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Authors

Santos, Maria J
Khanna, Shruti
Hestir, Erin L
et al.

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Measuring landscape-scale spread and persistence of an invaded submerged plant community from airborne remote sensing

MARIA J. SANTOS,^{1,2,5} SHRUTI KHANNA,¹ ERIN L. HESTIR,^{1,3} JONATHAN A. GREENBERG,^{1,4} AND SUSAN L. USTIN¹

¹Center for Spatial Technologies and Remote Sensing (CSTARS), Department of Land, Air and Water Resources, University of California, One Shields Avenue, Davis, California 95616 USA

²Department of Innovation, Environmental and Energy Sciences, Utrecht University, Heidelberglaan 2, P.O. Box 80115, 3508 TC Utrecht, The Netherlands

³Department of Marine, Earth and Atmospheric Science, North Carolina State University, Raleigh, North Carolina 27695 USA

⁴Department of Geography, University of Illinois, Urbana-Champaign, Illinois 61801 USA

Abstract. Processes of spread and patterns of persistence of invasive species affect species and communities in the new environment. Predicting future rates of spread is of great interest for timely management decisions, but this depends on models that rely on understanding the processes of invasion and historic observations of spread and persistence. Unfortunately, the rates of spread and patterns of persistence are difficult to model or directly observe, especially when multiple rates of spread and diverse persistence patterns may be co-occurring over the geographic distribution of the invaded ecosystem. Remote sensing systematically acquires data over large areas at fine spatial and spectral resolutions over multiple time periods that can be used to quantify spread processes and persistence patterns. We used airborne imaging spectroscopy data acquired once a year for 5 years from 2004 to 2008 to map an invaded submerged aquatic vegetation (SAV) community across 2220 km² of waterways in the Sacramento-San Joaquin River Delta, California, USA, and measured its spread rate and its persistence. Submerged aquatic vegetation covered 13–23 km² of the waterways (6–11%) every year. Yearly new growth accounted for 40–60% of the SAV area, ~50% of which survived to following year. Spread rates were overall negative and persistence decreased with time. From this dataset, we were able to identify both radial and saltatorial spread of the invaded SAV in the entire extent of the Delta over time. With both decreasing spread rate and persistence, it is possible that over time the invasion of this SAV community could decrease its ecological impact. A landscape-scale approach allows measurements of all invasion fronts and the spatial anisotropies associated with spread processes and persistence patterns, without spatial interpolation, at locations both proximate and distant to the focus of invasion at multiple points in time.

Key words: distribution; imaging spectrometry; invasive species; remote sensing; spread and persistence; submerged aquatic vegetation.

INTRODUCTION

Climate change, habitat loss and conversion, and biological invasions are the leading threats to global biodiversity and its processes, and are also associated with major economic impacts (Mooney and Cleland 2001, Pejchar and Mooney 2009). Invasive alien species affect native species, communities, and ecosystems in different directions, magnitudes, and extents. Invasive alien species can affect evolutionary processes (Mooney and Cleland 2001), decrease the abundance and diversity of resident species (Vilá et al. 2011), promote community disassembly (Sanders et al. 2002), enhance productivity and other ecosystem processes (Vilá et al. 2011), and affect human well-being (Pejchar and Mooney 2009).

The effects of invasions are felt at different organizational, spatial, and temporal scales as the process of invasion itself is phased throughout time and space. To fully assess the impacts of invasive alien species it is crucial to assess their processes of spread and patterns of persistence.

Spread and persistence are components of dispersal and establishment processes. While these processes are often long-term, they occur at a faster pace when a species becomes invasive, often limiting early control of invasions (Rejmánek 2000, Fletcher and Westcott 2013). Spread is a spatial process that occurs through gradual extension of occupied areas of suitable habitat, or through saltatorial or discontinuous occupation of distant habitat areas (Andow et al. 1990, Hastings et al. 2005). For invasive species, this process is exacerbated by the presence of multiple dispersal vectors, such as humans, wildlife, vehicles, etc., which increase their invasive potential (Neubert and Parker 2004). Spread is

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⁵E-mail: m.j.ferreiradossantos@uu.nl

often the time following introduction until the establishment in a new location. Spread limits and is limited by the ability of the species to persist in the new habitat. Persistence represents the survival of individuals over time at a given location (Weiher et al. 1996, Rouget and Richardson 2003). A sufficient supply of viable propagules (seeds, plantlets, rhizomes, and other plant fragments) allows a species to persist and maintain existing distributions. Both spread and persistence are influenced by species traits (Theoharides and Dukes 2007, Buoro and Carlson 2014), and by external factors such as disturbance (Firn et al. 2008) and resource availability (Funk and Vitousek 2007). However, the effectiveness of a trait, e.g., response to disturbance and resource use, is contextual and at different times the same traits may be advantageous, negligible, or even detrimental. Spread and persistence are also influenced by the extent of potential invasible area, connectivity, disturbance, temporally fluctuating resources, resource-use efficiency, competition–colonization trade-offs, storage effects, propagule pressure, species sorting, and genetic diversity (Hastings et al. 2005, Funk and Vitousek 2007, Theoharides and Dukes 2007, Davis 2009).

Assessments of spread and persistence are fundamental for understanding the dynamics of invasive species and the processes that govern their distribution (Ellner and Schreiber 2012, Buoro and Carlson 2014). This understanding is key for management activities that eradicate or reduce the effects of an alien invasive species on impacted ecosystems (Fletcher and Westcott 2013), and to developing process-based or statistical models that predict future rates of spread and new invasions (Ellner and Schreiber 2012, Ge et al. 2013). Yet, making observations of spread and persistence is a non-trivial challenge: spatial anisotropies in spread processes and temporal variations in the rates make estimates difficult (Gilbert and Liebhold 2010). While controlled replicated experiments have shown that spatial and temporal aspects of spread affect our predictions of invasion outcomes (Giometto et al. 2014), field surveys with large sample sizes are few and may provide only limited estimates of spread rates, especially when the origin of invasion is unknown (Gilbert and Liebhold 2010). The most accurate records come from mapping invasion fronts over successive years; however, these methods often fail to detect long-distance dispersal events (Hastings et al. 2005). The best estimates come from large data sets systematically acquired over extended time periods that cover large areas at sufficient spatial resolution (Fletcher and Westcott 2013). Remote sensing approaches provide synoptic information over large spatial scales, being able to measure both local and regional scales simultaneously (Mack et al. 2007). Remote sensing data can produce accurate species and community distributions at both fine spatial and temporal resolutions (Ackleson and Klemas 1987, Vis et al. 2003, Williams et al. 2003, Gullström et al. 2006, Silva et al. 2008, Santos et al. 2012). Such resolution scales

facilitate characterizing the spatial and temporal aspects of spread and persistence.

Of possible remote sensing technologies, imaging spectrometers that measure hundreds of contiguous narrow spectral bands for each pixel in a digital image have shown the greatest success in mapping invasive species (Lass et al. 2002, Ustin et al. 2002, Silvestri et al. 2003, Williams et al. 2003, Hestir et al. 2008), assessing patterns of establishment (Lass et al. 2002, Vis et al. 2003) and invasion processes (Ustin et al. 2002, Arzandeh and Wang 2003), as well as assessing the risk of invasion (Lass et al. 2002, Arzandeh and Wang 2003, Glenn et al. 2005, Bradley and Mustard 2006), understanding invasion's environmental context (Silvestri et al. 2003, Asner and Vitousek 2005, Andrew and Ustin 2008) its potential impacts (Santos et al. 2009, 2011), and management efficacy (Santos et al. 2009). Imaging spectrometers are also necessary to meet the challenges of detecting invasive species in the aquatic environment (Hestir et al. 2008).

The Sacramento San Joaquin River Delta system, California, USA has been subject to many invasion events in terrestrial and aquatic ecosystems (Cohen and Carlton 1995, 1998, Light et al. 2005). The submerged aquatic vegetation (SAV) has undergone several invasion events by species like European watermilfoil (*Myriophyllum spicatum*) and more recently (since 1999), Brazilian waterweed (*Egeria densa*) dominates the submerged aquatic vegetation community and it affects community structure and composition by facilitating persistence of nonnative species and making it less likely that native species establish (Santos et al. 2011, 2012). This makes the community ideal to test the use of high spectral, high spatial resolution remote sensing to measure rates of spread and patterns of persistence in an invaded submerged aquatic vegetation community. In this study we used airborne imaging spectroscopy data (also referred to as hyperspectral remote sensing) to estimate the rates of spread and map patterns of persistence of the invaded submerged aquatic vegetation community inhabiting the Sacramento–San Joaquin River Delta from 2004 to 2008. Specifically, we asked three questions in this study: (1) What is the distribution of the invaded SAV community and how does it change over time? (2) What is the rate of spread of the SAV community? (3) How much of the yearly growth persists from one year to the next and how much is lost? We will discuss the results in light of the potential mechanisms that can be driving the spread and persistence patterns of an invaded submerged aquatic plant community.

METHODS

Study area

The Sacramento–San Joaquin River Delta in the Central Valley of California has all the characteristics that facilitate spread and persistence of invasive aquatic species (Jassby and Cloern 2000, Lucas et al. 2002). The

ivers form an inverted inland delta that exits into San Francisco Bay through the Carquinez Strait. It comprises an area of 2220 km² of highly interconnected waterways (Fig. 1a). The Delta has two daily tidal stages that alter fresh water availability, water levels, thermal gradients, and create mixing of the multiple sources of organic matter and sediments (Jassby and Cloern 2000), all of which create diverse habitats for native and non-native species (Cohen and Carlton 1995, Lucas et al. 2002). The Delta's geographical setting, in close proximity to San Francisco Bay, which is a source of many invasions, results in high propagule pressure from multiple vectors (boats, populations, etc.), and dynamic species sorting (Cohen and Carlton 1998). At the submerged plant community level, the number of native to nonnative plant species is 1.25:1 (Santos et al. 2011, 2012). This ratio has been achieved over the last 30 yr, and currently the SAV community is composed of five native species (waterweed *Elodea canadensis* Michx., coontail *Ceratophyllum demersum* L., sago pondweed *Stuckenia pectinata* (L.) Börner, broadleaf sago pondweed *Stuckenia filiformis* (Pers.) Börner, and American pondweed *Potamogeton nodosus* Poir.) and four nonnative species (Brazilian waterweed *Egeria densa* Planch., Eurasian watermilfoil *Myriophyllum spicatum* L., Carolina fan-worth *Cabomba caroliniana* Aubl., and curlyleaf pondweed *Potamogeton crispus* L.). Brazilian waterweed is the dominant species, occurring by itself or dominating the mixed communities (Santos et al. 2011, 2012). Eighty to ninety percent of the submerged vegetation cover in the Delta is Brazilian waterweed, and it contributes

70–90% of the submerged vegetation biomass in the Delta (Cohen and Carlton 1995). This high proportion of nonnative species likely leads to competition–colonization trade-offs and potential for rapid shifts in species distributions and community composition (Santos et al. 2011).

Data collection

Submerged aquatic vegetation was mapped annually using airborne imaging spectroscopy data acquired in late June–early July in 2004, 2005, 2006, 2007, and 2008 (Hestir et al. 2008, Khanna et al. 2011). We acquired 64 flightlines each year using the HyMap sensor to cover the ~2500-km² extent of the Delta at a 3-m ground resolution (Fig. 1b). HyMap spectroscopic imagery contains information in 128 bands per pixel at 10-nm bandwidths in the visible and near-infrared (VNIR; 450–1500 nm), and 15–20 nm bandwidths through the shortwave infrared (SWIR; 1500–2500 nm). The flightlines were acquired in an east–west orientation, at an altitude of ~1510 m. Imagery was collected during low tides in late morning and early afternoon to maximize surface exposure of the submerged vegetation and to minimize sun glint at the water surface. The images were converted to apparent surface reflectance using the HyCorr atmospheric correction software (Hyvista, Sydney, Australia). We used an orthorectification algorithm (Analytical Imaging and Geophysics, Boulder, Colorado, USA) to orthorectify the imagery using the United States Geologic Survey National Elevation Set Digital Elevation Models

FIG. 1. (a) Location of the Sacramento–San Joaquin River Delta in California, USA. The Delta corresponds to the confluence area of the Sacramento (flowing from the north) and the San Joaquin (flowing from the south) rivers. The gray outline represents the legal Delta, which defines the jurisdiction for the study area water management. (b) Image of the 2005 HyMap flightline mosaic. It corresponds to 65 flightlines that have been radiometrically corrected and orthorectified at a root mean-square error (RMSE) < 1.0 pixel.

and a set of 1-foot (covering 30 flightlines) and 1-m (covering 34 flightlines) color orthophotos (1 foot = 0.3 m). A minimum of 20 ground control points with a total root mean-square error ≤ 1.0 pixel were used for each flightline (Fig. 1b).

Field data collection was conducted simultaneously with image data acquisition. Each year >700 locations of submerged aquatic vegetation and water were collected using Differential Global Positioning System (DGPS) during the period of imagery acquisition (total field locations were over 1000 every year; Table 1). DGPS locations of large ($\geq 3 \times 3$ m), homogenous patches of submerged aquatic vegetation, patch size, percent cover, dominant species and other co-occurring species, and algal cover were recorded by survey crews in six boats distributed across the study system. At DGPS locations of water we verified absence of macro/filamentous algae or vegetation and assessed turbidity with a Secchi disk.

Data analysis

Spectral properties of SAV.—Submerged aquatic vegetation has general spectral features similar to land plants; there are also characteristic differences (Fig. 2). The strong light absorption by plants between 400 and 700 nm, which is primarily a function of photosynthetic pigments, is influenced by the absorption and scattering processes in the water column caused by the dissolved and suspended material in the water column (Phinn et al. 2008, Brando et al. 2009, Hedley et al. 2012). Terrestrial vegetation typically exhibits high reflectance in the near-infrared (NIR; 700–1100 nm) due to multiple scattering of photons in the leaves and the canopy, and some absorption features, with some characteristic absorption features in the shortwave-infrared region (SWIR; 1100–2500 nm) due to leaf water, leaf carbon compounds, and other biochemicals such as nitrogen (Ustin et al. 2004). Thus, the near- and shortwave-infrared regions are most useful for discriminating submerged vegetation from water and emergent vegetation (Fig. 2).

The overlying water column influences the spectral signature of SAV, particularly in the visible region. The reflectance signal of SAV at the water surface can be reduced at depth due to attenuation of light as it passes through the water column (Fig. 2). Water depth in the Delta varies widely based on bathymetry and tidal variability, although we controlled for this as much as possible by acquiring imagery during low tides. Hestir et al. (2012) reports that in 2008 the mean depth of the water column to the SAV canopy was 0.53 m with a range of 0–4.9 m. The concentrations of in-water constituents (primarily suspended sediment and phytoplankton) also vary across the region (Cohen and Carlton 1995, Hestir et al. 2008, Santos et al. 2012) but did not vary significantly between 2004 and 2008 based on California state records. Additionally, nonlinear spectral mixing occurs as epiphytic algae that often grow on SAV, and emergent algal mats that form on top of SAV canopies, obscuring the spectral target. Nonetheless, because of water flows, epiphytes and mats only accumulate where they can anchor to the rooted SAV, thus in this system they can be used as indicators of the presence of SAV. While we know that certain SAV species are separable through the visible region (Santos et al. 2012), we opted not to separate SAV species in this analysis but to focus on the SAV community dynamics.

Hierarchical decision trees for SAV detection.—Given the spectral properties of SAV in the Delta, we used a combination of spectral unmixing (Spectral Mixture Analysis; SMA), spectral angle mapper (SAM), and red edge parameters to overcome the mixing problem and to discriminate SAV from other water constituents, and to isolate it from algae while taking variability between flightlines into account (Hestir et al. 2008). This method was implemented in a hierarchical decision tree (Hestir et al. 2008) and updated in Khanna et al. (2011), with the following nodes. Since it is a tree structure the nodes may or not be linear (see figures in Khanna et al. 2011):

Node 1: Remove land pixels: We used the US Bureau of Reclamation GIS layer of waterways to delineate water and land areas. The line maps of waterways were overlaid on the imagery, and the water

TABLE 1. Classification accuracies for submerged aquatic vegetation (SAV) for all the years analyzed, using all the field locations for all the classes (water, SAV, emergent, floating; Khanna et al. 2011).

Imagery date	Total data points	Accuracy		
		SAV User's	SAV Producer's	SAV kappa coefficient
2004	1900	98.97 (92.94)	61.98 (85.87)	0.98 (0.86)
2005	2329	94.70 (99.65)	72.48 (92.31)	0.92 (0.91)
2006	2753	93.81 (96.08)	84.39 (90.74)	0.88 (0.83)
2007	454	98.85 (89.09)	83.05 (80.05)	0.85 (0.82)
2008	685	90.91 (82.3)	62.35 (65.00)	0.91 (0.88)

Notes: Accuracy values are shown for training data (60% of field observations) and test data (40% of field observations; in parentheses). Kappa coefficient is also a measure of accuracy.

FIG. 2. (a) Spectral profiles for the SAV community and for epiphytic algae and water from 2004 to 2008 in the Sacramento–San Joaquin River Delta. Note: there is no spectral profile for algae in 2004. (b) Water (red) and SAV (blue) mNDVI (red-edge NDVI) on the x -axis and frequency on the y -axis.

boundaries matched with the edge of the water in the images. All land pixels outside the line boundary were masked.

Node 2: Because water levels are dynamic, we used spectral mixture analysis to remove remaining levee banks not masked in node 1. We used an unconstrained linear spectral mixture analysis (SMA) with spectral endmembers extracted from the imagery for aquatic vegetation, water, and soil, using overlying field locations. We defined all candidate aquatic pixels as those with a SMA-water fraction $\geq 10\%$.

Node 3: Pixels that had SMA-water $\geq 10\%$ and reflectance in the SWIR $\leq 4\%$ were classified as either SAV or turbid water. Because of absorption by the water column, submerged aquatic vegetation had $\leq 4\%$ reflectance in the wavelengths between 1599 and 1764 nm. Higher reflectance values within this region corresponded to either land or emergent plants (Hestir et al. 2008).

Node 4: The pixels previously classified as either SAV or turbid water were then sorted into those with red edge index > 0.1 . Chlorophyll in vegetation is characterized by a large switch between a low reflectance in the red due to absorption by leaf chlorophyll and a high reflectance in the near-infrared due to scattering in the entire interior of the leaf (red edge reflectance) and changes in the position of the red edge indicate plant condition (Fig. 2, Filella and Peñuelas 1994). We used the red edge reflectance (a normalized index between the spectral bands 674 and 731 nm) to separate turbid water from vegetated pixels. Higher red edge reflectance values correspond to submerged plants and lower red edge values to turbid water. The shape of the water spectra in Fig. 2a illustrates the turbidity of these waters. The frequency of mNDVI values is shown in Fig. 2b for both SAV and turbid water, showing the degree of overlap between the two classes.

Node 5: From previously identified vegetated pixels, SAV was separated from emergent vegetation using another SWIR threshold. Emergent wetland tule (*Schoenoplectus californicus*) patches have sparse canopies with erect-ophilic green photosynthetic culms and basal leaves which result in a highly mixed leaf–water pixel at the 3-m scale. The highest observed reflectance values for SAV overlap with the lowest observed reflectance values for tule in the SWIR (1599–1764 nm). We used this region for a new threshold to select pixels with reflectance in the SWIR $\leq 3\%$. This was a conservative threshold for SAV that ensured against false-positive identification of SAV.

Node 6: For the remaining pixels that had SMA-water $> 10\%$ that had not been previously classified as emergent vegetation, we included a two-tiered node that identified clear water, turbid water, SAV, and floating/emerged filamentous algae. This node used both a second SMA and the calculation of spectral angles. Because we implemented the second SMA on a reduced set of pixels and therefore spectral variability, we could use these four endmembers, which were relatively similar, and still obtain good unmixing results (Fig. 2). Again, the endmembers were obtained from the imagery by overlaying locations of field observations. The resulting SMA produced a better threshold of SMA-SAV versus SMA-water. Further we calculated spectral angles for further separation between water and SAV, and SAV from algae. We used reflectance in the visible and NIR (450–954 nm) to reduce the noise in the pixel spectra due to the mixing with water. Within this node we classified pixels as SAV if SMA-SAV $> 20\%$ (to separate from water) and if the spectral angle was close to SAV (to separate from epiphytic algae). Pixels that had SMA-SAV $> 20\%$ but a spectral angle far from SAV were classified as floating/emerged filamentous algae. Pixels that had SMA-SAV $< 20\%$ and spectral angle closest to emerged algae were classified as such; otherwise pixels were classified as water.

The decision tree was applied to each annual set of imagery, allowing for minor yearly adjustment of parameter estimates, because of some differences in image acquisition timing and atmospheric conditions (Hestir et al. 2008, Khanna et al. 2011). Map accuracy was assessed as overall yearly producer's and user's accuracies (Liu et al. 2007) and kappa statistics (Bloch and Kraemer 1989, Monserud and Leemans 1992, Liu et al. 2007). This was based on a data partition into training (60%) and testing (40%; Khanna et al. 2011). Yearly overall classification accuracy ranged from 62% to 99% (Table 1), which indicated sufficient classification accuracy to do the subsequent analysis (sensu Liu et al. 2007 a good classification accuracy is $> 70\%$).

Computation of spread rates and persistence.—Percent SAV cover was estimated for Delta waterways by dividing the area classified as SAV by the area of available waterways.

There are implications of the classification accuracies in the subsequent assessment of rates of spread and persistence of SAV. The producer's accuracy is the uncertainty of detection (or omission error or false negatives). Thus having a large uncertainty for any of the years will affect the calculated rates of spread from year to year, and interpretation of the results will need to be more careful for the years for which the producer's accuracy is lower. The users' accuracy (or commission error or false positives) could affect the measure of persistence, so pixels that appear to be persisting in the later years could actually just be commission errors leading to an over-prediction. Confidence intervals were used on area estimates to account for uncertainty in the SAV maps, using the producer accuracy (detection rate) as the metric of uncertainty (Liu et al. 2007).

To assess how the area and percent cover changed over time we subtracted the area of $t(y)$ from the area of $t(y + 1)$, for all combinations of years (y). We then computed spread and persistence from the classification maps. To assess whether the SAV community was spreading, we calculated the slope of the regression line between each pair of consecutive years of SAV area using the results from each year classification. If the slope of this line was positive, it indicated that SAV was expanding its distribution, thus spreading. If the slope of this line was negative, it indicated that SAV was contracting its distribution. If the slope was not different from zero it showed that SAV distribution was stable, neither spreading nor contracting.

To understand these patterns we then calculated how much SAV was spreading (i.e., new growth each year) and how much was persisting (i.e., survived to the next year). To calculate spreading, we calculated the common areas where SAV was found at each pair of years and used this area as the estimated survival per year. From the areas that were occupied in one year but not in the other, we estimated the areas that did not survive (occupied in year 1 but not in year 2) and those of new growth (occupied in year 2 but not in year 1).

Finally, we calculated the number of years that SAV persisted in the same pixels and the area of these pixels in the study area. To calculate the area of SAV, we used GIS to overlay all of the yearly SAV maps and extracted the areas that had SAV every year in the last 5 yr (2004–2008). We repeated this analysis to extract the areas that had SAV in each of the last 4 yr (2005–2008), 3 yr (2006–2008), and 2 yr (2007–2008). We assumed persistence values of 100% if all areas occupied by SAV continued to be occupied, otherwise persistence had a negative value indicating that with time SAV occurrence decreased.

RESULTS

Given the extent of waterways in the Delta (2220 km²), we present the statistics for the entire Delta but choose to show spread and persistence maps for four types of aquatic environments (Fig. 3). The represented areas correspond to the different environmental conditions that

support SAV in the Delta, and can be summarized into four categories: inundated islands (Fig. 3a), narrow channels (Fig. 3b), a deepwater channel maintained by dredging (Fig. 3c), and a large and deep tidal inundated island (Franks Tract, Fig. 3d). Inundated islands are former land areas that were inundated due to levee breaching and now have shallow and slow velocity water, often with higher water temperature than the surrounding flowing channels, and lower turbidity. Narrow channels are meandering, with variable flow shallow waters, lower

water temperature, and higher turbidity in comparison with inundated islands. The deepwater channel is a deep, straight channel with high flow, lower water temperature, and lower turbidity. Finally, Franks Tract is a unique site, a large inundated island with exposure to strong winds and fluctuating water levels due to tides and freshwater inflows. The island was flooded in 1936 and again in 1938 and has been the focus of directed management actions to control Brazilian waterweed since 2001 because it was thought to be a major source of propagules.

FIG. 3. Patterns of yearly spread (red and yellow) and persistence (green and brown) of the invaded SAV community in the Sacramento-San Joaquin River Delta ecosystem: (a) inundated island, (b) narrow and shallow channel, (c) wide and deepwater channel, and (d) Frank's Tract. Yearly spread estimated from imaging spectrometry data analysis is represented by different colors (left-hand side), yearly persistence estimated from imaging spectrometry data analysis is represented by different colors (right-hand side).

General spread and patterns of persistence vary in these different environmental conditions. In general, inundated islands and narrow channels show expanding concentric rings of SAV as the community expanded outward into available niches (Fig. 3a, b), and these are the areas where SAV persists the most from year to year. In the deepwater channel, SAV only colonizes the channel margins because the high depth and velocity of the water in the main channel impede establishment (Fig. 3c). Some persistence is observed in the channel margin environments. The largest decrease in SAV cover occurred in Franks Tract in 2007 and 2008 (Fig. 3d) following extensive chemical spraying.

Spread and persistence of submerged aquatic vegetation

About 6–11% of the Delta waterways were covered by SAV each year (Fig. 4a), with areas ranging from 17.29 to 32.2 km² (Fig. 4b). Spread rates were always below 1, suggesting a decrease from year to year (2004–2005, 0.79 km²/yr; 2005–2006, 0.98 km²/yr; 2006–2007, 0.89 km²/yr; 2007–2008, 0.78 km²/yr). New growth and persistence from previous years contributed equally to the SAV extent in all years, accounting almost 50% in

each year (Fig. 4c), with the exception of 2006–2007, where persistence was higher than new growth.

Submerged aquatic vegetation persistence decreased the longer it stayed in the system, with 2004–2005 persistence extent of ~12.7 km², and ~50% decrease each year thereafter (Fig. 4d), which was independent of the start year. We found an average persistence of 42% over 2 yr (out of four possible combinations of year to year persistence, for example from 2004 to 2005 or from 2005 to 2006; Table 2), 22% over 3 yr, 12% over 4 yr and 8.4% over the 5 yr of study (Table 3).

DISCUSSION

Each year ~6–11% of the Delta waterways were covered by SAV and this distribution remained relatively constant over a period of 5 years. The Delta's complex environment offers multiple habitats for SAV (Jassby and Cloern 2000, Lucas et al. 2002) and the interplay between the available habitat and the dynamics of spread and persistence may contribute to the observed relatively consistent yearly distribution area of SAV. The Delta multiple habitats are created by a combination of gradients in depth, water velocity, salinity, and temperature (Jassby

FIG. 4. (a) SAV extent in the Sacramento-San Joaquin River Delta in the 5 yr of study. SAV is shown in red, and overlaid in a 2005 true color image of the central area of the Delta. (b) Area and percent cover of SAV over the study area, (c) SAV area persisting from previous year, loss from previous year and new growth, (d) area of SAV that persisted over 1, 2, 3, and 4 yr; 1 yr persistence is the persistence from 2004 to 2005, 2 yr persistence is the persistence between 2004 and 2006, and so on.

TABLE 2. Persistence rates for all combinations of years.

Years	Number of combinations	Average persistence (%)
2	4	42
3	3	21.82
4	2	11.69
5	1	8.4

TABLE 3. Detailed persistence (%) per 3-yr and 4-yr time periods.

	Detailed persistence (%)
3-yr	
2004–2006	22.47
2005–2007	25.91
2006–2008	16.80
4-yr	
2004–2007	11.9
2005–2008	11.43

and Cloern 2000, Lucas et al. 2002). Habitat complexity is likely to promote the establishment of new species of SAV in areas previously unoccupied (Best 1981, Williams et al. 2003, Pennington 2007). In the last 30 years there has been a major change in the composition of SAV with an increase in nonnative species (Cohen and Carlton 1998, Jassby and Cloern 2000).

We observed diffusional or radial growth outward at local sites, and saltatorial colonization (or re-colonization) that allowed the discontinuous occupation of distant areas in the Delta. While we observed radial growth outward from pre-established patches, we think this process of spread only explains a small amount of the spread rate. We know that the SAV community in the Delta does not go through overwinter senescence (Santos et al. 2011), and we think this may enhance the radial spread of the invaded SAV community, as spread can begin earlier in spring in subsequent years. Despite most SAV species being annuals (Sculthorpe 1965, Pennington 2007), overwinter survival of SAV seems to be common in the eastern sloughs and other protected regions of the Delta where the water does not freeze (e.g., water temperature at Old River varies between 5°C and 25°C according to California Data Exchange Center station data from 2005 to 2008; Lucas et al. 2002). The observed overwinter survival also reduces the potential for underestimating spread rate, as it is unlikely that some of the persistence is local extinction and immediate recolonization by SAV.

Only through high propagule pressure can previously established areas maintain species presence and infill (Liu et al. 2006) and new areas be invaded via saltatorial spread, as we observed. A sufficient supply of viable propagules (seeds, plantlets, rhizomes, and other plant fragments) allows a species to expand its range and to persist and maintain existing distributions (Rouget and Richardson 2003). SAV propagule supply and distribution probably results from the periods of greater

admixture, as the higher velocity and admixture in the water likely created more propagules, and aided their dispersal to nearby and longer distances. This saltatorial spread could have also been aided by the increase in recreational boating in the Delta (CDBW 2002), mostly by small propeller boats (<8 m). High propagule pressure can compensate for the lack of persistence, suggesting that the Delta is yet to be saturated (i.e., all possible habitat is not yet occupied).

Despite the competitive advantage of overwinter survival, SAV communities exhibit surprisingly short-duration persistence (1–3 years). SAV persistence is likely conditioned by water flows. There were very high flows in May and June of 2005 and 2006, which likely resulted in higher water velocity, lower water temperature, higher turbidity, and higher admixtures of nutrients. These were followed by large flows in 2006, which probably contributed to flushing much of the SAV out of the system, and the higher (and colder) water velocities likely reduced SAV's ability to establish. Further, existing programs to control Brazilian waterweed (CDBW 2005, 2006) are likely associated with the decrease in SAV, especially in Franks Tract in 2007 and 2008 (Santos et al. 2009).

Our results show both radial growth and saltatorial spread, that the spread rates of the invaded SAV community are negative, and that the persistence is also low over time. This could suggest that the impact of invasive species in the native SAV community could diminish in the near future. Rates of spread are higher at the beginning of the invasion (Rejmánek 2000), and it is possible the SAV invasion has stabilized or even started declining. Nonetheless, cascading effects of such an invaded submerged community on fauna have already been noticed (Brown and Michniuk 2007, Ferrari et al. 2014). Interactions between anthropogenic use and natural processes (Neubert and Parker 2004, Gilbert and Liebhold 2010) may make predictions of future rates of spread quite challenging.

Other studies have focused on measuring dispersal rates and site-specific spread metrics and persistence patterns (for examples, see Best 1981, Andow et al. 1990, Arzandeh and Wang 2003, Bradley and Mustard 2006, Gilbert and Liebhold 2010), or have used replicated experiments to assess the effects of spatial and temporal variability in spread rates and patterns of persistence on the process of invasion (Giometto et al. 2014). Here we take a different approach and measure the landscape scale spread (i.e., new growth) and persistence of previous year SAV area over time. These landscape-scale remotely sensed measurements of spread and persistence can be influenced by classification success (Liu et al. 2007). Our estimates of new growth and persistence area of SAV could be affected by the producer's accuracy. The year 2004 had the lowest producer's accuracy so there are more false negatives, suggesting that the spread rate between 2004 and 2005 is potentially overestimated; while this spread rate is probably still negative, it may be of a smaller magnitude.

For example, Hestir et al. (2012) showed a much lower value of SAV in 2004 using a different method. We believe that the “true” value is somewhere in between, because 2004 was the first year in which we conducted our field sampling and analyzed the data, and therefore we believe is more subjective to error (Hestir et al. 2012). Overall, the relative spread rates would be the same, but the order of magnitude of the changes could be smaller. The persistence could be affected by the user’s accuracy but because this metric is generally large, we trust our measurements. Further, other fields within remote sensing, such as aquatic optics, take a process-based modeling approach (Dekker et al. 2005). For example, Dekker et al. (2011) presents a comparison of radiative transfer approaches that explicitly consider water depth and water column turbidity. While process-based models have the potential to produce more robust outputs because they are based in physics, their predictions of optical properties depend on our understanding of the processes affecting reflectance and how they are represented in the models (Ustin et al. 2009). Radiative transfer approaches may be more commonly available in the near future, as parameterization of such models can be more robust and in combination with hyperspectral and high temporal resolution remote sensing can present valid results for landscape-scale analysis. To our knowledge, there are no studies yet that use this method on deltaic data sets, certainly not for such a large area with such complex water quality issues (sediment, turbidity, flow rates and volumes, tidal patterns, salinity, algae, blue-green bacteria, etc.) in a reticulated landscape of water channels and active management of flows through gates as the Delta.

The landscape-scale approach allows measurements of all invasion fronts and the spatial anisotropies associated with spread processes and persistence patterns, without spatial interpolation, at locations both proximate and distant to the focus of invasion at multiple points in time. Explicit description of spatial spread (Andrew and Ustin 2008) and its variation over time is fundamental to understanding the process of invasion (Ge et al. 2013), and assessing whether this process is linked to spatial and temporal variation in dispersal traits (Ellner and Schreiber 2012, Buoro and Carlson 2014). Only through this knowledge can we design effective management actions (Fletcher and Westcott 2013).

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LITERATURE CITED

- Ackleson, S. G., and V. Klemas. 1987. Remote sensing of submerged aquatic vegetation in lower Chesapeake Bay: a comparison of Landsat MSS to TM imagery. *Remote Sensing of Environment* 22:235–248.
- Andrew, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1990. Spread of invading organisms. *Landscape Ecology* 4:177–188.
- Andrew, M. E., and S. L. Ustin. 2008. The role of environmental context in mapping invasive plants with hyperspectral image data. *Remote Sensing of Environment* 112:4301–4317.
- Arzandeh, S., and J. F. Wang. 2003. Monitoring the change of *Phragmites* distribution using satellite data. *Canadian Journal of Remote Sensing* 29:24–35.
- Asner, G. P., and P. M. Vitousek. 2005. Remote analysis of biological invasion and biogeochemical change. *Proceedings of the National Academy of Sciences of the United States of America* 102:4383–4386.
- Best, E. P. H. 1981. The submerged aquatic macrophytes in lake Maarsseveen I: species composition, spatial distribution and productivity. *Aquatic Ecology* 15:72–81.
- Bloch, D. A., and H. C. Kraemer. 1989. 2×2 kappa coefficients: measures of agreement or association. *Biometrics* 45:269–287.
- Bradley, B. A., and J. F. Mustard. 2006. Characterizing the landscape dynamics of an invasive Plant and risk of invasion using remote sensing. *Ecological Applications* 16:1132–1147.
- Brando, V. E., J. M. Anstee, M. Wettle, A. G. Dekker, S. R. Phinn, and C. Roelfsema. 2009. Physics based retrieval and quality assessment of bathymetry from suboptimal hyperspectral data. *Remote Sensing of Environment* 113:755–770.
- Brown, L. R., and D. Michniuk. 2007. Littoral Fish Assemblages of the Alien-dominated Sacramento-San Joaquin Delta, California, 1980–1983 and 2001–2003. *Estuaries and Coasts* 30:186–200.
- Buoro, M., and S. M. Carlson. 2014. Life-history syndromes: integrating dispersal through space and time. *Ecology Letters* 17:756–767.
- California Department of Boating and Waterways (CDBW). 2002. Sacramento-san Joaquin delta boating needs assessment 2000–2020. California Department of Boating and Waterways, Sacramento, CA, USA, 100 pp.
- California Department of Boating and Waterways (CDBW). 2005. *Egeria densa* control program. California Department of Boating and Waterways, Sacramento, CA, USA, 42pp.
- California Department of Boating and Waterways (CDBW). 2006. *Egeria densa* control program 2nd Addendum to 2001 environmental impact report. California Department of Boating and Waterways, Sacramento, CA, USA, 205 pp.
- Cohen, A. N., and J. T. Carlton. 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay Delta. United States Fish and Wildlife Service, National Sea Grant College Program.
- Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558.
- Davis, M. A. 2009. *Invasion biology*. Oxford University Press, Oxford, UK.
- Dekker, A., V. Brando, J. Anstee, S. Fyfe, T. Malthus, and E. Karpouzli. 2005. Remote sensing of seagrass ecosystems: use of spaceborne and airborne sensors. Pages 347–359 in A. W. D. Larkum, R. J. Orth, and C. M. Duarte, editors. *Seagrasses: biology, ecology, and conservation*. Springer, Berlin, Germany.
- Dekker, A. G., et al. 2011. Intercomparison of shallow water bathymetry, hydro-optics, and benthos mapping techniques in Australian and Caribbean coastal environments. *Limnology and Oceanography Methods* 9:396–425.

- Ellner, S. P., and S. J. Schreiber. 2012. Temporally variable dispersal and demography can accelerate the spread of invading species. *Theoretical Population Biology* 82:283–298.
- Ferrari, M. C. O., L. Ranåker, K. L. Weinersmith, A. Sih, and J. L. Conrad. 2014. Effects of turbidity and an invasive waterweed on predation by introduced largemouth bass. *Environmental Biology of Fishes* 97:79–90.
- Filella, I., and J. Peñuelas. 1994. The red edge position and shape as indicators of plant chlorophyll content, biomass, and hydric status. *International Journal of Remote Sensing* 15:1459–1470.
- Firn, J., T. Rout, H. Possingham, and Y. M. Buckley. 2008. Managing beyond the invader: manipulating disturbance of natives simplifies control efforts. *Journal of Applied Ecology* 45:1143–1151.
- Fletcher, C. S., and D. A. Westcott. 2013. Dispersal and the design of effective management strategies for plant invasions: matching scales for success. *Ecological Applications* 23:1881–1892.
- Funk, J. L., and P. M. Vitousek. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–1081.
- Ge, Z., H. Cao, and L. Zhang. 2013. A process-based grid model for the simulation range expansion of *Spartina alterniflora* on the coastal saltmarshes in the Yangtze Estuary. *Ecological Engineering* 58:105–112.
- Gilbert, M., & A. Liebhold. 2010. Comparing methods for measuring the rate of spread of invading populations. *Ecography* 33:809–817.
- Giometto, A., A. Rinaldo, F. Carrara, and F. Altermatt. 2014. Emerging predictable features of replicated biological invasion fronts. *Proceedings of the National Academy of Sciences* 111:297–301.
- Glenn, N. F., J. T. Mundt, K. T. Weber, T. S. Prather, L. W. Lass, and J. Pettingill. 2005. Hyperspectral data processing for repeat detection of small infestations of leafy spurge. *Remote Sensing of Environment* 95:399–412.
- Gullström, M., B. Lundén, M. Bodin, J. Kangwe, M. C. Öhman, M. S. P. Mtolera, and M. Björk. 2006. Assessment of changes in the seagrass-dominated submerged vegetation of tropical Chwaka Bay (Zanzibar) using satellite remote sensing. *Estuarine, Coastal and Shelf Science* 67:399–408.
- Hastings, A., et al. 2005. The spatial spread of invasions: new developments in theory and evidence. *Ecology Letters* 8:91–101.
- Hedley, J. D., C. Roelfsema, S. Phinn, and P. J. Mumby. 2012. Environmental and sensor limitations in optical remote sensing of coral reefs: Implications for monitoring and sensor design. *Remote Sensing* 4:271–302.
- Hestir, E. L., S. Khanna, M. E. Andrew, M. J. Santos, J. H. Viers, J. A. Greenberg, S. S. Rajapakse, and S. L. Ustin. 2008. Identification of invasive vegetation using hyperspectral remote sensing in the California Delta ecosystem. *Remote Sensing of Environment* 112:4034–4047.
- Hestir, E. L., J. A. Greenberg, and S. L. Ustin. 2012. Classification trees for aquatic vegetation community prediction from imaging spectroscopy. *IEEE Selected Topics in Applied Earth Observations and Remote Sensing* 5: 1572–1584.
- Jassby, A. D., and J. E. Cloern. 2000. Organic matter sources and rehabilitation of the Sacramento – San Joaquin Delta (California, USA). *Aquatic Conservation* 10:323–352.
- Khanna, S., M. J. Santos, S. L. Ustin, and P. Haverkamp. 2011. An integrated approach to a biophysiological based classification of floating aquatic macrophytes. *International Journal of Remote Sensing* 32:1067–1094.
- Lass, L. W., D. C. Thill, B. Shafii, and T. S. Prather. 2002. Detecting spotted knapweed (*Centaurea maculosa*) with hyperspectral remote sensing technology. *Weed Technology* 16:426–432.
- Light, T., T. Grosholz, and P. Moyle. 2005. Delta Ecological Survey (Phase I): Nonindigenous aquatic species in the Sacramento-San Joaquin Delta, a literature review. Final Report to the U.S. Fish and Wildlife Service. Sacramento, CA, USA.
- Liu, G., W. Li, J. Zhou, W. Liu, D. Yang, and A. J. Davy. 2006. How does the propagule bank contribute to cyclic vegetation change in a lakeshore marsh with seasonal drawdown? *Aquatic Botany* 84:137–143.
- Liu, C., P. Frazier, and L. Kumar. 2007. Comparative assessment of the measures of thematic classification accuracy. *Remote Sensing of Environment* 107:606–616.
- Lucas, L. V., J. E. Cloern, J. K. Thompson, and N. E. Monsen. 2002. Functional variability of habitats within the Sacramento-San Joaquin Delta: restoration implications. *Ecological Applications* 12:1528–1547.
- Mack, R. N., B. V. Holle, and L. A. Meyerson. 2007. Assessing invasive alien species across multiple spatial scales: working globally and locally. *Frontiers in Ecology and the Environment* 5:217–220.
- Monserud, R. A., and R. Leemans. 1992. Comparing global vegetation maps with the Kappa statistic. *Ecological Modelling* 62:275–293.
- Mooney, H. A., and E. E. Cleland. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences* 98:5446–5451.
- Neubert, M. G., and I. M. Parker. 2004. Projecting rates of spread for invasive species. *Risk Analysis* 24:817–831.
- Pejchar, L., and H. A. Mooney. 2009. Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution* 24:497–504.
- Pennington, T. G. 2007. Seasonal changes in allocation, growth, and photosynthetic responses of the submerged macrophytes *Egeria densa* Planch (Hydrocharitaceae) from Oregon and California. PhD. Dissertation, Portland State University, Portland, OR, USA.
- Phinn, S. R., C. M. Roelfsema, A. Dekker, V. Brando, and J. Anstee. 2008. Mapping seagrass species, cover and biomass in shallow waters: an assessment of satellite multi-spectral and airborne hyper-spectral imaging systems in Moreton Bay (Australia). *Remote Sensing of Environment* 112:3413–3420.
- Rejmánek, M. 2000. Invasive plants: approaches and predictions. *Austral Ecology* 25:497–506.
- Rouget, M., and D. M. Richardson. 2003. Inferring process from pattern in plant invasions: a semimechanistic model incorporating propagule pressure and environmental factors. *American Naturalist* 162:713–724.
- Sanders, N. J., N. J. Gotelli, N. E. Heller, and D. M. Gordon. 2002. Community disassembly by an invasive species. *Proceedings of the National Academy of Sciences* 100:2474–2477.
- Santos, M. J., S. Khanna, E. L. Hestir, M. E. Andrew, S. S. Rajapakse, J. A. Greenberg, L. W. J. Anderson, and S. L. Ustin. 2009. Use of hyperspectral remote sensing to evaluate efficacy of aquatic plant management in the Sacramento-San Joaquin River Delta, California. *Invasive Plant Science and Management* 2:216–229.
- Santos, M. J., L. W. J. Anderson, and S. L. Ustin. 2011. Effects of invasive species on plant communities: an example using submersed aquatic plants at the regional scale. *Biological Invasions* 13:443–457.

- Santos, M. J., E. L. Hestir, S. Khanna, and S. L. Ustin. 2012. Image spectroscopy and stable isotopes elucidate functional dissimilarity between native and non-native plant species in the aquatic environment. *New Phytologist* 193:683–695.
- Sculthorpe, C. D. 1965. *The biology of aquatic vascular plants*. Koeltz Scientific Books, Koenigstein, West Germany. 610 pp.
- Silva, T. S. F., M. P. F. Costa, J. M. Melack, and E. M. L. M. Novo. 2008. Remote sensing of aquatic vegetation: theory and applications. *Environmental Monitoring and Assessment* 140:131–145.
- Silvestri, S., M. Marani, and A. Marani. 2003. Hyperspectral remote sensing of salt marsh vegetation, morphology and soil topography. *Physics and Chemistry of the Earth* 28:15–25.
- Theoharides, K. A., and J. S. Dukes. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176:256–273.
- Ustin, S. L., D. DiPietro, K. Olmstead, E. Underwood, and G. J. Scheer. 2002. Hyperspectral remote sensing for invasive species detection and mapping. *Geoscience and Remote Sensing Symposium, IGARSS 2002*:1658–1660.
- Ustin, S. L., D. A. Roberts, J. A. Gamon, G. P. Asner, and R. O. Green. 2004. Using imaging spectroscopy to study ecosystem processes and properties. *BioScience* 54:523–534.
- Ustin, S. L., A. A. Gitelson, S. Jacquemoud, M. Schaepman, G. P. Asner, J. A. Gamon, and P. Zarco-Tejada. 2009. Retrieval of foliar information about plant pigment systems from high resolution spectroscopy. *Remote Sensing of Environment* 113:S67–S77.
- Vilá, M., J. L. Espinar, M. Hejda, P. E. Hulme, V. Jarosik, J. L. Maron, J. Pergl, U. Schaffner, Y. Sun, and P. Pysek. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702–708.
- Vis, C., C. Hudon, and R. Carignan. 2003. An evaluation of approaches used to determine the distribution and biomass of emergent and submerged aquatic macrophytes over large spatial scales. *Aquatic Botany* 77:187–201.
- Weiher, E., I. C. Wisheu, P. A. Keddy, and D. R. J. Moore. 1996. Establishment, persistence, and management implications of experimental wetland plant communities. *Wetlands* 16:208–218.
- Williams, D. J., N. B. Rybicki, A. V. Lombana, T. M. O'Brien, and R. B. Gomez. 2003. Preliminary investigation of submerged aquatic vegetation mapping using hyperspectral remote sensing. *Environmental Monitoring and Assessment* 81:383–392.