functioning, water primrose mats also have detrimental effects on human health by providing habitat for mosquitoes transmitting the West Nile virus and inhibiting effects of larvicides (Meisler 2009).

Data collection

Liberty Island and the Central Delta were imaged by the Airborne Visible and InfraRed Imaging Spectrometer—next generation (AVIRIS-ng) and by the airborne HyMap sensor. In June of 2004 and 2008, spectroscopy data from the HyMap sensor (126 bands: 400–2500 nm, bandwidth: 10–15 nm) were collected over the Delta at 3 m ground resolution by HyVista Corporation (Sydney, Australia). In Fall of 2014 and 2016, AVIRIS-ng data (~430 bands: 350–2500 nm, bandwidth: 5–7 nm) were collected over the Delta at 2.5 m ground resolution by the Jet Propulsion Laboratory (JPL, Pasadena, California, USA). Image dataset details are given in Table 2. Data

Table 2. Acquisition dates, sensor, number of flightlines, and pixel size of spectroscopy datasets flown in that year.

Year	Dates	Sensor	No. Flightlines	Pixel size (m)
2004	6/25 to 7/9	HyMap	65	3
2008	6/29 to 7/7	HyMap	48	3
2014	11/14 to 11/25	AVIRIS-ng	60	2.5
2016	10/8 to 10/9	AVIRIS-ng	22	2.5

Note: The analysis for this study included only the 22 common flightlines present in all years.

were collected in 2-h windows before or after solar noon to minimize sunglint and close to low tide to minimize water column height over submerged aquatic vegetation (SAV; Hestir et al. 2008). Although image acquisition occurred in two different seasons, we believe this is not problematic because water primrose shows active growth from June through October, and senescence occurs in November (public communication: ISC 2018). As for the other communities, riparian plants are perennial and the dominant invasive submerged species, *E. densa*, is known to grow throughout the entire year (Santos et al. 2010). The two sensors used to acquire data differ in the number of spectral bands they acquire (HyMap with 126 bands, 10–15 nm bandwidth) and AVIRIS-ng (457 bands, 5–7 nm bandwidth); however, this study applies a post-classification change detection method which is robust to

radiometric and spectral differences because it compares the classified maps, not the bands themselves (Coppin et al. 2004, Lu et al. 2004).

Concurrent with image collection, Global Positioning System (GPS) locations of aquatic species patches were acquired in all years with ~1000–2000 field data points per year. Each location was recorded at a vegetation patch dominated by one species and at least 3 × 3 m in size, the resolution of the HyMap imagery. Supplementary information such as patch size, orientation, percent cover of each species, health, phenology, and photographs was also collected for each field location. Patch locations were converted to polygons in ArcMap (ArcGIS 10; ESRI, 380 New York Street, Redlands, California, USA) based on patch-size information to include both inter-patch and intra-patch variability of the classes to be classified. Yearly field data were divided into training and validation subsets for image classification and independent validation as described in section *Image classification*.

Image preprocessing

Both HyMap data and AVIRIS-ng data were atmospherically calibrated to surface reflectance by HyVista and JPL, respectively. Preliminary geocorrection of the imagery was also completed by HyVista and JPL using onboard GPS and inertial navigation instruments obtained concurrent with the overflights. Images georeferenced based on this information often suffered from residual misalignment of 2–4 pixels (personal observation). We performed a second level of geocorrection on the HyMap data using an orthorectification algorithm from Analytical Imaging and Geophysics, Boulder, Colorado (Aspinall et al. 2002). The images were georegistered to the United States Geological Survey (USGS) Digital Elevation Model with a resolution of 30 m. Average root mean square error was about 3 m or 1 pixel after geocorrection. Additionally, the AVIRIS-ng images from 2016 were co-registered to 2014 images using an automated image registration technique (Koltunov et al. 2012) that combines robust band-wise compensation for radiometric differences in images (Koltunov et al. 2008) with an iterative gradient-based video-sequence alignment method by Irani (2002), using the affine image motion model. Areas of large or systematic change in the scene (e.g., cloud masses) were excluded from the image motion estimation. As a result of the image co-registration, the residual pixel misregistration was reduced to less than a pixel, allowing more accurate analysis of annual changes in species distribution.

Earlier HyMap imagery from 2004 and 2008 was acquired at a 3 × 3 m resolution. We did not resample HyMap imagery to AVIRIS-ng resolution or vice versa because this would have required interpolation between pixels which is unnecessary at this stage since we are interested in change, not in the classification itself. We preferred to classify the images at the best possible resolution, but were able to calculate change at the same resolution for all years.

Image classification

To produce a set of candidate input variables for the random forest (RF) classifier, we used multiple techniques that capture reflectance properties across different regions of the electromagnetic spectrum and represent different biochemical properties of plants. To capture plant water content and cellulose, we calculated band indices and continuum removals over water and cellulose absorption features centered at 980 nm, 1200 nm, and 2100 nm wavelengths (Clark and Roush 1984). To estimate the proportion of water, soil, non-photosynthetic vegetation (NPV), green vegetation, and submerged vegetation within a pixel, we used spectral mixture analysis (Huete 1986, Smith et al. 1990, Adams et al. 1995). Finally, we created a spectral library of all emergent and floating species and used it to run a spectral angle mapper algorithm to detect species identity based on the angles between reflectance in consecutive bands and regions of the electromagnetic spectrum (Kruse et al. 1993, Alberotanza 1999, Hirano et al. 2003). The full list of input variables is described in Appendix A. All of these indices could be calculated, and procedures could be run on both sensor datasets using the same wavelengths.

We used these input variables in a RF machine learning algorithm (Breiman 2001) to classify (1) water, (2) submerged, (3) water primrose, (4) water hyacinth, (5) emergent, and (6) non-photosynthetic vegetation (a term for the dry, non-green plant materials in the image). Pennywort was classified in 2004 and 2008; however, in 2014 and 2016, the species occurred rarely in the Delta and therefore was not mapped as a separate

class. The three floating species, water primrose, water hyacinth, and pennywort, were classified at the genus level because we wanted to focus on the impact of water primrose on other floating species, and on the emergent and submerged plant communities. The attenuation of the submerged spectral signature by water, which absorbs almost all of the near-infrared and short-wave-infrared electromagnetic radiation, makes it difficult to differentiate submerged species (Hestir et al. 2008, Santos et al. 2012). More specifically, the less abundant native species can be differentiated while some non-native are more difficult to differentiate with airborne spectroscopy data because they have higher variability in their spectral signatures due the wider range of environments they can survive and persist in Santos et al. (2012). Because of this, we kept the submerged as a class and decided against differentiating native and non-native species, which should not be a problem as we expect that both native and non-native submerged species will respond similarly to light limitation imposed by the presence of water primrose.

Random forest is an automated algorithm that builds hundreds of classification-tree models by randomly selecting a subset of the training data to develop each tree (Breiman 2001). Each tree is grown to the largest extent possible, and there is no pruning or simplification of the tree. This is repeated many times to produce a large set of trees that are then used to determine the best fit class type for each pixel based on consistency across tree predictions, and each tree keeps a tally for each class for all pixels. Because the classifier produces a forest of trees and then chooses the most frequently selected class, it limits the problem of over-fitting (Breiman 2001). To classify a new object, it passes the input vector for that object (comprising of values for all the input variables listed in Appendix S1), down each of the classification trees in the forest.

We assessed accuracy of the classification using two metrics: overall accuracy, which is the percentage of all target classes that were correctly classified and ranges from 0 to 100% (Congalton 1996); and Cohen's kappa statistic, which is an indicator of the level of agreement between field data and the classification map that accounts for the probability of random agreement (Rosenfield and Fitzpatrick-Lins 1986).

Kappa values range from 0 to 1 where values >0.5 indicate good agreement and values >0.8 indicate excellent agreement.

Change detection

We calculated change detection (CD) statistics for three time-steps: 2004–2008, 2008–2014, and 2014–2016. For convenience, we will call them "change-pairs" and refer to them by the years included, for example, 2004–2008. Co-registration between images is critical for detecting change across multiple years. It has been shown that a sub-pixel registration accuracy of one-fifth of a pixel can nevertheless lead to CD errors as high as 10% (Townshend et al. 1992, Shi and Ehlers 1996, Dai and Khorram 1998). The Optimal Scale Change Detection (OSCD) algorithm as a way to overcome this limitation (Khanna et al. 2012). The OSCD is relatively robust to small co-registration errors between images because it detects change at a coarser spatial scale than the spatial resolution of the imagery. Using this method in a previous study, we determined the optimum scale of CD as 30 m for the HyMap 2004–2008 data (Khanna et al. 2012). To be consistent across years, we maintain this scale for all years. Hence, the CD window for HyMap 3 m data becomes 10 × 10 pixels while that for the AVIRIS-ng 2.5 m data becomes a 12 × 12 pixel window. For each CD window, we calculated change with Eq. 1:

$$\Delta P_{CS} = P_{CSt1} - P_{CSt2} \qquad (1)$$

where P_{CSt} is the percentage of pixels of class C in window S at time t (C = W: water, SAV: submerged, EAV: emergent and NPV, WH: water hyacinth, WP: water primrose). Change of 10% of pixels or less was considered to show no change to account for minor misalignment of images which can cause spurious detection of change. We extracted the number of CD windows where water primrose had either increased or decreased, that is, $|\Delta P_{LD}| > 10$, and labeled these as n^+ for the number of windows where $\Delta P_{LD} > 10$, and n^- for the number of windows where $\Delta P_{LD} < -10$. Further, for every class, C, we used the same notation with n_C^+ corresponding to the number of windows where $|\Delta P_C| > 5$ and $\Delta P_{LD} > 10$, and n_C^- corresponds to the number of windows where $|\Delta P_C| > 5$ and $\Delta P_{LD} < -10$. Thus, $n_C^+ < n^+$ and $n_C^- < n^-$ is always true.

Next, for each class, we calculated two metrics, response (r) and effect size. Response is a metric of whether the change in a particular class is ubiquitous throughout the Delta or site specific. We calculated it for both increases greater than (r_C^+) and decreases smaller (r_C^-) than 10% of the window (see Eq. 2).

$$r_C = (n_C/n) \times 100 \qquad (2)$$

A low response for a class c indicates infrequent change in the same geographic areas where water primrose changes, while a high response indicates frequent change coincident with changes in water primrose. Although we call this a response, we do not imply that it describes a direct response to change in water primrose cover. Instead, it describes the number of windows that show changes in cover of a class that coincide with changes in water primrose cover. The response variable describes change in location at the measured time step (2, 4, or 6 yr, in this case); any transitions occurring at smaller time-steps are not evaluated.

Effect size (Cohen 1969) is a useful method that standardizes the difference between two means (in our case, deviation from zero change) by quantifying the percent overlap between two sample distributions. Unlike significance tests, effect size provides a statistic that is independent of sample size and range of values. The effect size (e) indicates the direction (positive or negative) and the consistency and magnitude of change in the windows that show a response. Essentially, it is a metric of the effect of changing water primrose cover on each class since we are only looking at windows that show changes in water primrose cover and only in the immediate 900 m^2 (30 × 30 m) neighborhood. A strong effect size, that is, standardized departure from no change, combined with a strong response for class c indicates a ubiquitous and consistent change in a single direction, but a strong effect size combined with a weak response shows that while the change is consistent and unidirectional it is also site-specific.

$$e_C = (\mu_C/\sigma_c) \qquad (3)$$

where μ_C is mean and σ_c is the standard deviation of ΔP_C for all n_C windows. We repeated the calculation for both + and − change windows. This metric might be affected by the temporal

span of the change-pairs especially if the change is unidirectional and consistent, and the longer the intervening time, the stronger will be the effect. If the trend is scattered or weak, then it will not have much effect on the magnitude of effect size. Therefore, this metric is appropriate to detect the magnitude of the change driven by invasion of water primrose.

Our previous study in this region indicated that pixels were on average spatially autocorrelated up to a distance of 42 m (Khanna et al. 2012). Hence, we only included CD windows more than 42 m apart from any other window. We used the results of the CD analysis to determine the dominant direction of movement of water primrose within a window and for the delta in general. Simultaneously, we also ascertained the movement of other plant communities within that window. By evaluating this information, we could assess whether water primrose leads succession along the expected pathway or reverses it by encroaching into emergent marshes and converting them back to water primrose floating communities.

RESULTS

Water primrose in the Delta

Water primrose has increased fourfold in the two study areas of the Delta between 2004 and 2016, from 122 ha to 471 ha. The increase was slower from 2004 to 2014 (on average 12.7 ha per year), but it has accelerated in the past two years (110.9 ha per year; Table 3), and it was especially fast in Liberty Island.

The overall accuracy and Kappa coefficients for all four years (2004, 2008, 2014, and 2016) RF classification are shown in Table 4. Accuracies were over 85% and Kappa coefficients were over 0.82, which indicates excellent agreement between field data and image classification and

Table 3. Water primrose cover in hectares in Central Delta and Liberty Island from 2004 to 2016.

	Water primrose cover in hectares			
Location	2004	2008	2014	2016
Central Delta	84.8	106.5	216.2	388.3
Liberty Island	37.0	51.3	33.2	82.9
Total	121.8	157.8	249.4	471.3

Table 4. Kappa coefficients and overall accuracies for years of imagery classified.

Year	Overall accuracy (%)	Kappa coefficient (%)	Primrose kappa (%)
2004	86.9	84.0	82.0
2008	93.1	91.1	97.3
2014	86.7	83.5	89.3
2016	88.8	86.4	86.9

therefore a successful classification for change detection.

Community turnover due to primrose invasion

Central Delta.—In the Central Delta, water primrose increased from 85 ha to 107 ha from 2004 to 2008 (Table 3). From 2008 to 2014, water primrose extent doubled, to cover 216 ha. In just the last two years, from 2014 to 2016, there was

again a considerable increase in water primrose cover to 388 ha.

From 2004 to 2008, almost the same number of CD windows showed an increase and a decrease in water primrose. Water primrose increased in cover in 524 CD windows, while it decreased in 447 CD windows (Table 5). Percent increase and decrease per window was also similar and averaged between 24% and 26%. From 2008 to 2014, there were more CD windows showing increase in water primrose than decreases. 1300 CD windows recorded an increase in water primrose compared to only 551 showing a decrease in cover. Further, within a CD window, the percent increase was higher than the percent decrease, with average increase in a CD window of 37% while average decrease was 23%. In the last two years (from 2014 to 2016), there was again a higher number of CD windows where water

Table 5. Change detection statistics for all three change-pairs for four classes (water, submerged aquatic vegetation (SAV), emergent aquatic vegetation (EAV), and water hyacinth (WH)) with respect to change in water primrose cover in the Central Delta.

Central delta	Class	n/Class	Mean of ΔP	Standard deviation	Response r	Effect size, e
2004–2008						
Increase in water primrose >10% ($n = 524$)	Water	245	−0.124	0.339	0.468	−0.367
	SAV	*248*	*−0.040*	*0.294*	*0.473*	*−0.137*
	EAV	386	−0.097	0.242	0.737	−0.401
	WH	196	−0.196	0.233	0.374	−0.843
Decrease in water primrose >10% ($n = 447$)	*Water*	*137*	*0.083*	*0.412*	*0.306*	*0.202*
	SAV	185	0.208	0.357	0.414	0.583
	EAV	**324**	**0.213**	**0.220**	**0.725**	**0.971**
	WH	**198**	**−0.124**	**0.105**	**0.443**	**−1.188**
2008–2014						
Increase in water primrose >10% ($n = 1300$)	**Water**	**941**	**−0.511**	**0.320**	**0.724**	**−1.595**
	SAV	955	−0.081	0.341	0.735	−0.237
	EAV	*935*	*0.021*	*0.261*	*0.719*	*0.080*
	WH	**658**	**0.254**	**0.207**	**0.506**	**1.229**
Decrease in water primrose >10% ($n = 551$)	Water	170	−0.103	0.250	0.309	−0.414
	SAV	252	−0.054	0.249	0.457	−0.216
	EAV	**520**	**0.335**	**0.221**	**0.944**	**1.514**
	WH	138	0.092	0.237	0.250	0.386
2014–2016						
Increase in water primrose >10% ($n = 1719$)	*Water*	*333*	*−0.052*	*0.277*	*0.194*	*−0.189*
	SAV	745	−0.067	0.288	0.433	−0.233
	EAV	**1399**	**−0.237**	**0.202**	**0.814**	**−1.173**
	WH	755	−0.182	0.273	0.439	−0.664
Decrease in water primrose >10% ($n = 422$)	**Water**	**155**	**0.303**	**0.265**	**0.367**	**1.144**
	SAV	**296**	**0.237**	**0.331**	**0.701**	**0.715**
	EAV	293	0.056	0.248	0.694	0.226
	WH	231	−0.162	0.250	0.547	−0.645

Note: Combinations of high response and high effect size are highlighted in bold while effect sizes <0.2 are italicized.

primrose increased relative to the number of windows where it decreased. We found that 1719 CD windows recorded an increase in water primrose while only 422 recorded a decrease. Average increase was 30% while average decrease was 24%.

From 2004 to 2008, increases in water primrose came at the expense of water hyacinth (effect size: −0.8; Table 5; Fig. 2) and to a smaller extent, of emergent marsh and open water (effect size: −0.4). From 2008 to 2014, water primrose mainly grew over open water (effect size: −1.6), and water hyacinth increased in cover in close proximity to water primrose (effect size: 1.2). But in the last two years, 81% of the time, water primrose replaced emergent marsh vegetation (effect size: −1.2).

Areas that saw a decrease in water primrose between 2004 and 2008 were colonized by emergent marsh (effect size: 1.0) and, to a lesser extent, by SAV (effect size: 0.6). Areas where water primrose cover decreased between 2008 and 2014 were almost exclusively (94% of the time) and strongly (effect size: 1.5) occupied by emergent marsh in 2014. Finally, between 2014 and 2016, areas with decreased cover of water primrose were colonized 70% of the time by SAV (effect size: 0.7) and occasionally reverted to open water (effect size: 1.1).

Liberty Island.—In Liberty Island, the rates of water primrose growth were more variable than in the Central Delta, and fast growth was observed especially between 2014 and 2016. Water primrose increased in cover from 37 ha to

51 ha from 2004 to 2008. It decreased to 33 ha from 2008 to 2014, and then, it more than doubled to 83 ha from 2014 to 2016 (Table 3).

Spatially, from 2004 to 2008, water primrose cover in Liberty Island increased in twice as many CD windows as decreased; it increased in 199 CD windows while it decreased in 107 (Table 6). Average increase in a CD window was 24%, while average decrease was 19%. Between 2008 and 2014, the pattern was reversed with twice as many CD windows showing a decrease in cover compared to CD windows showing an increase in cover. But the average percent increase in a CD window was higher (38%), compared to the average decline in cover (22%). In the last two years, increase in cover was observed in 332 CD windows, while only 49 showed a decline in cover. Average increase per CD window was 30%, while average decrease was 19% (Table 6).

From 2004 to 2008, 67% of the time, water primrose expanded over open water (effect size: −1.4; Table 6; Fig. 3). In the few sites where water hyacinth decreased, water primrose moved into the emptied niche (effect size: −0.8). From 2008 to 2014, water primrose continued to expand strongly toward open water and also started to encroach on submerged mats. By 2014, most of the open water and submerged area sandwiched between emergent marshes was already taken over by water primrose (Fig. 4). Hence, as availability of open water and submerged vegetation decreased, water primrose primarily displaced emergent marsh, 92% of the
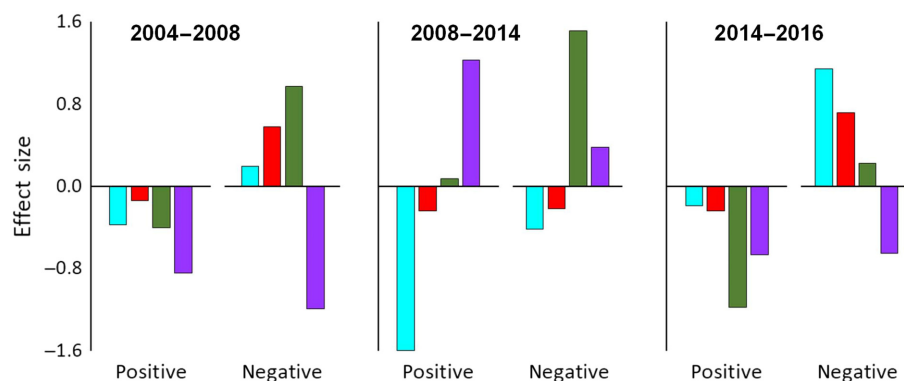

Fig. 2. Cohen's effect sizes for all three-year pairs in the Central Delta showing direction (sign) and magnitude (value) of change (*y*-axis) in water (cyan), SAV (red), EAV (green), and water hyacinth (purple).

Table 6. Change detection statistics for all three change-pairs for four classes (water, submerged aquatic vegetation (SAV), emergent aquatic vegetation (EAV), and water hyacinth (WH)) with respect to change in water primrose cover in the Liberty Island region of the Delta.

Liberty island	Class	n/Class	Mean of ΔP	Standard deviation	Response r	Effect size, e
2004–2008						
Increase in water primrose >10% (n = 199)	**Water**	134	−0.465	0.342	**0.673**	**−1.361**
	SAV	98	0.123	0.241	0.492	0.510
	EAV	151	0.061	0.260	0.759	0.232
	WH	37	−0.112	0.140	0.186	−0.798
Decrease in water primrose >10% (n = 107)	*Water*	*35*	*0.015*	*0.164*	*0.327*	*0.094*
	SAV	*16*	*0.020*	*0.142*	*0.150*	*0.144*
	EAV	93	0.266	0.206	**0.869**	**1.290**
	WH	36	−0.094	0.121	0.336	−0.781
2008–2014						
Increase in water primrose >10% (n = 140)	**Water**	92	−0.522	0.326	**0.657**	**−1.598**
	SAV	82	−0.229	0.376	0.586	−0.610
	EAV	101	0.109	0.285	0.721	0.384
	WH	38	0.141	0.163	0.271	0.865
Decrease in water primrose >10% (n = 273)	Water	96	−0.097	0.153	0.352	−0.635
	SAV	98	−0.052	0.198	0.359	−0.262
	EAV	256	0.276	0.206	**0.938**	**1.345**
	WH	43	0.084	0.142	0.158	0.591
2014–2016						
Increase in water primrose >10% (n = 332)	Water	30	−0.121	0.238	0.090	−0.509
	SAV	91	−0.195	0.296	0.274	−0.659
	EAV	306	−0.290	0.204	**0.922**	**−1.420**
	WH	82	0.108	0.208	0.247	0.518
Decrease in water primrose >10% (n = 49)	*Water*	*12*	*0.020*	*0.158*	*0.245*	*0.124*
	SAV	22	0.118	0.213	0.449	0.555
	EAV	38	0.110	0.195	0.776	0.563
	WH	*29*	*−0.051*	*0.268*	*0.592*	*−0.191*

Note: Combinations of high response and high effect size are highlighted in bold while effect sizes <0.2 are italicized.
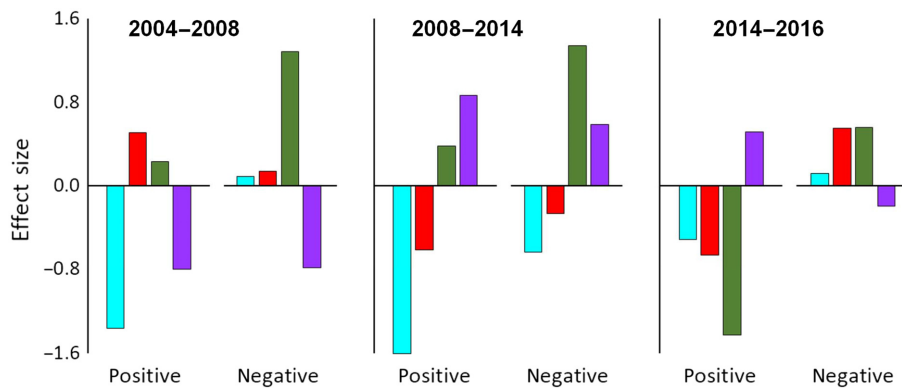

Fig. 3. Cohen's effect sizes for all three-year pairs in Liberty Island region showing direction and magnitude of change in water (cyan), SAV (red), EAV (green), and water hyacinth (purple).

time (effect size: −1.4). On the other hand, whenever water primrose retreated, emergent marsh increased in that area strongly and universally throughout the 13-yr period in this region.

Discussion

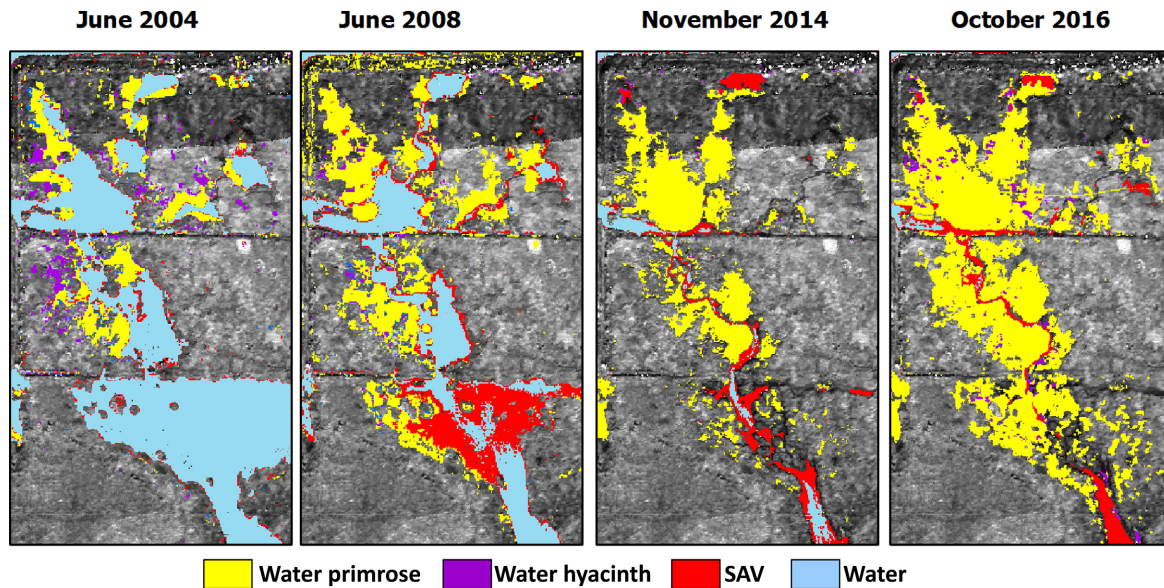In the early 2000s, the floating community in the Delta was dominated by water hyacinth,

Fig. 4. Water primrose expansion into open water and submerged vegetation habitat (June 2008 and November 2014) and finally into emergent marsh habitat (October 2016).

pennywort, and water primrose (Khanna et al. 2012). However, over the past decade, pennywort cover has reduced considerably and water primrose cover has surged. Until 2016, water hyacinth was chemically treated as part of California's management strategy, but the state did not have permission to spray water primrose (Division of Boating and Waterways, personal communication). In this study, we found that over the last 12 yr (2004–2016), there was a fourfold increase in water primrose area. Until 2014, the majority of this expansion was over open water and into areas freed of water hyacinth, but in the last two years, water primrose started to encroach into areas previously dominated by emergent marsh.

Many studies have remarked on the amphibious nature of water primrose and documented its presence in both aquatic habitat and wet to seasonally wet meadows (Meisler 2009, Thouvenot et al. 2013a, Haury et al. 2014). But, to our knowledge, very few studies have previously documented this encroachment of water primrose over emergent marshes, with the exception of Dutartre et al. (public communication, 2013) who mention that water primrose has replaced several hectares of reed beds in Erdre Valley, France. Here, we document that between 2004 and 2014, water primrose spread into open water habitat 63% of the time. During the same period, any retreat in water primrose was followed, 87% of the time, by a strong expansion of the emergent marsh. This suggests that water primrose colonization accelerated the terrestrialization of the aquatic habitat, likely by increasing sedimentation and making it easier for emergent marsh to expand into the region when water primrose retreated. Water primrose is known to increase sedimentation leading to hyper-sedimentation, silting, and lowering sediment transport capacity (Dandelot et al. 2005, Nehring and Kolthoff 2011). Water primrose also has a denser and more intricate root network under the mat (Rejmánková 1992) than for example water hyacinth, increasing its effectiveness in trapping sediment by acting as both a submerged and a floating plant (Thouvenot et al. 2013a, Haury et al. 2014). Thus, water primrose invasion and retreat likely leads to lateral expansion of the emergent marsh moving the boundary of the pulse stability that keeps the submerged, floating, and emergent communities in relative equilibrium.

However, we also found that once the aquatic habitat was fully occupied, water primrose switched from growing over water to growing

over emergent marsh, slowly taking over and expanding into both tule and cattail marsh beds, 87% of the time between 2014 and 2016 (Figs. 4, 5a). Armitage et al. (2013) described two forms of water primrose, one aquatic and one terrestrial, showing that the terrestrial form had more root biomass, shorter internodes and stems, and more secondary ramifications, being generally more stressed and exhibiting slower growth than the aquatic form (Meisler 2009, Lambert et al. 2010, Haury et al. 2014). These characteristics suggest that the terrestrial form of water primrose cannot spread as fast as the aquatic form, likely explaining why we observed water primrose occupying aquatic habitats first and then, when it was not able to occupy deeper open water, it expanded over the terrestrial habitat. Thus, our change detection analysis revealed that water primrose can change successional pathways, either by promoting succession when it moves into open water or arresting or reversing succession when it expands into emergent marsh and eventually replaces it.

This study also shows that water primrose acts somewhat differently than water hyacinth, the other major aggressive floating invasive in this ecosystem. Our previous study showed that water hyacinth spread over submerged mats as often as it spread over open water habitat (Khanna et al. 2012), while our current results show water primrose spreading into open water far more effectively (average effect size: −0.94) than over the submerged mats (average effect size: −0.06). And yet, this does not mean that the open water areas that water primrose spread into were not previously occupied by submerged vegetation as this could be an artifact of the time span between measurement periods. The water hyacinth analysis was an annual analysis with 1-yr time-steps, and our current study is over larger time-steps of 2, 4, and 6 yr. These larger time-steps might mask the intermediate step of submerged vegetation expansion into open water before it is then taken over by water primrose. Analysis at a finer temporal scale would be necessary to determine whether water primrose favors habitat already colonized by submerged vegetation or open water. Nonetheless, water hyacinth has less root material and more aerenchyma tissue than water primrose, and because it is a true-floating macrophyte, it might require the anchoring support offered by submerged vegetation

before spreading into open water (Khanna et al. 2012). Water hyacinth is also more tolerant of deeper water since it is a truly floating macrophyte (Penfound and Earle 1948) while water primrose is a rooted emergent plant known to expand by creeping over the water column (Rejmánková 1992). We believe that the stabilizing and flow-reducing characteristics of submerged vegetation are important for water hyacinth to survive in otherwise high-flow channel environments, where otherwise it would be swept away in the current. The only habitat where water hyacinth is able to capitalize on its ability to grow over much deeper waters is flooded islands where water flow velocities are very low. Because of this dynamic, water hyacinth does not have such a strong effect in sedimentation as reported for water primrose; thus, its ability to provide substrate for other plants is probably lacking. In our previous study, we found a similar push-pull relationship of water hyacinth with the emergent marsh—marsh expands in regions when water hyacinth retreats and vice versa (Khanna et al. 2012). Water hyacinth mats can surround tule stands and slowly push them out (Fig. 5b) but water hyacinth does not climb over the tule stands as we found with water primrose (Fig. 5a) and this relationship is hence much weaker (Khanna et al. 2012). When water hyacinth is managed/removed or decreases in area, the emergent marsh area increases (response: 77%; effect size 0.35 for local change <25%, 0.92 for local change >30%) but again, not as strongly and universally as it does in response to decrease in water primrose (response: 86%; effect size 1.07). Thus, water primrose presents a bigger threat to emergent marsh in the Delta than water hyacinth.

Water primrose cover in the study area has increased more than fourfold from 2004 (122 ha) to 2016 (471 ha) exhibiting almost exponential growth in recent years. Taking into account both submerged and floating macrophytes, invasive species cover in the Delta has increased from 9.5% of waterways in 2008 to more than a third of the waterways area in 2016. Thus, as hypothesized by Gaertner et al. (2014), it appears likely that the Delta ecosystem is rapidly undergoing a regime shift from a sparsely vegetated intertidal region with turbid water to a heavily vegetated intertidal region with clear water (Nichols et al. 1986, Hestir et al. 2013, 2016). But longer time
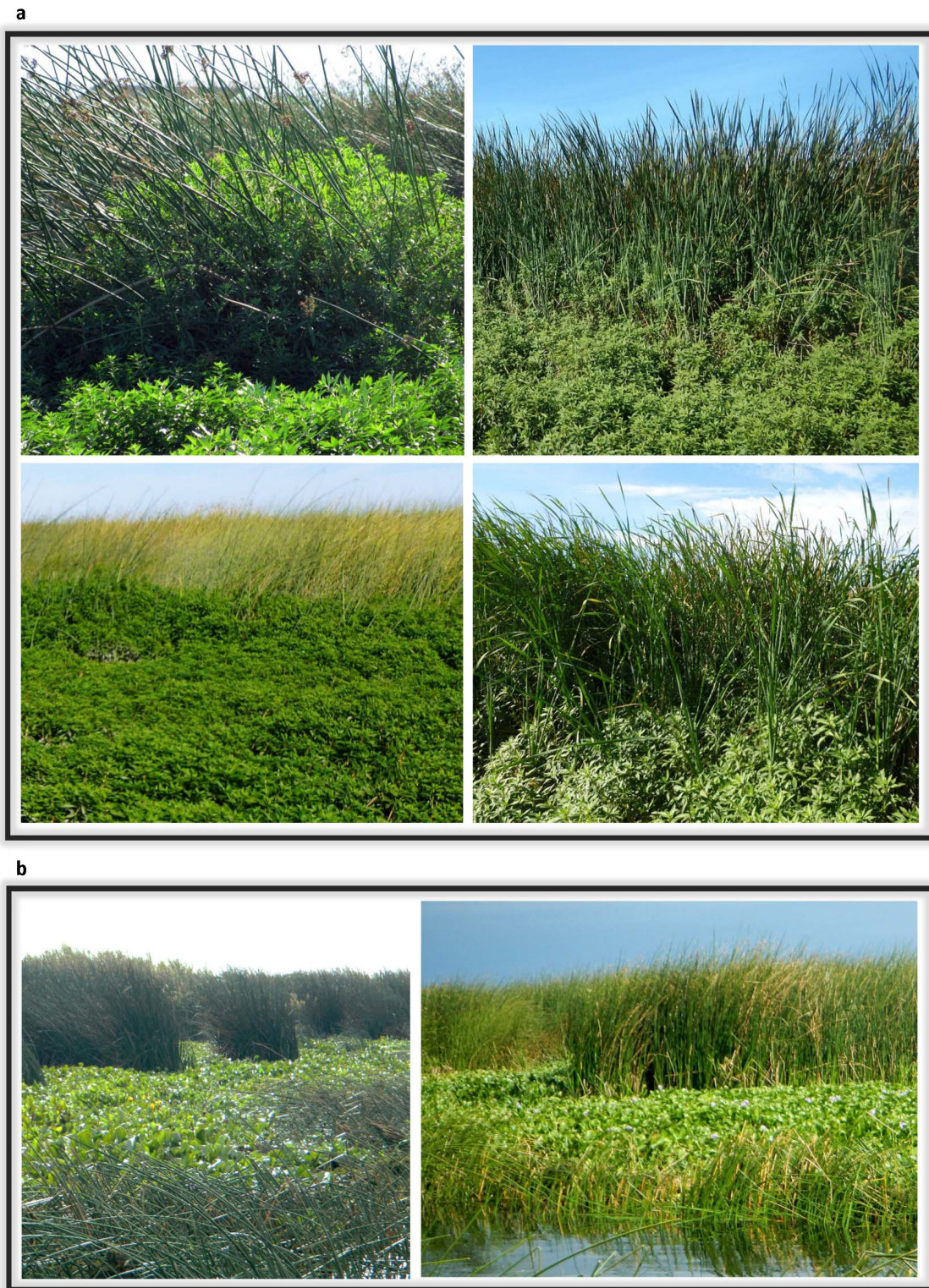
a

b

Fig. 5. Encroachment into tule (left panel) and cattail (right panel) marsh beds by (a) water primrose and (b) water hyacinth.

series and more study is needed to confirm such a shift and estimate its magnitude and long-term impact on ecosystem dynamics.

Conclusion

The Sacramento-San Joaquin Delta has been invaded by many invasive species that have acted as ecosystem engineers and continue to mold the ecosystem to their advantage (Cohen and Carlton 1998, Hestir et al. 2016). One of the two major invasive floating aquatic macrophytes in the Delta, water primrose has seen an almost exponential increase since 2004, its area matching that of water hyacinth. Active management for this species has been approved as of 2016 using chemical spraying, while water hyacinth has been managed since the 1990s. Our study illustrated the potential for water primrose to change successional pathways, thereby profoundly affecting the balance of various plant communities in the Delta. The dual successional effects of water primrose invasion might make it a more problematic invasive species, and it may become more threatening to the native marshes of the Delta. Hence, it is imperative to develop and implement an effective integrated management plan for controlling the spread of both water primrose species present in the Delta today.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2418/full