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Maintaining channel abandonment processes increases riparian plant diversity within fluvial corridors

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ABSTRACT

Within dynamic alluvial riverine corridors, abandoned channels form and experience hydrogeomorphic processes that are distinct from similar elevation surfaces along active channels. Compared with the relatively well-studied role of fluvial disturbance on floodplain plant communities along active channels, the drivers of plant diversity and community dynamics along terrestrializing abandoned channels have received much less attention. In this study, we addressed several related questions within the context of the Sacramento River (California, USA): (1) Do abandoned channels host different plant species compared with the surrounding floodplain? (2) How do plant communities vary among abandoned channels in relation to time since cutoff and disturbance regime? (3) Do understory plant species within an abandoned channel display distinct zonation along a disturbance gradient from the wetted edge laterally to upland areas? Our results show that although species richness is similar to floodplain sites, abandoned channels support a different species pool, notably due to presence of more wetland-associated species, and this contributes to increase biodiversity within the fluvial corridor. We found substantial shifts in species composition that occurred since channel abandonment, likely related to decreases in the strength of hydromorphic disturbance through time. Lastly, we found that lateral environmental gradients within abandoned channel sites were significant, although much weaker drivers of understory vegetation patterns than typically found along active channel banks. These results argue for a management approach that preserves and promotes natural processes of channel migration and sediment dynamics.

KEY WORDS abandoned channel; sedimentation; understory vegetation; flood disturbance; floodplain forest; channel cutoff; riparian vegetation

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INTRODUCTION

Process-based approaches to riparian management and restoration have gained prominence in recent decades with our increased understanding of the strong physical and biological linkages within these systems (Naiman *et al*., 2005). Variation in hydrogeomorphic conditions – particularly the disturbance regime – profoundly influences riparian vegetation communities, both in the pioneer phase of colonization and in later stages as communities develop (Bendix and Stella, 2013). These physical drivers include flood intensity, frequency, timing and inundation duration, sedimentation, scour intensity and water availability (Menges and Waller, 1983; Hupp, 1992; Van Coller *et al*., 1997; Bendix and Hupp, 2000; Steiger *et al*., 2005). Studies beginning in the early to mid-20th century established that biological diversity at the valley-bottom scale is related to the presence of fluvial landforms such as channel banks, point bars and floodplain scrolls that exhibit strong gradients of topography and hydrology (Hefley, 1937; Johnson *et al*., 1976; Hupp and Osterkamp, 1985; Budke *et al*., 2008). Better quantification of the links between physical drivers and vegetation responses spurred the development of a process-based understanding of fluvial systems and approach to their restoration (Boon *et al*., 1992; Auble *et al*., 1994; Dufour and Piégay, 2009; Stella *et al*., 2013). Rather than establishing a fixed pattern of topography or vegetation distribution, a process-based approach seeks to restore the underlying physical regimes such as flooding, channel morphodynamics and sediment transport that generate and maintain diverse aquatic and floodplain habitats (Ward *et al*., 2001; Hughes *et al*., 2005).

Lateral channel mobility is one of the main hydromorphological processes that influences riparian vegetation pattern and diversity, primarily because it shapes a complex mosaic of sediment deposits (with regard to depth, texture and organic material), topographic conditions (e.g. elevation above the water table) and terrestrial and aquatic habitats (Salo *et al*., 1986; Florsheim *et al*., 2008). Lateral channel mobility also drives the creation of

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abandoned channels, which are distinct features in the floodplains of many mobile rivers (Vogt, 1965; Lewis and Lewin, 1983; Shankman, 1993; Stella *et al.*, 2011). Abandoned channels are often marginal semi-aquatic features (i.e. topographic depressions) yet experience less intense and less frequent physical disturbance compared with similar elevations along main channel margins (Constantine *et al.*, 2010).

After the initial cutoff event, abandoned channels become progressively disconnected from the main channel, and this process is a critical factor that drives the rate and pattern of sediment filling within the aquatic zone (Citterio and Piégay, 2009; Constantine *et al.*, 2010). As hydrologic and sedimentary conditions diverge relative to conditions in the main channel and adjacent floodplain (Gagliano and Howard, 1984; Piégay *et al.*, 2008; Stella *et al.*, 2011), the aquatic part of abandoned channels adds habitat heterogeneity, thus improving floodplain biological diversity by supporting specific pools of species and providing refugia during floods (Pautou, 1984; Kalliola *et al.*, 1991; Amoros and Wade, 1993; Bornette *et al.*, 1998; Godreau *et al.*, 1999).

Most studies on abandoned channels have focused on processes and patterns in the aquatic zone, particularly gradients of hydrological connectivity (Hudson *et al.*, 2012; Phillips, 2013), sedimentation and geomorphological patterns (Bravard, 1982; Gagliano and Howard, 1984; Shields and Abt, 1989; Citterio and Piégay, 2009; Constantine *et al.*, 2010; Delhomme *et al.*, 2013; Dieras *et al.*, 2013), impacts of nutrient load and hydrogeological fluxes (Bornette *et al.*, 2001), and diversity of aquatic vegetation and animal communities (Amoros and Bornette, 2002; Obolewski, 2011; Besacier-Monbertrand *et al.*, 2012; Meyer *et al.*, 2013; Toth *et al.*, 2013). However, the larger floodplain environment that develops as abandoned channels fill has received much less attention, in particular the composition, biodiversity and temporal changes of the terrestrial plant community and its distribution along hydrogeomorphic gradients (but see Shankman, 1993; Holland *et al.*, 2000). Additionally, riparian vegetation associated with abandoned channels is often the most extensive remnant within large river floodplains that have experienced significant land conversion (Stella *et al.*, 2011), because their semi-aquatic condition makes them less likely to have been converted to other land uses. Thus, a better understanding of their vegetation dynamics and contribution to biodiversity within the fluvial corridor is essential for both prioritizing conservation efforts and for designing feasible restoration approaches.

The objective of this paper is to assess the community composition and temporal changes of riparian plant species that colonize abandoned channels within the fluvial corridor of the middle Sacramento River, a large, meandering, gravel-bed river in central California. We aim to understand the contributions of these environments to plant diversity within the river corridor, the drivers of plant diversity and community dynamics along terrestrializing abandoned channels, and to assess the potential benefits of process-based management strategies in promoting their sustainability. We include gross comparisons in woody species composition and dominance among abandoned channel types, but we focus with more detail on patterns of understory vegetation because it is the most diverse component of the vascular flora and the most sensitive to local (or fine scale) physical gradients characteristic of abandoned channels (Dufour and Piégay, 2008, 2010). Specifically, we addressed three questions: (1) Do abandoned channels host different plant species compared with the surrounding floodplain? (2) How do plant communities vary among abandoned channels in relation to time since cutoff and flood disturbance regime (i.e. inundation frequency and overbank sediment deposition magnitude)? (3) Do understory plant species within an abandoned channel display distinct zonation along a disturbance and water availability gradient from the wetted edge laterally to upland areas?

On the basis of prior riparian studies by the present authors and others, we predicted that a distinct pool of species would be associated with abandoned channels compared with similar elevation environments within or adjacent to the active channel due to their wetter and more stable abiotic conditions. We also expected younger, more recently abandoned channels to have greater levels of local specificity in terms of community composition, diversity and abundance of disturbance-adapted species, due to the strength of hydrogeomorphic factors that drive the early phase of succession (Corenblit *et al.*, 2007; Stella *et al.*, 2011). With time since cutoff, we expected a decrease in diversity and a rapid homogenization of the plant community, due to rapid attenuation of floodplain sediment deposition and increases in plant resource competition, particularly for light (Stella *et al.*, 2011). For older abandoned channels that remain hydraulically connected to the main channel, we expected these shifts to be weaker because of a relatively high disturbance regime compared with disconnected backwater abandoned channels. Lastly, we expected to see a distinct lateral community pattern within each abandoned channel that followed the gradients of disturbance magnitude and frequency and water availability from lower to higher elevations (Pautou *et al.*, 1985; Lite *et al.*, 2005).

MATERIAL AND METHODS

Study reach

The Sacramento River catchment is the largest in California, draining 68 000 km^2 from the Sierra Nevada and Klamath Mountains, Coast Ranges, and the southern end of the Cascades and Modoc Plateau, through the northern half of the Great Central Valley to the San

Francisco Bay-Delta. The middle reach of the river extends for 160 river kilometres, from a major diversion dam in Red Bluff (Tehama County) downstream to the overflow weir in Colusa (Colusa County) (Figure 1). The area experiences a Mediterranean climate, with hot, dry summers and cool, wet winters. Average annual precipitation in the valley is 56 cm, over 80% of which typically falls between December and February (DWR, 1994). The average annual temperature is approximately 17 °C, reaching highs of 32–47 °C in summer and lows around freezing in winter (DWR, 2006). Land use in the floodplain of the study reach is predominantly agricultural, dominated by fruit and nut orchards. On the basis of classification proposed by Dodds *et al.* (1998), water quality data indicate that the mainstem in this reach is typically oligotrophic in total nitrogen and mesotrophic in total phosphorus (Domagalski *et al.*, 2000).

We selected this reach because it is generally unconfined, actively shifting with many abandoned channels, and new knowledge on linked geomorphological and ecological processes is needed to inform river conservation strategies. This reach is primarily a single-thread, gravel-bed, meandering section of stream set within a fine-grained floodplain alluvium.

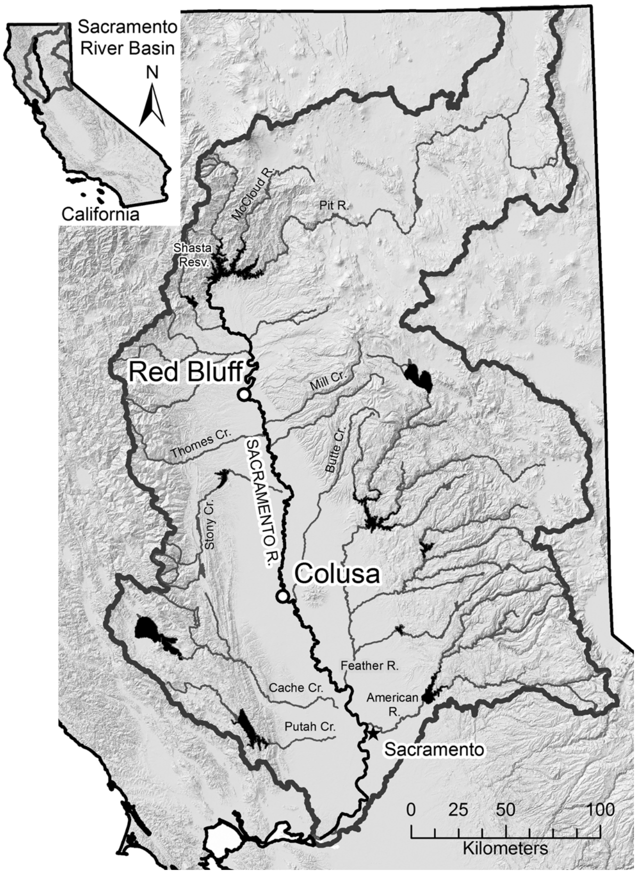

Figure 1. Sacramento River study area. The middle reach extends between Red Bluff and Colusa.

Bankfull channel width averages 300 m, and channel slope ranges from $0{\cdot}0007\ \mathrm{m\,m^{-1}}$ at the upstream end to $0{\cdot}0002\ \mathrm{m\,m^{-1}}$ at the downstream end (Micheli *et al.*, 2004; Constantine, 2006). The study reach is underlain by tertiary and quaternary sedimentary deposits (DWR, 1994), with banks that range from very hard, cemented material to coarse, non-cohesive alluvium (Constantine, 2006). Alluvial deposits over the last century typically include a silty upper layer of overbank material on top of non-cohesive gravel and sand channel deposits (Constantine, 2006). The median grain size of the main channel bed ranges from 15 to 35 mm (Micheli *et al.*, 2004), with much finer sand and silt deposits in the abandoned channels.

The mainstem is regulated at Shasta Dam, built in 1942 to capture peak flows for irrigation supply and hydropower generation. All major tributaries are regulated by either storage or overflow dams. Despite significant flow regulation with truncated peak flows, reduced sediment supply and elevated base flows, geomorphically significant events still occur and result in active channel migration and cutoffs (Larsen *et al.*, 2007; Singer, 2007; Micheli and Larsen, 2010). New abandoned channels appear to be created with similar frequency as in pre-dam conditions, but they are typically smaller in length and surface area, reflecting an increase in chute versus neck cutoffs that has resulted from the complex interplay of land-use changes, historical timing of large floods, and effects of dams and bank revetment on channel migration (Michalkova *et al.*, 2010). Despite an estimated loss of 90% of riparian forest area throughout the Central Valley since European settlement, the middle Sacramento River corridor has the largest network of pioneer and mature forest stands remaining in California (Buer *et al.*, 1989). A significant fraction (54%) of these extant pioneer forest stands formed within abandoned channels (Stella *et al.*, 2011).

Abandoned channel selection and sampling strategy

In order to compare differences between flora in abandoned versus active channel floodplain environments, we collected field data at ten abandoned channel sites and compared them with existing floodplain community data surveyed in 2003 (Vaghti *et al.*, 2009 and Viers *et al.*, 2011; see Section on Floodplain Vegetation Data Set). All sites had some remnant wetland or lake feature, and experienced varying degrees of sedimentation and vegetation colonization since abandonment. To analyse variability of vegetation patterns both among and within abandoned channels, the ten sites were selected to span a range of time (15–100 years) since cutoff (Stella *et al.*, 2011) and represented a range of geomorphic (notably sedimentation) and historical (i.e. plant colonization) conditions from a total of 30 abandoned channel sites found within the study reach (see Michalkova *et al.*, 2010 for geomorphic analysis of the full 30 sites). For each site selected, its assigned age corresponded to the mid-point year between a sequential set of aerial photos that show the site before and after abandonment (Stella *et al*., 2011).

To highlight the role of time and disturbance regime, we grouped the sites on the basis of a combination of age and hydrogeomorphic considerations. Field observations and aerial photo analysis by Kondolf *et al*. (2006) indicated that three of the six older (i.e. >35 years) abandoned channels retained hydraulic connectivity to the main channel, largely driven by their planform shape and orientation. These three sites shared a straighter channel morphology, resulting in a more active disturbance regime, with more frequent connection to upstream flows and significantly coarser sediments deposited in the aquatic zone. The other three older channels functioned as backwaters connected upstream only at high discharge, resulting in a lower disturbance frequency (Figure 2). There were no young channels located in corresponding backwater areas evident along the Sacramento River. Thus, our analysis across sites compared three geomorphic types that represent different time and disturbance regime conditions: four young active sites (hereafter named 'YA', all <25 years old); three old active sites ('OA'; >35 years old) and three old backwater sites ('OB', >35 years old). Median upstream overbank discharges were, respectively, 198, 395 and 1086 $m^3 s^{-1}$ for the young active type, old active type and old backwater type (C. Gomez, unpublished data).

In late April and early May 2007, we surveyed the vegetation and key physical drivers within the boundaries of the former wetted channel that had filled with sediment and were currently vegetated (*sensu* Citterio and Piégay, 2009). This was carried out to ensure we only sampled vegetation that colonized after abandonment. Sampling was conducted along three transects on the inner (convex) bend of each channel. All transects were oriented perpendicular to the abandoned channel centreline, began at the transition between aquatic and terrestrial vegetation and extended upslope away from the aquatic zone for 45 m. This distance was a conservative estimate of floodplain area that developed within the wetted width of the original channel; aerial photographs confirmed that all transects were located on areas that experienced bedload and fine sediment infilling and not on point bars colonized prior to channel cutoff (Michalkova *et al*., 2010). At each site, one transect was randomly placed within the upstream, middle and downstream thirds of the abandoned channel segment (i.e. a total of 30 transects).

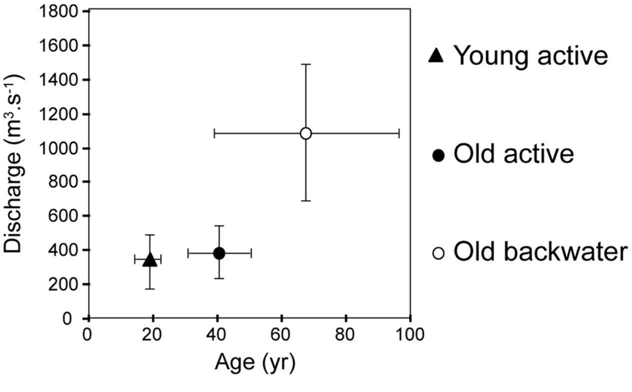

Figure 2. Means and range of ages and connecting discharges for the ten abandoned channel sites: young active (YA, $n = 4$), old active (OA, $n = 3$) and old backwater (OB, $n = 3$).

Measurement of physical variables

To assess current conditions in terms hydrosedimentary conditions, we surveyed topography along each transect relative to the summer baseflow surface water elevation in the river using an autolevel (Model AT-G4, Topcon Corp., Tokyo). The surveys were completed during a 10-day period when the mean flow was, respectively, 266 at Vina-Woodson Bridge (DWR gauge ID: VIN), 220 at Hamilton City and 221 $m^3 s^{-1}$ at Ord Ferry.

Moreover, as we focused on understory vegetation (see Section on Understory Survey), we assessed the grain size of surface sediment as a proxy of current flood disturbance regime (Dufour and Piégay, 2010). We used a 10 cm diameter × 20 cm deep soil auger to collect sediment samples at four locations per transect: in the aquatic zone and at 4, 20 and 44 m from the wetted edge. Grain size analysis was carried out using a Laser granulometer Malvern Mastersizer 2000.

Lastly, we characterized mean hydrosedimentary conditions using long-term average net sedimentation rates derived by Stella *et al.* (2011), which were based on measuring the accumulation of fine sediment above the former gravel bar surface since time of cutoff (Piégay *et al*., 2008).

Canopy survey

Along each transect, we sampled the overstory canopy composition by the line intercept method (Krebs, 1999). We quantified the frequency of each species along a transect scale by considering 45 points regularly spaced with interval of 1 m along the transect and counting the presence or absence of the species at each point. These data were included primarily to relate to compositional patterns in the understory vegetation, and secondarily to understand gross differences in woody species composition and dominance between the different habitats.

Understory survey

We sampled understory vegetation composition and abundance within ten, 1 × 2 m plots along each 45-m transect, with the longer side of the plot perpendicular to the transect. We expected more variation in topographic and hydrologic patterns nearest to the aquatic part of the abandoned channel; therefore, we placed five plots within the first 15 m (regularly spaced every 3 m) and five plots between 15 and 45 m (every 6 m). Within each plot (30 plots per abandoned channel; $N = 300$ total), we identified all vascular plant species and estimated abundance by percent cover using modified Braun-Blanquet (1932) cover classes: absence, <2%, 2–5%, 5–10%, 10–25%, 25–50% and >50%. Bare ground, litter and coarse woody debris were also noted using the same cover classes. Species identification was based on Hickman (1993). Nomenclature was updated to follow the second edition (Jepson Flora Project, 2012), which was published after our surveys were completed.

Floodplain vegetation data set

We compared the understory vegetation sampled in abandoned channels (described above) with understory data from an existing 2003 study within the Sacramento River active channel floodplain (hereafter ‘floodplain’ data) that comprised 91 plots located within the same range of elevation relative to water surface and landform age as our abandoned channel plots (for details, see Vaghti *et al.*, 2009 and Viers *et al.*, 2011). The previously surveyed floodplain plots were 200 m^2. Because sampling methods and plot sizes were different, we only compared species composition and not abundance.

Data analysis

For the Abandoned Channel (AC) versus Floodplain (FP) comparison (Question #1), abundance was measured based on presence/absence data (due to differences in sampling methods and plot sizes) and limited to those species present in ≥10% of plots (i.e. frequently encountered species). For comparison among and within the three abandoned channel types (Questions #2 and #3), abundance was evaluated by percent cover using the median value of each cover class. Means and standard deviations are thus based on these median cover values.

We used a complementary suite of analyses to quantify differences in plant community composition, abundance and diversity. We first tested for significant differences between species pools found in AC versus FP plots (Question #1) and among the three AC types (Question #2) with a multiple response permutation procedure (MRPP). MRPP is an analogous nonparametric procedure to discriminant analysis that tests the hypothesis of no difference between or among pre-defined plant communities (McCune and Grace, 2002).

We then documented the nature of any differences with the Chao–Jaccard similarity index, measures of species richness and diversity, and an indicator species analysis. We chose the Chao–Jaccard similarity index because it has been shown to reduce the risk of sampling bias when using only species presence/absence data (Chao *et al.*, 2005). We calculated a 95% confidence interval as SE × 1·96 where SE is the standard error. We considered non-overlapping intervals between groups as an indicator of significant dissimilarity between species pools. We compared species diversity and richness using well-established diversity indices (Magurran, 1988), including Simpson’s D, and Shannon’s H’, and an asymptotic estimation of richness (Chao, 1987). All similarity and diversity analyses were conducted using EstimateS 8.2 (Colwell, 2006).

Our indicator species analysis was based on the general approach of Dufrene and Legendre (1997), and corrected for use of presence/absence data (for AC vs FP comparison) following the methods of Tichý and Chytrý (2006). Indicator species were those species that were both common (as measured by abundance) and had high fidelity to one habitat type (e.g. predominantly found only in floodplain sites), as defined by distinct environmental conditions (Dufrene and Legendre, 1997). We focused only on those indicator species with a p-value of $\leq 0{\cdot}05$. Species characteristics and habitat information came from four main sources: the Jepson Flora (Jepson Flora Project, 2012), Calflora database (http://www.calflora.org), the California Invasive Plant Council Inventory Database (http://www.cal-ipc.org/paf/), and United States Fish and Wildlife Service wetland indicator status information (http://plants.usda.gov/wetland.html).

To evaluate whether differences in species pools among AC types were driven by differences in hydrogeomorphic disturbance regime (Question #2), we first determined whether there were statistical differences in physical characteristics among the three abandoned channel types. Statistical significance of differences in mean values for sedimentation rate, relative elevation and sediment grain size between abandoned channel types were tested using ANOVA (normal data) or Kruskal–Wallis (non-normal data) tests in R3.0.2-software (R Core Team, Vienna, Austria). Post hoc tests (Tukey’s and Scheffe’s tests) and a multiple comparison test (Dwass–Steel–Critchlow–Fligne method) were used to identify which groups differ from others, respectively, for ANOVA and Kruskal–Wallis tests.

Finally, we used multivariate ordination to evaluate the influence of disturbance regime and other environmental gradients on understory species composition patterns among and within AC sites (Questions #2 and #3). Given our interest in quantifying the role of specific local drivers, we applied canonical correspondence analysis (CCA), a form of direct gradient analysis. Our data fit the CCA assumptions of multivariate normality; therefore, this parametric ordination procedure was most appropriate. The results of CCA express the pattern of variation in species composition in relation to an observed set of variables (Palmer, 1993; Ter Braak, 1995). As potential drivers, we included canopy openness, the abundance of overstory cottonwood (*Populus fremontii*) trees (expressed as relative basal area), relative elevation above the former channel, surface sediment grain size and distance from the abandoned channel aquatic edge. We also included the site-scale variables of age since abandonment and geomorphic type (i.e. young active, old active and old backwater). Geomorphic type was included as a categorical variable by coding two 'dummy variables'. We treated young active as the baseline state. The ordination included 291 samples (because 9 quadrats had no plants) and 70 species. All ordinations were conducted in PC-ORD (MjM Software Design, Gleneden Beach, Oregon). To more specifically assess the effect of lateral gradients within abandoned channels (Question #3), we also ran three additional CCA's for each of the geomorphic categories (e.g. young active, old active and old backwater) but with only two environmental variables: relative elevation and distance from water.

RESULTS

Abandoned channel versus floodplain understory vegetation

There were significant differences in species composition based on presence/absence between abandoned channel and floodplain plots (MRPP test, $p < 0{\cdot}0001$). An asymptotic estimation of species richness showed that abandoned channels significantly contribute to species diversity of the fluvial corridor. Floodplain and abandoned channels had, respectively, a richness of 69 (95% CI = 61–94) and 68 (64–82) species, with a total richness of 104 (97–129) for all plots together. Similarity analyses also indicated that abandoned channels represent a distinct plant community. Of the 70 species observed, respectively, in floodplain and abandoned channel environments, only 33 species were shared between the two groups (Chao–Jaccard similarity index = 0·61; SE = 0·12). Shared species included similar dominance (by frequency) of four common species: two species of *Rubus*, the native perennial wetland herb *Artemisia douglasiana* and the weedy annual *Galium aparine* (Table I). The main differences were (1) abandoned channels had fewer indicator species, 10 versus 26 in floodplain plots ($p \leq 0{\cdot}05$), (2) a higher proportion of these indicators were native wetland-associates (70% vs 38%) and (3) many were particularly associated with slow-water areas, whereas the slow-water species found in floodplain sites were mostly infrequent (present in <3% of plots; Supplemental Information: Appendix 1).

Among and within-abandoned channel patterns: changes in disturbance regime through time

Plant community patterns among abandoned channel types. The overstory tree community that colonized abandoned channels was similar in composition among the three geomorphic types. There were no pairwise differences based on similarity index if we look at the mean ±1·96 SE (i.e. all overlap 1) (Table II). There was no difference in

Table I. Understory species present in ≥10% of abandoned channel and/or floodplain plots (total richness = 104), listed here in rank order by percent frequency in AC plots.

					Abandoned Channel Plots ($n = 291$)		Floodplain Plots ($n = 73$)	
Species	Family	Growth habit	Native	Wetland indicator status	% Freq.	Rank	% Freq.	Rank
Artemisia douglasiana	Asteraceae	Perennial	Y	FACW	24·4	1	31·5	2
Rubus ursinus	Rosaceae	Shrub	Y	FAC	23·4	2	30·1	4
Galium aparine	Rubiaceae	Annual	Y	FACU	20·6	3	28·8	5
Rubus armeniacus	Rosaceae	Shrub	N	FACW	18·6	4	16·4	10
Boehmeria cylindrica	Urticaceae	Perennial	N	OBL	18·2*	5	1·4	58
Lycopus americanus	Lamiaceae	Perennial	Y	OBL	18·2*	6	—	—
Equisetum laevigatum	Equisetaceae	Annual/fern	Y	FACW	17·9*	7	—	—
Cyperus eragrostis	Cyperaceae	Perennial	Y	FACW	13·4*	8	5·5	19
Leersia oryzoides	Poaceae	Perennial	Y	OBL	12·0*	9	—	—
Anthriscus caucalis	Apiaceae	Annual	N		6·5	15	31·5*	1
Bromus diandrus	Poaceae	Annual	N		2·1	30	30·1*	3
Elymus glaucus	Poaceae	Perennial	Y	FACU	6·5	16	23·3*	6
Vitis californica	Vitaceae	Vine/shrub	Y	FACW	9·6	10	20·5*	7
Carex barbarae	Cyperaceae	Perennial	Y	FACW	7·2	14	19·2*	8
Aristolochia californica	Aristolochiaceae	Vine/shrub	Y		4·1	22	16·4*	9
Brassica nigra	Brassicaceae	Annual	N		0·3	61	13·7*	11
Stipa miliaceum var. *miliaceae*	Poaceae	Perennial	N		—	—	11·0*	12

Asterisk (*) denotes a species that was considered a good indicator for the habitat type ($p < 0{\cdot}05$), based on indicator species analysis. Wetland indicator status are OBL, Obligate Wetland; FACW, Facultative Wetland; FAC, Facultative; FACU, Facultative Upland; UPL, Obligate Upland.

Table II. Similarity analyses (Chao–Jaccard) of riparian vegetation among three abandoned channel types, based on site age and hydrodynamic status.

	Canopy vegetation			Understory vegetation		
Comparison	Mean	SE	CI	Mean	SE	CI
YA versus OA	0·65	0·19	0·28–1	0·79	0·09	0·61–0·97
YA versus OB	0·82	0·13	0·57–1	0·95	0·10	0·75–1
OA versus OB	0·87	0·14	0·59–1	0·98	0·04	0·90–1

YA, Young active; OA, Old active; OB, Old backwater; SE, standard error. Confidence intervals (CI) are based on a significance level of 0·05 and calculated as the mean ± 1·96SE, with an upper boundary of 1. 1 = all shared species; 0 = no shared species.

Populus fremontii abundance; however, there was more *Salix* (specifically *Salix exigua* and *Salix lasiandra*) in young active abandoned channels than in other geomorphic types (Table III).

There were significant differences in understory species composition among the three abandoned channel types (overall and pairwise MRPP tests, $p < 0{\cdot}001$). However, although similarity analysis indicated that understory vegetation in young active abandoned channels was distinct from vegetation in the old active, there were no other pairwise differences (Table II). There were 59 total species found in the young active abandoned channels, 39 in old active and 36 in old backwater, with 22 species shared across all three abandoned channel types. On the basis of the comparison of diversity among geomorphic types of abandoned channels, there were more unique species, higher species richness and higher indices of diversity in the young active abandoned channels than in the old ones (Table IV). The young active abandoned channels were the most species-rich because of a large fraction (42/59) of low abundance (<0·2% mean cover) and infrequent species (26/59 species occurred in only 1–2 plots), resulting in lower evenness. In contrast, species with low abundance in the two older types were frequently encountered in low abundances everywhere.

Indicator species for young active abandoned channels were dominated by species typically associated with areas of very slow- or standing water (marshes and ponds), such as *Typha* sp. and *Paspalum distichum* (Supplemental Information: Appendix 3). Species abundant in the two older types, but absent or rare in the young active abandoned channels, were typically associated with drier and/or more heavily disturbed areas, and were dominated by perennials (e.g. *Carex barbarae*, *Elymus glaucus*, *Bromus hordeaceus* and *Arundo donax*). We also observed that young active abandoned channels were more similar to

Table III. Abundance (Mean and SE of absolute abundance) for five *Salix* species and *Populus fremontii* in riparian forests that colonized abandoned channels (based on canopy survey, 1 means the species is present all along the transects).

	All *Salix*	SAEX	SAGO	SALAE	SALAS	SALA	POFR	Open
YA (*n* = 12)	0·74 (0·07)	0·55	0·26	0·02	0·08	0·27	0·16 (0·05)	0·16 (0·07)
OA (*n* = 9)	0·13 (0·06)	0·15	0·33	0·00	0·16	0·14	0·17 (0·05)	0·06 (0·05)
OB (*n* = 9)	0·37 (0·10)	0·06	0·20	0·00	0·00	0·01	0·12 (0·06)	0·24 (0·07)

SAEX, *Salix exigua*; SAGO, *Salix gooddingii*; SALAE, *Salix laevigata*; SALAS, *Salix lasiolepis*; SALA, *Salix lasiandra*; POFR, *Populus fremontii*; and open, canopy absent (i.e. grassland). YA, Young active; OA, Old active; OB, Old backwater.

Table IV. Understory vegetation diversity within abandoned channels.

	Young active	Old active	Old backwater
N	120	90	90
Observed number of species	59	36	39
Number of unique species (SE)	18 (3)	6 (3)	6 (2)
Richness (95% CI)	79 (63–129)	41 (35–69)	37 (33–55)
Simpson 1/D (SE)	22·1 (1·0)	14·6 (1·4)	15·8 (2·0)
Shannon H’ (SE)	3·4 (0·0)	3·0 (0·1)	3·0 (0·1)

old backwater than old active abandoned channels (Table II). The shared species that were relatively abundant were wetland-associates, including *Lycopus americanus*, *Ludwigia peploides* and *Cyperus eragrostis*.

Environmental gradients driving patterns of understory composition among and within abandoned channels. The three abandoned channel types corresponded to different physical templates for vegetation. Young active and old backwater abandoned channels were sited at lower relative elevations (with respect to the active channel) compared with old active abandoned channels (Figure 3A; one-way ANOVA, $p < 0{\cdot}0001$). Young active abandoned channels sustained higher sedimentation rates (Figure 3B; one-way ANOVA, $p < 0{\cdot}001$). Grain size metrics indicated a lower magnitude of current disturbance in old backwater abandoned channels; indeed, the smaller surface sediment grain size (D_{50}) indicated a lower level of energy during floods in both the terrestrial and aquatic zones (Figure 3C and D).

From the aquatic part of the abandoned channel to the higher floodplain, we observed a lateral and vertical gradient of flood disturbance regime and water availability. Water availability was assessed using the proxy of elevation above the baseflow water level, which ranged from 0·0 to 5·8 m above the baseflow water level with a median of 1·0–2·2 m in young active abandoned channels, 1·2–2·0 m in old backwaters and 3·5–4·0 m in old active abandoned channels. The latter elevation range corresponds to a discharge of 2500–3000 $m^3 s^{-1}$, or approximately a 5- to 10-year flood return interval at the Hamilton City gauge. The correlation between relative elevation and distance along the transects from the aquatic zone of the abandoned channel is relatively low ($r = 0{\cdot}27$) but significantly different from zero ($p < 0{\cdot}001$).

Canonical analysis indicated that patterns of species composition were significantly related to environmental gradients that occur both among and within sites (randomization test for the species-environment correlation, $p = 0{\cdot}001$), although the variables we measured accounted for only a small fraction of the observed variability (Figure 4). The most important abiotic variable was median grain size of overbank fine sediment, which increased (i.e. coarsened) in the direction of young active plots as discussed previously. The first axis was correlated with age, as well as lateral gradients of relative elevation (not on the figure because it did not rank as an important correlation), and distance from edge of aquatic zone, all of which covaried positively. *Populus* cover and open cover (percent of canopy transects that have no trees) were inversely correlated and explained the second axis. However, the eight environmental variables we included (i.e. distance to water, relative elevation, geomorphic status, age, canopy openness, *Populus* abundance and surface sediment grain size) explained less than 10% of the total variation in understory species composition among plots. There are thus other factors shaping the understory vegetation that were not included in our ordination. We

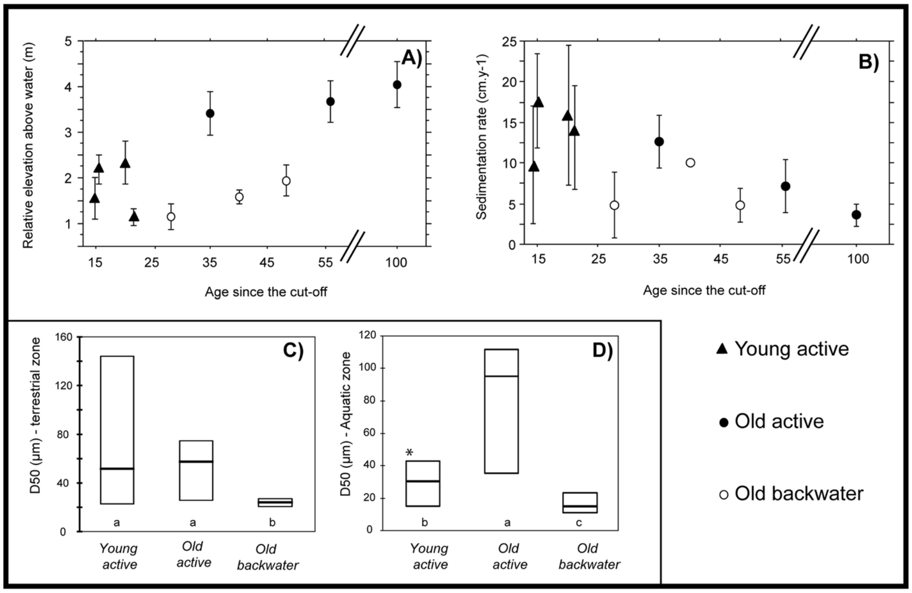

Figure 3. Chronosequence of physical conditions observed in the abandoned channels: (A) relative elevation as a function of abandoned channel age, with standard deviation as error bars, based on relative elevation measured for all understory vegetation plots; (B) time-averaged sedimentation, as the ratio between overbank deposits thickness and year since the cutoff, based on two measurements for each transect (Stella *et al*., 2011); (C) boxplot of grain size distribution of terrestrial sediment (with first quartile, median and third quartile values); and (D) boxplot of grain size distribution of aquatic sediment (* these data are missing for one AC) (with first quartile, median and third quartile values). For (C) and (D), small letters indicate statistical differences between abandoned channel types from a Kruskal–Wallis one-way analysis of variance (where each abandoned channel type is a group).

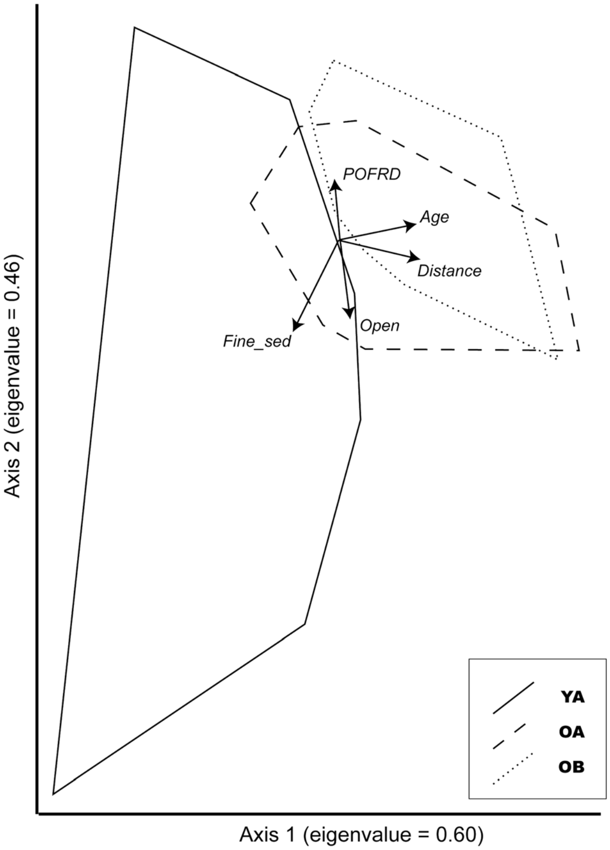

Figure 4. Canonical correspondence analysis of understory vegetation within abandoned channels. The polygons represent overlays that enclose all the samples within a geomorphic classification: solid line = young active abandoned channels; dashed line = old active abandoned channels; dotted line = old backwater abandoned channels. Correlated variables include the following: Fine_sed = surface sediment grain size; Open = measure of canopy cover; Distance = distance from water's edge perpendicular to flow direction; POFRD = the relative dominance of *Populus fremontii* in the canopy (see text); and age = years since channel abandonment.

also ran three additional CCA's for each of the geomorphic categories (e.g. young active, old active and old backwater) but with only two environmental variables: relative elevation and distance from water. There were significant relationships between understory species and the two variables at all abandoned channels (randomization test, $p \leq 0{\cdot}01$). The two variables corresponded most closely with the first axis that captures a reasonably strong gradient (eigenvalue $> 0{\cdot}25$). However, the two variables only explain a smaller fraction of the understory species pattern captured by the first axis (3·1%, 3·9% and 5·2% the total variation, respectively, for young active, old active and old backwater).

DISCUSSION

This study shows that the terrestrial part of abandoned channels support a unique plant community that differs in composition from floodplains adjacent to active river channels, that differences in sedimentation dynamic and degree of hydrological connection to the channel drive the variation we see among abandoned channels and that lateral environmental gradients, although significant, were much weaker drivers of species composition patterns than typically found along active channel banks.

Other studies have shown that at the valley scale, landforms with environmental gradients of elevation and age typically support different species assemblages, from flood tolerant to upland species (Hupp and Osterkamp, 1985; Pautou *et al.*, 1996; Nakamura *et al.*, 1997; Vadas and Sanger, 1997). Differences in disturbance regimes within a particular landform type also drive vegetation composition and pattern both in aquatic (Bornette and Amoros, 1996) and terrestrial ecosystems (Vivian-Smith, 1997; Wolfert *et al.*, 2002; Dufour and Piégay, 2008, 2010). Our results indicate that landforms with the same range of elevation and age but with distinct hydrodynamic position in the floodplain are occupied by distinct plant species assemblages. Despite similar richness and a pool of generally common species between abandoned channels and floodplains, we observed significant differences, notably in the presence and abundance of wetland species. For example, species typical of slow/slack water areas, such as marshes and wetlands (as opposed to along streambanks), were unique to or present at higher frequency in abandoned channels. This included indicator species such as *Persicaria hydropiperoides* and *Paspalum distichum*, and less abundant species of *Typha* and *Juncus*. These species indicate that after abandonment, hydrologic and geomorphic drivers generate relatively benign conditions in terms of disturbance even for low-elevation plots that are frequently flooded. Abandoned channels create persistent wetland habitats within a matrix of floodplain that is succeeding to upland (or at least later successional) species.

The analysis of the vegetation among abandoned channels highlights the temporal changes that occur after channel abandonment. Along a gradient of young to old channels, we observed a decrease in *Salix* abundance (specifically *Salix exigua* and *Salix lasiandra*) (coherent with Shankman, 1991), a decrease in understory diversity and a shift in the understory composition toward species typically associated with drier and/or more heavily disturbed areas such as roadsides, ditches, levees or fields (even if older channels still support some wetland species). These changes could be related to a shift in abiotic conditions from young active abandoned channels (i.e. high sedimentation rate and low relative elevation, Figure 3) to old active and old backwater ones. Indeed, the species richness of young active abandoned channels is driven largely by infrequent, low abundance species, supporting the hypothesis that resource availability and recruitable space are higher in newly abandoned channels than in older ones where vegetation establishment limits resources. This hypothesis that, quickly after abandonment, the terrestrial part of the channel shifts from abiotic to biotic controls (except for lowest elevation plots) is also supported by the fact that significant differences in physical conditions in abandoned channels older than 35 years (e.g. old active plot elevations were significantly higher than old backwater AC) do not result in significant differences in vegetation composition. This differs somewhat from the results obtained in the aquatic part of the abandoned channel where organisms appear more sensitive to differences in disturbance regime (Bornette and Amoros, 1996; Barrat-Segretain *et al*., 1999; Obolewski, 2011; Besacier-Monbertrand *et al*., 2012).

As in many other riparian studies, the within-site understory vegetation pattern is significantly linked to local environmental gradients (distance from water and elevation above water) (Pautou *et al*., 1985; Vadas and Sanger, 1997; Lyon and Sagers, 1998; Lite and Stromberg, 2005; Lite *et al*., 2005; Goebel *et al*., 2006). However, in the case of abandoned channels, these gradients explain only a small part of the understory vegetation pattern. The relatively low importance of distance from and elevation above water, which are typically strong drivers on active channel banks, may be due to an attenuated disturbance regime for the abandoned channel and its surrounding margins as a whole, due to the distance and isolation from the active channel (Dufour and Piégay, 2010; Helfield *et al*., 2012). On the Sacramento River, the low duration and frequency of flooding relative to other rivers may contribute to this phenomenon. Additionally, the drought stress gradient that typically influences plant recruitment along river banks in this system (Stella and Battles, 2010) may be less pronounced in abandoned channels because of the finer sediment grain size and less dynamic water table compared with the main channel. Thus, water availability would be less of a limiting factor in abandoned channels, and would not contribute to the strong sorting patterns of plant species typically observed along a local water availability gradient (Holland *et al*., 2000; Lite *et al*., 2005; Battaglia and Sharitz, 2006; Rodríguez-González *et al*., 2010).

Beyond hydrodynamic and canopy variables, there are clear factors shaping the understory vegetation that were not included in our study; these include nutrient availability, propagule pressure and seed rain composition, hazard of seed and branch arrival, flood chronology and impacts, more accurate measures of light availability and biological controls. For example, surrounding vegetation can influence the composition and diversity of vegetation that colonizes newly abandoned channels (Holl and Crone, 2004). Moreover, flood timing and the sequencing of floods of different magnitudes and their associated sediment deposits over time can strongly influence the dispersal, recruitment, survival and growth of particular species (Johnson, 2000; Dixon, 2003; Stella *et al*., 2006).

To conclude, our results emphasize the importance of a processes-based approach for floodplain biodiversity management, focusing on the physical mechanisms that continuously create these unique habitats and drive their morphological changes. We demonstrate that the terrestrial part of an abandoned channel is a specific biomorphological feature that contributes to habitat heterogeneity at the floodplain scale. It increases the overall richness of the fluvial corridor, just as the aquatic part (Bornette *et al*., 1998) or temporary pools (Ishida *et al*., 2010) do. It not only adds to understory diversity but also is an important feature in the population dynamics of woody pioneer species such as *Populus* or *Salix* (Stella *et al*., 2011). Because maximizing diversity requires a broadly distributed range of abandoned channel ages, promoting new cutoff events is as important as preserving older abandoned channels and the mature plant communities they support. Process-based restoration approaches should therefore focus on channel migration and cutoff events, which create the initial habitat units, and sediment transport and supply, which drive their subsequent shift from aquatic to terrestrial habitats (Bravard *et al*., 1986; Bornette *et al*., 1998; Piégay *et al*., 2000; Greulich *et al*., 2007; Micheli and Larsen, 2010; Stella *et al*., 2011).

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