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HIGHLIGHTS

- Landscape modification reduces net primary production (NPP) supporting other species.
- Wetlands are being lost faster than forests but the associated loss of NPP is unknown.
- We show that 77% loss of habitats from a large wetland ecosystem reduced NPP by 94%.
- Success at meeting habitat restoration targets could recover 12% of lost NPP.
- Estimated losses of ecosystem functions from habitat loss can guide restoration plans.

GRAPHICAL ABSTRACT
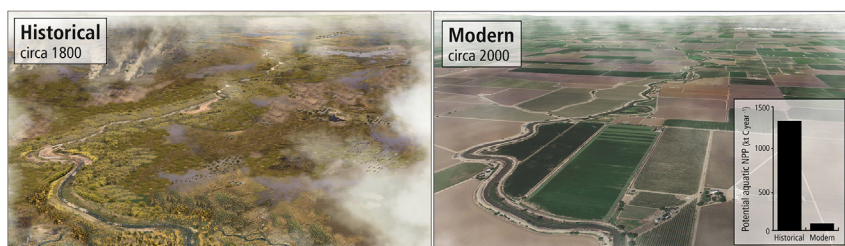
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ABSTRACT

Humans are changing the Earth's surface at an accelerating pace, with significant consequences for ecosystems and their biodiversity. Landscape transformation has far-reaching implications including reduced net primary production (NPP) available to support ecosystems, reduced energy supplies to consumers, and disruption of ecosystem services such as carbon storage. Anthropogenic activities have reduced global NPP available to terrestrial ecosystems by nearly 25%, but the loss of NPP from wetland ecosystems is unknown. We used a simple approach to estimate aquatic NPP from measured habitat areas and habitat-specific areal productivity in the largest wetland complex on the USA west coast, comparing historical and modern landscapes and a scenario of wetland restoration. Results show that a 77% loss of wetland habitats (primarily marshes) has reduced ecosystem NPP by 94%, C (energy) flow to herbivores by 89%, and detritus production by 94%. Our results also show that attainment of habitat restoration goals could recover 12% of lost NPP and measurably increase carbon flow to consumers, including at-risk species and their food resources. This case study illustrates how a simple approach for quantifying the loss of NPP from measured habitat losses can guide wetland conservation plans by establishing historical baselines, projecting functional outcomes of different restoration scenarios, and establishing performance metrics to gauge success.

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1. Introduction

Wetlands are unique transitional zones situated between land and water. Once viewed as wastelands to be drained, we now recognize that wetlands provide ecosystem services valued higher (per unit area) than other biomes (de Groot et al., 2012). Wetlands have and continue to be lost at a rapid rate, primarily through human appropriation for agriculture and urban spread (Davidson, 2014). More than half of the wetland ecosystems of North America, Europe, Australia, and China have been lost since the early 20th century (Moreno-Mateos et al., 2012), and the rate of loss is accelerating in some regions such as NE China where two thirds of its wetlands were lost to agricultural land use from 1975 to 2004 (Zhang et al., 2010). Landscape change at this scale has many ramifications, including decreased net primary production (NPP) available to support ecosystems and their biological communities (Vitousek et al., 1986). Lost NPP from landscape change reduces the energy available to consumers, their diversity, and the ecosystem services they provide. Thus, "insuring a sustainable future entails sharing NPP with a great host of other species" (Field, 2001).

Human activities have reduced global NPP available to terrestrial ecosystems by nearly 25% (Haberl et al., 2007). The loss of NPP from wetland ecosystems is unknown, but it could be large because the fractional loss of wetlands, estimated between 33% (Hu et al., 2017) and 87% (Davidson, 2014), exceeds the estimated 20–50% loss of terrestrial wildlands (Oakleaf et al., 2015). The elimination of wetlands and their ecological functions has contributed to widespread population declines of wetland-dependent species (Millennium Ecosystem Assessment, 2005), and lost biodiversity now motivates wetland conservation and restoration plans around the globe (Zedler and Kercher, 2005). A missing link in this strategy is the quantification of lost ecosystem functions and their potential for recovery through habitat restoration. The aim of our study was to develop and apply a simple method for converting metrics of habitat loss and restoration into corresponding losses and recovery of ecosystem functions that support wetland biodiversity.

Our first objective was to develop quantitative relationships between wetland landscape configuration (areal extent of different habitat types) and two life-supporting ecosystem functions – NPP and carbon (C) supply to consumers. The second objective was to apply these relationships to estimate losses and potential recovery of those functions in California's Sacramento-San Joaquin Delta, an example of a large (2300-km^2) wetland ecosystem that has been transformed by conversion for agricultural and urban uses. Our investigation shows that landscape transformation of this river-delta system has resulted in a nearly complete loss of NPP by natural plant communities. This is, to our knowledge, the first estimate of human appropriation of NPP from a large wetland ecosystem. Our investigation also provides estimates of the fraction of lost NPP that could be recovered if current habitat-restoration targets are met.

This case study illustrates how simple approaches for quantifying changes in ecosystem functions from landscape change can guide wetland restoration plans by providing historical baselines, projecting outcomes of habitat-restoration scenarios, and placing bounds on the extent to which lost functions can be recovered. Results from this case study also suggest that the fraction of NPP appropriated globally by wetland conversion might be larger than the fractional loss of NPP in terrestrial ecosystems.

2. Study area

Our study site (California's Sacramento-San Joaquin Delta, hereafter Delta) was once the largest estuarine wetland system on the contiguous U.S. west coast (Fig. 1). Of this historical 2300-km^2 system of hydrologically connected freshwater wetland, tidal channels, and riparian habitats, nearly all tidal and floodplain wetlands have been drained and converted for agriculture or open-water habitat, along with substantial loss of riparian forest habitats (Whipple et al., 2012). The modern landscape is largely disconnected from its rivers by levees and flow regulation from upstream dams. River deltas across the world are on a similar trajectory. Fifteen other large deltas, including the Indus, Hunge He, Yukon and Zambezi lost a mean 36% of their wetlands from the 1980s to 2002 (Coleman et al., 2008).

The reconstruction of landscape change in the Sacramento-San Joaquin Delta is spatially explicit and allowed us to estimate NPP in five wetland habitat types having distinct producer communities, rates of primary productivity, and inundation patterns (tidal, seasonal, annual). We estimated potential NPP for three landscapes: (1) the Delta prior to Euro-American transformation (historical); (2) the contemporary transformed landscape (modern); and (3) a future scenario of attaining marsh and floodplain restoration goals.

3. Materials and methods

We computed potential aquatic NPP (PANPP) in each habitat type from the products of habitat area and habitat-specific areal productivity of five primary-producer groups. Specifically, PANPP measures annual production of organic C available to aquatic food webs in hydrologically connected habitats, defined as those connected by riverine or tidal water flows. Detailed methods are provided in Supplementary material sections 1–2. Areal productivities were based on peak biomass (marsh plants) or photosynthetic rates (phytoplankton) measured in the Delta, or published measurements in other ecosystems (attached microalgae, inputs from woody riparian plants) or of dominant species (aquatic plants). All original data sources are referenced in Supplementary material sections 2.1–2.5 We estimated PANPP for two different hydrologic conditions (wet years, dry years) in three different landscapes: historical (ca. 1800 prior to significant Euro-American landscape transformation); modern (ca. 2010); and a future scenario based on current restoration targets. PANPP is the magnitude of ecosystem NPP expected for these different landscapes in today's climatic, hydrologic, and water-quality setting. The computed quantities reported here have multiple sources of uncertainty (Supplementary material section 2), so we report them with only one or two significant digits.

3.1. Determining habitat parameters

We first quantified the extent of hydrologically connected areas of five dominant habitat types in each landscape: open water, tidal marsh, nontidal marsh, riparian forest/scrub, and other seasonal floodplain areas (Table 1). Historical habitat areas were derived from a spatially explicit reconstruction of Delta land cover in the early 1800s developed from hundreds of historical texts, photographs, and cartographic sources (Whipple et al., 2012). Modern areas were derived from detailed vegetation and land cover maps (Robinson et al., 2014).

We define hydrologically connected habitats as the habitat extent where hydrologic connections allow for surface-water mediated transfer of energy, matter, and organisms between landscape elements (Pringle, 2003). The extent of hydrologically connected habitats was quantified for both wet and dry years ("water year type"), defined respectively as the median duration of inundation estimated from upper and lower quintiles of measured annual river inflow for the period 1980–2019 (CDWR, 2019). All areas in the historical Delta mapped by Whipple et al. (2012) as open water, tidal marsh, nontidal marsh, or riparian forest/scrub were considered hydrologically connected in wet years. In dry years there were slight decreases in the extent of hydrologically connected open water and more substantial differences in the extent of riparian forest/scrub (Table 1), described below. For the modern landscape, the same habitat types were considered potentially connected, but we accounted for the effect of levee infrastructure on hydrological connections using the California Levees Database (CDWR, 2013)
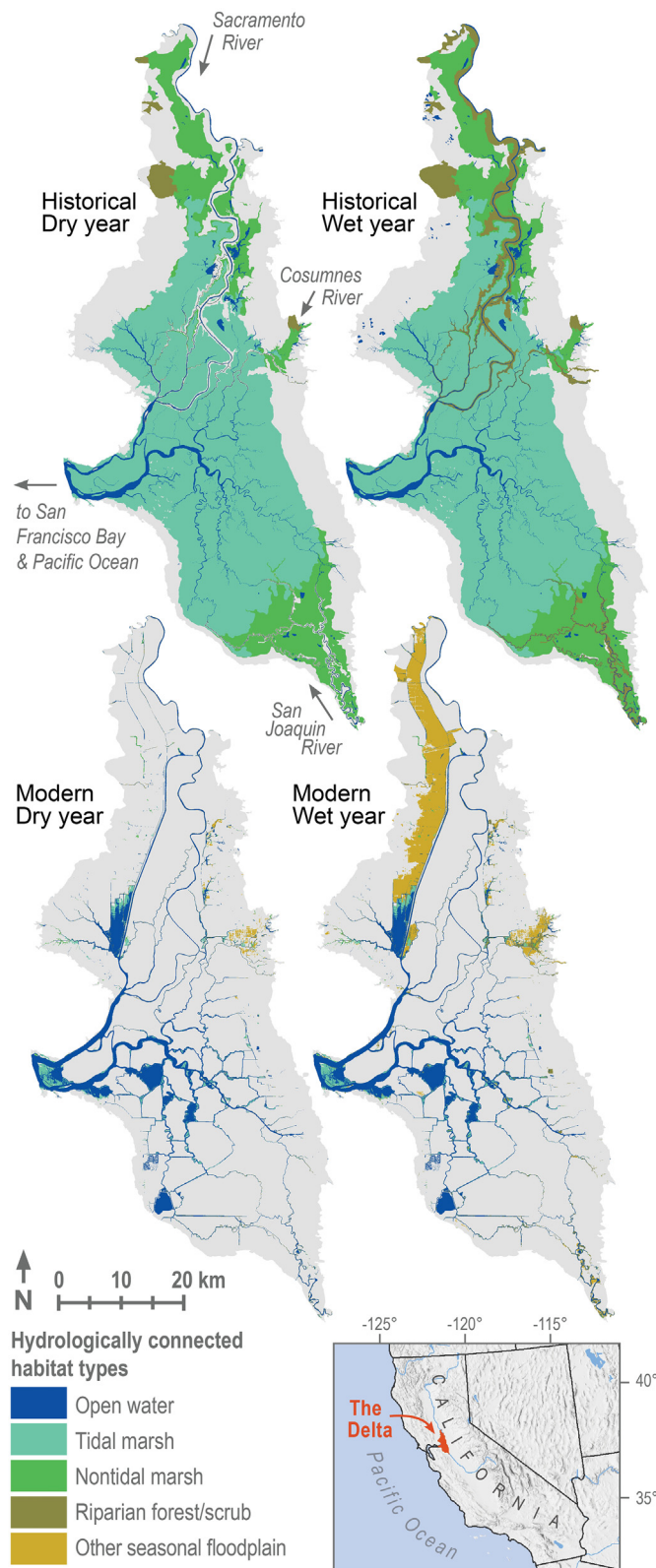
Fig. 1. Maps showing the historical and modern extent of five habitat types in the Sacramento-San Joaquin Delta that are connected by surface water flows to the aquatic ecosystem. Comparisons between dry and wet years show the expansion of inundation during periods of high river inflow.

Hydrologically connected habitat types

- Open water
- Tidal marsh
- Nontidal marsh
- Riparian forest/scrub
- Other seasonal floodplain

to mask out areas located entirely behind levees. For dry years in both the historical and modern landscape, the extent of hydrologically connected riparian forest/scrub was prescribed as a function of distance to

the nearest channel. Only areas of willow riparian scrub and valley foothill riparian within 25 m of open water were considered hydrologically connected in dry years versus the full extent in wet years (see Supplementary material section 1.3.3). Other seasonal floodplain habitat, present only in the modern period, included all other areas subject to periodic inundation (not included in the above habitat types or located behind a levee), as mapped by Pekel et al. (2016) in wet and dry years.

For each habitat type, we also quantified the depth and duration of inundation based on bathymetric data, hydrodynamic models, and assumptions grounded in published historical and contemporary observations. Areas mapped as open water were assumed to be perennially inundated, with depths determined from digital elevation models of the historical and modern Delta (Fregoso et al., 2017; Robinson et al., 2014). The depth and duration of inundation in tidal marshes were based on historical observations and contemporary measurements in remnant tidal marshes (Enright et al., 2013). Inundation duration in nontidal marsh and other seasonal floodplain habitats was determined from daily flow records (CDWR, 2019) to compute the median number of days each month in which flows exceed floodplain inundation thresholds. We accounted for interannual differences in inundation parameters in nontidal marsh and other seasonal floodplain habitats by calculating inundation duration for wet and dry years. Inundation depths in these habitat types (Supplementary material Table 1) were determined using hydrodynamic modeling results. Detailed methods for estimating habitat areas and inundation patterns are provided in Supplementary material section 1.

3.2. Marsh plant primary production

Delta wetlands consist mainly of tidal freshwater marshes dominated by *Schoenoplectus* (bulrush) spp. We used previously collected, peak aboveground biomass measurements (Byrd et al., 2017, 2018, 2020) to estimate NPP of the marsh plant producer group. We assumed that these communities are composed entirely of emergent vascular plants and that tidal, nontidal, slightly brackish, and freshwater emergent marsh communities have equal areal NPP. We also assumed that areal NPP does not vary between wet and dry years and has not changed between historical and modern periods. A statistical summary of aboveground peak biomass measurements is provided in Supplementary material Fig. 2. Carbon production was estimated as the product of biomass and 0.441, the mean plant organic C content in tidal marshes ($n = 1384$, 95% C.I. = 43.99%–44.37% (Byrd et al., 2018)). We report PANPP based on the median areal NPP of marsh plants, 5.76 Mg C ha^{-1} yr^{-1} (Table 2). Our estimates of marsh plant NPP based on peak biomass ranged from 0.52 to 28.13 Mg C ha^{-1} yr^{-1} (Supplementary material Fig. 2), resulting in a broad range of PANPP estimates (Supplementary material Fig. 3).

3.3. Aquatic plant primary production

To estimate primary production of submersed (SAV) and floating (FAV) aquatic vegetation in the modern landscape, we selected the numerically dominant native and introduced species present today (Santos et al., 2011; Ustin et al., 2015) and compiled 116 areal productivity rates of these species from 30 peer-reviewed studies (Supplementary material section 2.4.4). We reduced annual C production by 1/3 to account for low productivity in winter months and calculated the median value for each species (Table 2). For the modern landscape, we used remote sensing data at 2.5-m resolution to estimate the areas occupied by FAV and SAV (15 and 85% of total, respectively; Ustin et al., 2015) and parsed these areas based on relative abundance of each species (Santos et al., 2011; Ustin et al., 2015). We calculated total PANPP of aquatic plants in the modern landscape from areas of FAV or SAV coverage across depths (to 9 m or 3 m, respectively), the median areal productivity rate for each species, and the proportion of the total represented by that species. For the historical landscape, we assumed that FAV and SAV comprised

Table 1

Landscape change as altered areal extents of five hydrologically connected wetland habitat types in the Sacramento-San Joaquin Delta by era (historical vs. modern) and water year type (wet vs. dry).

Habitat type	Historical Dry (km^2)	Modern Dry (km^2)	Historical Wet (km^2)	Modern Wet (km^2)	Percent change Dry	Percent change Wet
Open water	139	253	146	253	+82%	+74%
Tidal marsh	1462	32	1462	32	−98%	−98%
Nontidal marsh	442	6	442	6	−99%	−99%
Riparian forest/scrub	70	22	223	49	−68%	−78%
Other seasonal floodplains	0	10	0	190		
Total	2113	323	2273	530	−85%	−77%

15% and 85% of coverage, respectively, as in the modern landscape, and were composed of the common native species today in the same relative abundances. To estimate historical aquatic plant PANPP, areas of potentially available habitat in the historical landscape were corrected for the proportion of each depth occupied by FAV or SAV in the modern landscape; these values were multiplied by the median areal productivity rate for each species (Table 2), adjusted for the proportion of the total represented by that species.

3.4. Inputs from woody riparian plants

C inputs from woody riparian vegetation enter the Delta's food web as litterfall, lateral migration of rivers, and plant mortality. Given the absence of historical data, we assumed that litterfall rates and plant mortality do not differ between wet and dry years and that plant community structure was similar in the historic and modern periods.

Litterfall was estimated by multiplying the hydrologically connected area of each riparian habitat type by the average litterfall rates measured in the Central Valley of California (Matzek et al., 2016). For areas

mapped as riparian forest, we used the average rate of 5.21 Mg C ha^{-1} yr^{-1} reported for remnant forests (Matzek et al., 2016). For areas mapped as willow scrub, we used the average rate of 1.65 Mg C ha^{-1} yr^{-1} reported for young restoration sites (Matzek et al., 2016). We assumed that C constituted 50% of dry biomass. We also assumed that litterfall from the full extent of riparian habitats contributes to the aquatic food web in wet years when floods inundate the riparian corridor. However, we assumed that only riparian areas within 25 m of water contribute litter to the aquatic food web in dry years because this is the average maximum distance from which litterfall is input to adjacent water bodies (Collins et al., 2006).

C captured via channel meandering (lateral movement) was estimated using river lengths and average annual lateral migration rates to estimate the area of riparian forest/scrub captured each year (Larsen et al., 2006; Whipple et al., 2012), and then applying measured C stocks in California riparian plant communities (Matzek et al., 2018). In areas without active channel migration, we estimated the inputs of large woody debris associated with age-related mortality. There is considerable variability in this complex process (Table 2) and a number of

Table 2

Summary of wetland primary producer groups with descriptions of each, example taxa, habitat types occupied, and summary statistics (median, interquartile range) of primary productivity measurements compiled from the scientific literature and used to estimate PANPP across different Delta landscapes. Data are insufficient for summary statistics of woody riparian plants; ranges are provided.

Primary producer group	Description	Habitat types	NPP units	Median and (interquartile range) of compiled NPP measurements
Phytoplankton	Planktonic microscopic algae including diatoms, cryptophytes, chlorophytes and cyanophytes	Open water Tidal marsh Nontidal marsh Other seasonal floodplain	mg C m^{-2} d^{-1}	123 (69–188)
Attached microalgae	Microscopic benthic or epiphytic unicellular or filamentous algae - e.g., *Navicula* spp., *Amphora* spp.	Open water Tidal marsh Nontidal marsh Riparian forest/scrub Other seasonal floodplain	g C m^{-2} yr^{-1}	Epiphytes on marsh plants: 44 (14–71) Epiphytes on aquatic plants: 24 (9–29) Non-shaded sediment: 40 (33–162)
Marsh plants	Emergent freshwater macrophytes growing in tidal or nontidal marshes	Tidal marsh Nontidal marsh	g C m^{-2} yr^{-1}	576 (388–917)
Aquatic plants, native (N) and introduced (I)	Submersed aquatic or floating vegetation (SAV or FAV)	Open water	g C m^{-2} yr^{-1}	*Stuckenia pectinata* (N, SAV): 330 (150–668) *Ceratophyllum demersum* (N, SAV): 335 (177–425) *Elodea canadensis* (N, SAV): 131 (60–346) *Egeria densa* (I, SAV): 326 (243–532) *Myriophyllum spicatum* (I, SAV): 97 (30–119) *Potamogeton crispus* (I, SAV): 23 (18–41) *Hydrocotyle umbellata* (N, FAV): 1118 (730–1252) *Eichhornia crassipes* (I, FAV): 2087 (583–2741) *Ludwigia peploides* (I, FAV): 3914 (2703–4380)
Woody riparian plants	Riparian trees, shrubs, scrub, and herbaceous understory plants.	Riparian forest/scrub	g C m^{-2} yr^{-1}	Litterfall: range = 83–261 Channel meandering: range = 4996–9306 Tree mortality: range = 4319–8413
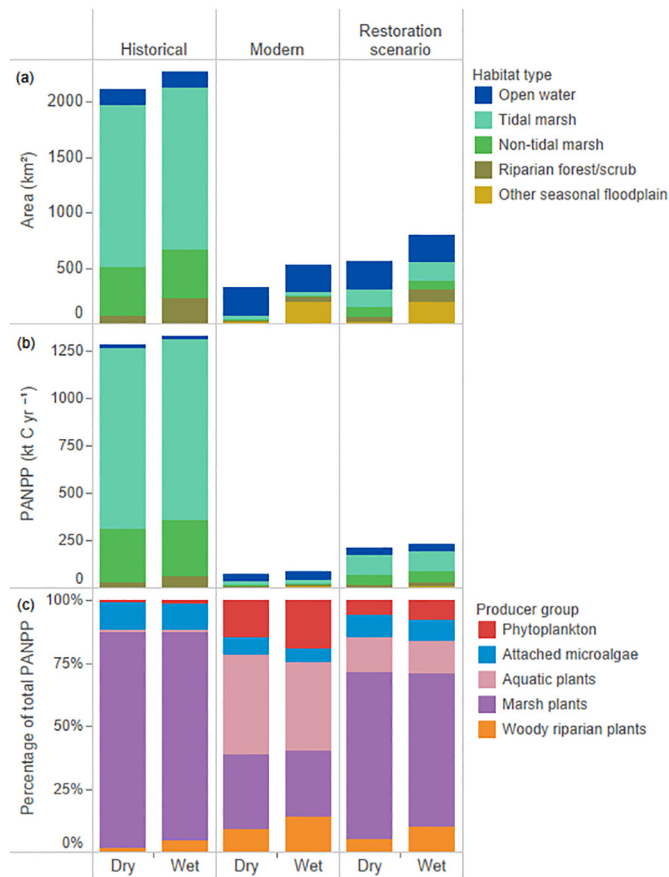
Fig. 2. (a) Hydrologically connected areas of five habitat types in the Sacramento-San-Joaquin Delta during wet and dry years for the historical and modern landscapes and a scenario of future habitat restoration. (b) PANPP generated within each of those habitat types and (c) the fractional contribution to total PANPP from each of five primary producer groups.

assumptions were required, most significantly that C inputs from tree mortality arise from a 3-m band width for willow scrub habitat types and 15-m width for riparian forest. Mortality rates were set at 1% annually with the mature age of the willow scrub community being 30 years and 100 years for riparian forests. The available literature (Supplementary material section 2.5) suggests that only 30% of plants experiencing age-related senescence fall toward the channel.

Estimated inputs from each riparian process and habitat (Supplementary material Table 3) were summed to estimate PANPP from the woody riparian plants.

3.5. Attached microalgae primary production

Few direct measurements of epiphyte or benthic microalgal NPP have been made in the Delta. We used 44 peer-reviewed scientific publications (Supplementary material Section 2.2) to obtain estimates for analogous habitat types. We considered NPP by 3 categories of attached microalgae: epiphytes on emergent vegetation, epiphytes on aquatic plants, and benthic microalgae on non-shaded sediments. Rates for benthic microalgae on shaded sediments (beneath the plant canopy) were adjusted to account for light attenuation by emergent vascular plants using the fraction of light above plant canopies that reaches the sediment surface f. The factor f has not been systematically measured in Delta tidal marshes, but it has been measured in freshwater marshes of the central USA with similar plant communities (Williams et al., 2017). We used the mean value $f = 0.68$ from light profiles measured in 25 *Schoenoplectus acutus* stands of those freshwater marshes

(Williams et al., 2017). Similarly, NPP estimates for sediments submerged by 0–1 m of water were obtained using $f = 0.05$. For sediments submerged by 1–2 m of water, we used $f = 0.01$.

The median and interquartile ranges were calculated for each of the NPP rate categories (Table 2). The median value was used to estimate NPP for each habitat type. The upper and lower quartiles were used to illustrate the uncertainty in the estimates. Respective areal rates of NPP were multiplied by the habitat area for wet/dry years and historical/modern landscapes to obtain habitat-type NPP for attached microalgae in units of kt C y^{-1}.

$$NPP = t * f * R * a * \left(1.0 \times 10^{-9}\right) \tag{1}$$

t = fraction of the year the habitat is wetted ($\times$/365)
f = light attenuation factor
R = median rate of NPP from literature (g C m^{-2} y^{-1})
a = area of habitat (m^2)

3.6. Phytoplankton primary production

Daily phytoplankton primary productivity PP has been measured as ^{14}C assimilation rates across a range of open-water habitat types in the Delta (Jassby et al., 2002; Sobczak et al., 2002). The data set includes 210 measurements having an overall mean of 152 and range of 7 to 1551 mg C m^{-2} d^{-1}. From these data, we built a Generalized Additive Model of log-transformed PP as a function of habitat depth d (m) and season (month number m), using R package *rms* (Harrell, 2017). We used this model (Supplementary material Fig. 1) to estimate monthly phytoplankton carbon production C_m (mg C month $^{-1}$) as:

$$C_m = a * PP(d, m) * t, \tag{2}$$

where a is the area of habitat (m^2) and t the number of days per month. Phytoplankton PANPP in open water habitats was estimated as the sum of monthly values of C_m over all months and habitat depths partitioned into 1-m depth bins (Supplementary material Table 1).

We applied the open-water PP model to estimate C_m in tidal wetlands, assuming they are inundated half of each photoperiod, and the depth (d) and areal extent (a) of inundated habitat vary between spring and neap tides (Supplementary material Section 1.4). We accounted for light attenuation by emergent vascular plants using the factor $f = 0.68$ (see above). Phytoplankton PANPP in tidal wetlands was computed as the sum of monthly production C_m:

$$C_m = 0.5 * a * PP(d, m) * t * f \tag{3}$$

Phytoplankton PP has been measured in a Delta floodplain when it was inundated in 2003. From these measurements (Lehman et al., 2008), we computed mean daily PP_m for each month; these ranged from 50 to 540 mg C m^{-2} d^{-1}. Then, for each month of the wet season (December–June) we estimated total monthly production as:

$$C_m = a * PP_m * t * f \tag{4}$$

where a and t varied by month and between wet- and dry year-scenarios. We used values $f = 1$ for unvegetated other seasonal floodplains and $f = 0.68$ for vegetated nontidal marshes.

The approach used to estimate phytoplankton PANPP has multiple sources of uncertainty (Supplementary material Section 2.1.2) including errors in the PP model, assumptions we made about the depths of tidal inundation and area of inundation during the photoperiod, the absence of data to validate our estimates of phytoplankton PP in tidal marshes from a model based on measurements in open-water habitats, and the small number of PP measurements made in nontidal marshes.

3.7. Future primary production gains from habitat restoration

We used the same methods described above to estimate PANPP in a future landscape scenario of achieving habitat restoration goals. We assumed that increases in the extent of each habitat type will come from areas that are now hydrologically disconnected. Other simplifying assumptions are described in Supplementary material Section 3.

3.8. Carbon flows to consumers

Organic C produced in wetlands can be exported, buried, or transferred to consumers. For each landscape-hydrology scenario, we estimated the fractions of PANPP consumed by herbivores and converted into detritus. Our estimates were based on the meta-analysis of Cebrian and Lartigue (2004) who compiled measured fates of NPP by different primary producers. For example, most of marsh-plant NPP (median 94%) is converted to detritus, whereas most of phytoplankton production (median 56%) is consumed by herbivores.

4. Results and discussion

4.1. Wetland habitat loss

Wetlands are being lost globally at a rate three times higher (0.78% yr^{-1}) than that of forests (0.24% yr^{-1}) (Ramsar Convention on Wetlands, 2018). Our reconstruction of the transformation of the Sacramento-San Joaquin Delta illustrates what that loss means when applied at the landscape scale (Fig. 1). The wetland system of the early 19th century included 1900 km^2 of marshes dominated by vascular plants (green colors, Fig. 1; Fig. 2A) that have mostly been leveed and converted to agricultural lands, largely croplands and pasture. The major outcome of landscape change has been a 98% loss of tidal and nontidal marshes (Whipple et al., 2012; Table 1). Other changes included a loss of 47 km^2 (dry years) to 170 km^2 (wet years) of hydrologically connected riparian forest/scrub, expansion of open water from 140 to 150 km^2 to 250 km^2, and replacement of up to 190 km^2 of perennial marsh with seasonally flooded agriculture and managed wetlands. This transformation is a microcosm of landscape changes occurring globally. For example, the areal extent of wetlands in Africa, Asia and Europe all decreased more than 30% between 1970 and 2013 (Ramsar Convention on Wetlands, 2018).

4.2. Lost primary production

Wetlands provide habitat for nearly 20,000 plant and animal species (Ramsar Convention on Wetlands, 2018). That biological diversity is supported by the diversity of hydrologically connected habitat types and the high primary productivity of wetland ecosystems (Moreno-Mateos et al., 2012). In our study we asked how production at the base of aquatic food webs is disrupted by human modification of wetlands as exemplified by transformation of the Delta described above. Our results show that annual PANPP in the historical landscape was ~1300 kt C, mostly in marshes by plants (~1100 kt C) and attached microalgae (~140 kt C) (Fig. 2B; Table 3). These two sources are nearly completely gone, so PANPP in the modern landscape is only ~80 kt C. This difference of 1220 kt C is an estimate of the annual NPP appropriated from aquatic food webs by landscape change. PANPP was 3% higher in wet than dry years in the historical landscape but is now 12% higher in wet years because of larger woody riparian plant inputs and an additional 5 kt C from microalgal production in other seasonal floodplains (Table 3). The Delta example illustrates how transformation of a hydrologically connected river-wetland-estuarine ecosystem to a hydrologically disconnected landscape of leveed farmland, open waters, and novel seasonal floodplains reduced NPP available to aquatic species by over 90%. To our knowledge, this is the first quantitative assessment of lost NPP resulting from landscape transformation of a multi-habitat wetland ecosystem.

The magnitude of NPP sets a limit on the abundance of consumer organisms supported by plant communities (Cebrian and Lartigue, 2004). We know, for example, that fisheries yield in oceans and freshwaters is strongly correlated with annual primary production (Nixon, 1988). The products of NPP enter aquatic food webs through grazing by herbivores and consumption of detritus. Both pathways are important in the modern Delta where invertebrates and fish assimilate organic matter from all primary producer groups (Young et al., 2020). We estimate from the losses of NPP that the annual flow of organic C (energy) to herbivores has decreased by 89% (166 to 18 kt C), and detritus production has decreased by 95% (1136 to 62 kt C; Table 4, wet scenario). These greatly reduced C flows to primary consumers are presumed to be a significant change underlying population collapses of multiple fish species and their invertebrate prey (Sommer et al., 2007).

Fish and other vertebrate populations are decreasing across the world's wetland ecosystems as agricultural and urban landscapes expand. Forty percent of the world's species live and reproduce in wetlands. A quarter of those species, including 29% of freshwater fish species, are at risk of extinction (Ramsar Convention on Wetlands, 2018). Human appropriation of wetland NPP and the resulting reduction of energy flow to primary consumers have not yet been assessed at the global scale. However, the magnitude of changes reported here suggest that a key process underlying population declines of wetland-dependent species is the reduction of energy supplies supporting aquatic food webs.

4.3. Restructured producer communities

Wetland ecosystems are mosaics of different habitat types supporting different primary producer communities and rates of productivity (Table 2). Conversion of wetlands can alter the composition of those mosaics by contraction of some habitat types and/or expansion of others. For example, nearly 16,000 km^2 of wetlands were lost from 14 of the world's largest deltaic plains in recent decades, two thirds from conversion for agricultural and urban use and one third to expansion of open waters (Coleman et al., 2008). A similar, but more extreme shift has occurred in the Delta: 98% of its historical marshes have been lost while open waters expanded more than 70% (Table 1). Thus, differential habitat modifications transformed a marsh-dominated ecosystem where tidal and

Table 3
Estimated potential aquatic net primary production (PANPP, kt C yr^{-1}) across three Delta landscapes and two water-year types for five primary-producer groups (bold), binned by habitat types.

Primary producer group Source habitat type	Historical		Modern		Future	
	Dry	Wet	Dry	Wet	Dry	Wet
Phytoplankton	**12**	**20**	**11**	**16**	**12**	**19**
Open water	6	6	11	11	11	11
Tidal marsh	7	7	0	0	1	1
Nontidal marsh	0	8	0	0	0	2
Other seasonal floodplain			0	5	0	5
Attached microalgae	**140**	**140**	**5**	**5**	**20**	**19**
Open water	1	1	1	1	1	1
Tidal marsh	100	100	2	2	12	12
Nontidal marsh	32	29	0	0	6	5
Riparian forest/scrub	4	4	1	1	1	1
Other seasonal floodplain			0	0	0	0
Aquatic plants	**13**	**14**	**30**	**30**	**30**	**30**
Open water	13	14	30	30	30	30
Marsh plants	**1100**	**1100**	**22**	**22**	**140**	**140**
Tidal marsh	840	840	18	18	94	94
Nontidal marsh	250	250	4	4	48	48
Woody riparian plants	**21**	**59**	**6**	**12**	**10**	**23**
Riparian forest/scrub	21	59	6	12	10	23
Total	**1300**	**1300**	**74**	**84**	**210**	**230**

Bold entries are summed values for each producer group and the total of all producer groups.

nontidal marshes contributed 94–97% of PANPP (Table 3) to a new ecosystem type where most PANPP is in open waters. Marsh vascular plants contributed more than 80% of PANPP in the historical landscape compared to 26–30% now (Fig. 2C), and they now contribute less to PANPP than aquatic plants (35–40%) (Fig. 2C). Phytoplankton was a minor (2%) component of PANPP but now contributes 15–19%. Therefore, loss of marshes and expansion of open-water habitats not only reduced PANPP more than tenfold, but they also restructured the primary producer community by transposing the relative contributions of marsh vs. aquatic plants and of vascular plants vs. phytoplankton.

This restructuring of producer communities has an important implication for scaling up the results of place-based assessments of NPP loss. Our results show that the 94% loss of PANPP (Table 3, wet scenario) exceeded the 77% loss of hydrologically connected habitat area (Table 1) due to the selective elimination of high-productivity marsh habitats (~650 g C m^{-2} yr^{-1}) and expansion of lower-productivity (~140 g C m^{-2} yr^{-1}) open-water habitats. Thus, losses of NPP and wetland area do not necessarily scale 1:1. They will exceed that ratio if high-productivity habitats are selectively lost. Assessments of regional or global losses of wetland NPP will therefore require spatially explicit landscape analyses that account for this variability of areal primary productivity rates across habitat and vegetation types.

4.4. Prospects for and challenges of remediation

Our results illustrate how the disruption of ecosystem functions by landscape change can reduce the capacity of wetlands to support populations of consumers and their food resources. The continuing and accelerating loss of wetlands has prompted conservation plans to halt and reverse their degradation. The Ramsar Convention is an example of a global-scale agreement between 170 nations to "promote wetland conservation, wise use, and sustainability of biodiversity" (Ramsar Convention on Wetlands, 2018). Local-scale efforts are exemplified by the Delta Plan to restore its lost habitats, their connectivity, and the functions they provide to support native, resident and migratory species (Delta Stewardship Council, 2019). Current proposed targets include restoring 131 km^2 of tidal marsh, 77 km^2 of nontidal marsh, and 66 km^2 of riparian forest/scrub. However, this plan has no targets for improved ecological functions such as primary production or C flow to consumers. We estimate that if the Delta habitat restoration targets were met, annual PANPP would increase from 74 –84 kt C to 210–230 kt C (Fig. 2B, Table 3). This gain would recover 12% of lost PANPP and increase PANPP from 6% to 17% of its historical magnitude. This scale of habitat restoration would amplify the energy supply to consumers by doubling C flow to herbivores and tripling the current rate of detritus production (Table 4, wet years). These kinds of quantitative estimates are critical steps toward developing performance measures required to manage wetlands for ecosystem functions (Fulford et al., 2020). Reversion toward a marsh-dominated wetland has implications beyond the magnitude of NPP. Successful habitat restoration would also increase the marsh plant fraction of PANPP from ≤30% to >60% and decrease the aquatic plant fraction from 35 – 40% to <15%, re-balancing their relative contributions toward those in the historical landscape.

These projections must be tempered by the recognition that wetland restoration does not always recover ecosystem functions to their original levels (Moreno-Mateos et al., 2012). The value of restored primary production in supporting aquatic food webs in floodplain-pulse and tidal-pulse ecosystems depends not only on its magnitude, composition, and nutritional quality (e.g., marsh-based detritus vs. algal biomass), but also on the accessibility of production to higher-level consumers, which depends on physical habitat structure, the timing and transport of biomass, and hydrologic connectivity (Polis et al., 1997; Garcia et al., 2017; Colombano et al., 2021). In the Delta, for instance, riverine (often managed) floodplains provide important habitat for imperiled native fish like Sacramento splittail and Chinook salmon, which rely on seasonal floodplain habitats and their abundant food resources to spawn and/or rear (Jeffres et al., 2008, Moyle et al., 2004). Managing these floodplains for hydrologic connectivity — particularly in dry years — may become increasingly important in determining the availability of NPP as the region experiences greater climate extremes (Knowles et al., 2018; Swain et al., 2018).

The success of wetland restoration in recovering ecosystem functions can be modulated by other drivers of change that transform restored wetlands into alternative states, different from their condition before degradation. Two examples emerged from our study. First, phytoplankton production is now the largest source of organic C to herbivores (Table 4). However, that source is small because phytoplankton areal productivity across the Delta is low (~70 g C m^{-2} yr^{-1}; Jassby et al., 2002). This is partly a consequence of fast grazing and strong top-down control of phytoplankton biomass by two clam species introduced in the 20th century. Phytoplankton production is elevated (16 kt C) in wet years compared to dry years (11 kt C, Table 3), and this reflects the management action of inundating floodplains during spring of wet years to support high secondary production and growth of juvenile salmonids (Sommer et al., 2001). This management action depends upon water availability, and its long-term sustainability is uncertain given projected shifts toward drier spring months as global warming proceeds (Knowles et al., 2018). Finally, 30% of phytoplankton biomass produced in the Delta is lost with water exports and diversions (Jassby et al., 2002) and therefore unavailable to support local food webs. Thus, the shift from plants to phytoplankton (Fig. 2C) established an ecosystem where C flow to pelagic herbivores is constrained by other human disturbances beyond landscape change including species introductions, water management and climate change.

Second, aquatic plants have displaced marsh plants as the largest source of organic C supporting detritus production (Table 4). The aquatic plant community is now dominated by introduced species

Table 4

Net primary production and carbon flows in three wetland landscapes. PANPP is estimated potential aquatic net primary production in the Sacramento-San Joaquin Delta comparing historical and modern landscapes and a future landscape after habitat restoration for the wet-year scenario. C flows to herbivores and to detritus production were estimated using median values of the fractions of NPP routed to those pathways from the meta-analysis of Cebrian and Lartigue (2004).

	PANPP (kt C yr^{-1})	Fraction of PANPP to herbivores	Carbon flow to herbivores (kt C yr^{-1})	Fraction of PANPP to detritus production	Carbon flow to detritus (kt C yr^{-1})
Historical landscape					
Phytoplankton	20	0.56	11	0.35	7
Attached microalgae	140	0.46	64	0.23	32
Aquatic plants	14	0.15	2	0.81	12
Marsh plants	1100	0.08	88	0.94	1000
Woody riparian	59	0.03	2	0.93	55
Total	**1300**		**170**		**1100**
Modern landscape					
Phytoplankton	16	0.56	9	0.35	6
Attached microalgae	5	0.46	2	0.23	1
Aquatic plants	30	0.15	4	0.81	24
Marsh plants	22	0.08	2	0.94	21
Woody riparian	12	0.03	0	0.93	11
Total	**84**		**18**		**62**
Future landscape					
Phytoplankton	19	0.56	10	0.35	6
Attached microalgae	19	0.46	9	0.23	4
Aquatic plants	30	0.15	4	0.81	24
Marsh plants	140	0.08	11	0.94	130
Woody riparian	23	0.03	1	0.93	21
Total	**230**		**35**		**190**

such as _Egeria densa_, which forms dense beds at the expense of native plants (Borgnis and Boyer, 2016) and provides rearing habitat for non-native predatory fish (Conrad et al., 2016). The Delta fish community has become increasingly dominated by non-native species as invasive aquatic plants have expanded in recent decades (Brown and Michniuk, 2007; Young et al., 2018). This expansion was facilitated by managed inflows to repel salinity intrusion. Although invasive plants are a source of organic C used by consumers (Young et al., 2020), their modification of open-water habitats threatens sustainability of indigenous fish (Ferrari et al., 2014) and counters restoration goals.

5. Conclusions

Current estimates of global wetland areal loss (33%–87%) imply that humans have appropriated a percentage of global wetland NPP that is 1.3 to 3.5 times larger than the 25% of NPP appropriated from terrestrial ecosystems (Haberl et al., 2007). Human appropriation of wetland NPP is even larger where vegetated marshes have been selectively lost or converted to open water. The pace of global landscape change is accelerating as the human population grows to a projected 9.6 billion by 2050, risking the loss of 20% of Earth's remaining natural lands (Oakleaf et al., 2015). Four lessons emerged from our study that can be applied to anticipate ecological outcomes of future wetland losses and remediation of past losses through habitat restoration.

1. Wetland loss reduces NPP supporting aquatic food webs, and the magnitude of loss depends on the degree to which high-productivity habitats, such as marshes, are lost relative to lower-productivity habitats, such as open water.
2. Transformation of wetlands can restructure primary-producer communities, leading to shifts in food quality and the pathways of organic C routing to consumers.
3. Habitat restoration can be a feasible remediation step for returning lost NPP to transformed wetlands. Simple methods can project functional outcomes of different restoration scenarios and establish performance metrics to gauge success.
4. The challenge of wetland restoration is confounded by other human disturbances such as species introductions, water management, and climate change. Thus, the ultimate outcomes of wetland conservation and restoration plans will depend on our capacity to both conceptualize and manage the multi-stressor problem as exemplified in the Sacramento-San Joaquin Delta.

Data statement

All datasets analyzed here are available from the references cited.

CRediT authorship contribution statement

James E. Cloern: Conceptualization, Investigation, Formal analysis, Funding acquisition, Writing – original draft. **Samuel M. Safran:** Conceptualization, Investigation, Formal analysis, Writing – original draft, Visualization. **Lydia Smith-Vaughn:** Conceptualization, Investigation, Formal analysis, Writing – original draft, Visualization, Project administration. **April Robinson:** Conceptualization, Investigation, Project administration, Funding acquisition, Writing – review & editing, Visualization. **Alison A. Whipple:** Conceptualization, Investigation, Formal analysis, Writing – review & editing, Visualization. **Katharyn E. Boyer:** Conceptualization, Investigation, Formal analysis, Writing – original draft. **Judith Z. Drexler:** Conceptualization, Investigation, Formal analysis, Writing – original draft. **Robert J. Naiman:** Conceptualization, Investigation, Formal analysis, Writing – original draft. **James L. Pinckney:** Conceptualization, Investigation, Formal analysis, Writing – original draft. **Emily R. Howe:** Conceptualization, Investigation, Writing – review & editing. **Elizabeth A. Canuel:** Conceptualization, Investigation, Writing – review & editing. **J. Letitia Grenier:** Conceptualization, Investigation, Project administration, Funding acquisition, Writing – review & editing, Visualization.

Appendix A. Supplementary material

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