

1 Title:
2 Patterns of regional and local riparian plant diversity in the California Sacramento – San Joaquin
3 Valley
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38 Abstract

39 The widespread degradation of riparian ecosystems requires that we more fully understand
40 patterns of plant diversity at multiple scales to inform restoration and conservation efforts locally
41 and regionally. We analyzed the distribution of riparian plant diversity in California's
42 Sacramento – San Joaquin Valley, focusing on patterns found at three spatial scales, to support
43 present and future large river habitat restoration initiatives. We examined species richness and
44 complementarity between sample units at the riverscape, inter-riverine, and intra-riverine scales.
45 At the coarsest riverscape scale, spatial patterns of native riparian richness were driven by
46 herbaceous species, while woody species were largely cosmopolitan. Riverscape riparian species
47 richness centered over the California Bay-Delta region, forming a natural geographic ecotone
48 between the two largest watersheds. Inter-riverine richness and turnover between six watershed
49 study locations also indicated native riparian flora shifts mid-valley. Fine-scale, intra-riverine
50 riparian floras from the Sacramento and Cosumnes River floodplains had spatial patterns among
51 sites that relate to successional sequences. These fine-scale patterns suggest flood-induced
52 disturbance is an important factor in promoting heterogeneous habitats and herbaceous species
53 turnover. Our results are consistent with modern riverscape ecological theory; wherein natural
54 disturbances initiate patterned structural diversity that in turn promote aquatic and terrestrial
55 biodiversity. If biodiversity is to be a goal of future ecosystem restoration efforts, these findings
56 suggest that hydrological processes promoting diversity and distribution of native riparian
57 herbaceous flora need more attention. Furthermore, to be effective, large ecosystem restoration
58 efforts require multi-scale approaches to assess baseline patterns of distribution and to develop
59 appropriate benchmarks.

60

61 (A) **Introduction**

62 Ecological restoration is increasingly recognized as a critical component the conservation of
63 biodiversity worldwide (Gann & Lamb 2006). As the human ecological footprint expands, it
64 becomes ever more critical that we make working landscapes more conducive to the persistence
65 of biodiversity, by retaining and promoting ecosystem services and habitats that are functionally
66 intact, even as we extract human-derived benefits from those lands (Rosenzweig 2003). Riverine
67 landscapes are of particular importance due their interface between aquatic and terrestrial
68 ecosystems and their elevated biodiversity (Naiman *et al.* 1993; Naiman & Decamps 1997), and
69 because of their global manipulation and modification (Tockner & Stanford 2002). This paper
70 explores how patterns and measures of riparian plant diversity observed at multiple spatial scales
71 can inform riverscape restoration efforts.

72

73 Riverscapes indicate the broadest level of ecosystem processes inherent to riverine landscapes
74 (Fausch *et al.* 2002; Allan 2004). River ecologists recognize an inherent linkage between aquatic
75 and terrestrial ecosystem processes that is promoted by the structural and functional diversity of
76 riverscapes Allan (2004), Naiman & Decamps (1997). Biotic and abiotic fluxes in freshwater
77 systems maintain this linkage at the riparian interface (Stanford & Ward 1993), and form a
78 spatiotemporal continuum (Vannote *et al.* 1980), where ecological connectivity between aquatic
79 and terrestrial ecosystems is maintained by hydrological pulsing (Junk 1999; Tockner *et al.*
80 2000). These disturbance processes (i.e., floods) create heterogeneous riverscapes, which result
81 in patterned structural diversity (i.e., habitats) that in turn support aquatic and terrestrial
82 biodiversity (Ward & Tockner 2001).

83

84 The interaction of hydrology and geology greatly influences riparian vegetation (Malanson
85 1995), particularly for unimpeded rivers (Hardy 2005). Mosaics of riparian habitat are created by
86 a river's flood pulse (Tockner *et al.* 2000) which creates distinct alluvial landforms, such as
87 oxbow lakes and backwater sloughs (Mount 1995). Natural flow regimes sustain these habitat
88 mosaics through variable disturbance over space and time (Poff *et al.* 1997), which in turn has
89 profound effects on vegetation structure, composition, and patterns of distribution, including
90 patch dynamics (Pautou & Decamps 1985; Harris 1987; Trush *et al.* 2000; Stromberg 2001).
91 Patch dynamism is a highly significant factor in the creation and maintenance of riparian
92 ecosystems (Junk *et al.* 1989, Poff & Ward 1989, Petts 1990, Naiman & Decamps 1997), due to
93 hydrologic processes that help drive the cycle of disturbance, establishment and succession. Poff
94 and Ward (1989) found riparian patch persistence to be directly correlated to flooding events, in
95 that the seral composition of riparian vegetation within patches followed a successional
96 trajectory until a disturbance event reset the patch composition to an earlier seral phase.
97 Spatiotemporal dynamics in riverscape systems result in heterogeneous outcomes, as measured
98 by composition, structure, and pattern in constituent habitats, which are expressed at multiple
99 scales. Although river dynamism and riparian patch heterogeneity remain significant in human
100 dominated systems (Lyon & Gross 2005), we need to examine riparian ecosystems at multiple
101 scales and across broad riverscapes to provide insight into biogeographic trends.
102
103 Human derived benefits from riverscape ecosystem services include drinking water, ground
104 water recharge, flood-flow mediation, recreation, as well as cultural and aesthetic resources,
105 whose economic value is well described (Costanza *et al.* 1997; Jackson *et al.* 2001; Baron *et al.*
106 2002; National Research Council 2005). However, humans occupy a large proportion of

107 floodplains worldwide, which are increasingly impaired and unable to provide full ecosystem
108 services (Tockner & Stanford 2002). Restoration and recovery of riverscape ecosystems is
109 paramount if we are to maintain environmental benefits derived from their ecological
110 functioning. Riparian vegetation restoration efforts increasingly focus on promoting connectivity
111 and process (Stanford *et al.* 1996; Junk 1999; Tockner & Stanford 2002; Ward *et al.* 2002), to
112 create heterogeneous habitats and to maintain biotic and abiotic fluxes. However, determining
113 objectives (e.g., floral composition) and appropriate spatial scale for restoration activities is an
114 area largely uninformed by riverscape scale ecology.

115

116 In practice many riparian vegetation restoration efforts focus on large, charismatic species,
117 possibly at the expense of biodiversity. For example, considerable effort has been expended to
118 restore stands of riparian oak (*Quercus lobata* Née) by propagation, planting, and irrigation in
119 California's Central Valley (e.g., Alpert *et al.* 1999); but minimal attention has been paid to
120 whether this action helps meet other objectives such as promoting biodiversity in general or
121 native riparian plant diversity in particular. In part, this approach to riparian vegetation
122 restoration is due to a lack of multi-scale assessments of the species composition of riparian
123 floras, whose development could inform a broader range of restoration practices in regards to
124 both location and technique. That is not to imply that ecologists do not recognize the importance
125 of riverscape scale patterns and processes in restoration (Holl *et al.* 2003), but that in practice
126 restoration efforts are often constrained by time, money, and mandate (Wohl *et al.* 2005; Young
127 *et al.* 2005). By using differing measures of diversity (Sabo *et al.* 2005) and multiple scales of
128 analysis (Bornette *et al.* 2001), we explore patterns of riparian plant diversity to help guide

129 ongoing adaptive management efforts aimed at restoring California's Bay-Delta and its
130 contributing watersheds.

131

132 **Study Area**

133 The study area is located in California's (USA) Central Valley, a large area drained by two major
134 rivers, the Sacramento and San Joaquin (154,000 km² including its headwaters). Although
135 headwaters for the Central Valley extend to the crest of the Sierra Nevada Mountains, Mt.
136 Shasta, and the Klamath Mountains, this study focuses on the lowland valley setting, typically
137 below elevations of 1000m. The boundaries for this study are further delimited by the spatial
138 units used in CalJep (Viers *et al.* 2006), a geodatabase containing distribution data from two
139 prominent California floras, and corresponding to restoration management units (Figure 1).

140

141 The Central Valley is dominated by the confluence of its two large rivers, which drain
142 approximately 40% of California and transport 34,000 GL of freshwater annually (CADWR
143 1993). With a hydrologic cycle fed by the Pacific Ocean, the Central Valley receives
144 precipitation directly from rainfall and indirectly from snowmelt in headwaters. Under natural
145 conditions, the large rivers and tributaries of the Central Valley balanced sediment transport,
146 alluvial deposition, and channel geometry, creating meandering waterways prone to avulsion
147 (Mount 1995). These waterways are now largely out of balance, due in part to mining debris,
148 dams, and levees, resulting in myriad environmental effects. In addition, the hydrologic,
149 geomorphic and biological processes that create and maintain functioning Central Valley riparian
150 ecosystems have been greatly altered by modern water and land management practices (Mount
151 1995). Endemic vegetation in the Central Valley has largely been replaced by agricultural and

152 urban land cover (Williams *et al.* 2005; Schwartz *et al.* 2006). Only 5-12% of the riparian
153 vegetation habitats are estimated to remain (Hunter *et al.* 1999), thus impeding the ecological
154 services provided by riparian ecosystems.

155

156 Restoration of riparian vegetation in the Central Valley is a recognized priority by the California
157 Bay-Delta Authority (CBDA) (CALFED 2000), an ecosystem management entity comprised of
158 multiple state and federal agencies responsible for water policy and mediating consumptive
159 water demands. A stated goal of CBDA is the restoration of riparian habitats, and in particular
160 the rehabilitation of natural processes that promote habitat complexity and connectivity
161 (CALFED 2000); to date, however, there has not been a comprehensive examination of the
162 relationship between multi-scale patterns of riparian diversity and their implication for
163 restoration. In addition to the stated objectives of CBDA, riparian restoration efforts in general
164 have strived to reestablish: natural flow regimes (including flood pulses) (Richter *et al.* 2003);
165 fluvial geomorphological dynamism (Florsheim & Mount 2002); and regeneration of native plant
166 communities (Richter & Richter 2000; Stromberg 2001).

167

168 Historically, the Central Valley supported a variety of hydrological regimes, in which winter and
169 spring floods deposited sediments in channels and floodplains, creating backwater marshes and
170 distributaries and modifying the geomorphology of its defining riverine features (Thompson
171 1961; Katibah 1984). By understanding the distribution and diversity of riparian dependent flora
172 at multiple scales and under various hydrogeomorphic conditions, we can assist restoration
173 planning efforts and evaluate post-restoration ecosystem recovery (Ward *et al.* 2001). Therefore,
174 baseline patterns of native riparian diversity can be used as *a priori* estimates of expectation to

175 evaluate restoration practices and success within an adaptive management framework (Wohl *et*
176 *al.* 2005). Long term maintenance and conservation of riparian plant diversity is dependent upon
177 the successful restoration of hydrological processes, but first we must understand the inherent
178 patterns of diversity at multiple scales within the study system.

179

180 **(A) Methods**

181 We analyzed the regional distribution of plant diversity in the riparian flora. We examined
182 species richness (α diversity) and complementarity (β diversity) between sample units at three
183 scales. At the finest resolution, we also examined patterns of variation in species composition
184 among sites in relation to factors representing successional gradients and dynamic environments.

185

186 Proximity of observations within a landscape matrix challenges the statistical independence of
187 many species-environment correlation measures (Wagner & Fortin 2005). Furthermore, spatial
188 dependence and heterogeneity often acts at multiple scales (Wagner & Fortin 2005),
189 complicating boundary definition for the study system. Our approach, in addition to accounting
190 for area and distance effects within specific scales, was to implement a multi-scale analysis
191 utilizing independent data at each scale. Rather than defining causal environmental mechanisms
192 (Legendre *et al.* 2005), we explore the spatial dependence of riparian diversity at multiple scales.

193

194 All GIS analyses were conducted in ArcGIS 9.0 (ESRI, Redlands, CA) using a personal
195 geodatabase (Microsoft Access 2003, Redmond, WA). All statistical analyses were conducted in
196 JMPIn 5.1 (SAS Institute, Cary, NC).

197

198 (B) *Riverscape Analysis*

199 For the broadest, riverscape scale analysis, we implemented a geographical information system
200 (GIS) to examine CalJep (Viers *et al.* 2006), a spatial database reconciliation of electronic
201 versions of the two prominent floras for California: CalFlora (Dennis 2000) and Jepson
202 (Hickman 1993). The CalJep database is a useful data source for biogeographers and ecologists
203 and has been used in a number of recent studies (e.g., Harrison *et al.* 2000; Williams *et al.* 2005;
204 Schwartz *et al.* 2006). CalJep records 7887 plant species, subspecies and varieties across the
205 state of California (410,000 km²), represented by 228 map units with corresponding
206 distributional information for species at varying levels of confidence. Map units are demarcated
207 by a combination of natural landscape features used for ecoregional boundaries and political
208 borders of counties and sub-counties. We selected the 24 CalJep map units that corresponded
209 most closely with CBDA management zones for the Central Valley (see CALFED 2000; Figure
210 1.2); hereafter referred to as study units (Figure 2). We limited analyses to plant taxa defined as
211 either riparian or wetland affiliates by the California Rivers Assessment (Viers *et al.* 1998, J.
212 Hunter pers. comm.), whose records include subspecies and varieties and which we will refer to
213 here as species.

214

215 We analyzed patterns of riparian plant diversity at the riverscape scale using three methods. First,
216 we calculated α diversity for each of our study units using the probable distribution of native
217 riparian plant taxa from CalJep, which infers 4 definitions of distributional confidence (present,
218 probable, possible, not recorded) (Viers *et al.* 2006). Second, we calculated pairwise
219 dissimilarity matrices for each combination of study units using 1 - Jaccard Similarity Index,
220 denoted as DI_j ; we also subdivided native riparian species into woody and herbaceous categories

221 to examine dissimilarity by life form. DI_j is an association index that ranges from 0 to 1, where 1
 222 indicates study units without common species and 0 indicates perfect commonality among study
 223 units. DI_j can take the form of Equation 1, from van Tongeren (1995), where c is the number of
 224 species shared between units; A and B are the total number of species in each unit A and B,
 225 respectively.

$$226 \quad DI_j = 1 - \frac{c}{A+B-c} \quad \text{Equation 1.}$$

227 Third, we derived species complementarity for each of our study units by calculating a mean DI_j
 228 value for all pairwise unit comparisons. Whittaker's (1960) initial description of β diversity
 229 advised partitioning biotic diversity into geographic components, in which local diversity (α)
 230 refers to the number of species within a single site; γ or total diversity is the number of species in
 231 a large collection of sites; and β diversity is the turnover of unique species. The β score is highest
 232 when each site contains different species, and lowest when the same species are found at every
 233 site. Our proxy for β diversity follows contemporaries (Harrison & Inouye 2002; Renofalt *et al.*
 234 2005), who use dissimilarity scores for exploring rates of turnover between vegetation plots

235

236 (B) Inter-riverine Analysis

237 The inter-riverine scale of study is across natural watershed boundaries. This intermediate scale
 238 allows cross comparison of field data collected within the Central Valley. More importantly, this
 239 scale is indicative of the scale at which meta-analyses can be performed. This scale helps form a
 240 benchmark for adaptive management in that either studies or particular river systems can be held
 241 as controls – in essence, reference ecosystems – to be analyzed as baseline conditions. Analysis
 242 focused on six rivers within the CBDA management zone, and used previously published data
 243 from seven studies. We cataloged, tabulated, and compared native riparian species presence and

244 absence from vegetation studies which focused on, from north to south, the Sacramento River
245 (Conard *et al.* 1980; Vaghti 2003), Putah Creek (Sutter & Dawson 1986), Cosumnes River (Tu
246 2000), Stanislaus River (Quinn 1993), Tuolumne River (McBain & Trush 2000), and San
247 Joaquin River (Moise & Hendrickson 2002). This scaled analysis relies also on measures of
248 species richness and between-study dissimilarity (DI_j as above), in relation to geographic
249 position and connectivity.

250

251 *(B) Intra-riverine Analysis*

252 The intra-riverine scale is within natural watershed boundaries. Our analysis at this scale
253 consisted of two independent floristic datasets that were examined for patterns in community
254 composition by underlying habitat structure. We examined data from a study on the Sacramento
255 River, a heavily modified river (Vaghti 2003; Holl & Crone 2004), and the Cosumnes River, one
256 of the last unimpounded rivers in California (Tu 2000; Ahearn *et al.* 2005). The relatively fine
257 scale of this analysis was important as it represents the typical restoration project scale of
258 implementation, and the scale amenable to adaptive monitoring, as outlined by Florsheim *et al.*
259 (In Press).

260

261 The analysis of intra-riverine Sacramento River native riparian flora was based on the collection
262 that Vaghti (2003) used to describe and classify vegetation units in relation to environmental
263 gradients. Sample sites were stratified for floodplain age and relative elevation and randomly
264 chosen in areas previously mapped as “riparian” (Greco & Plant 2003); plot sizes were 800m²
265 for high vegetation and 200m² for medium and low vegetation. In all, 91 sites were surveyed
266 along 122 km of the Sacramento River (River KM 230 – River KM 352) in summer 2002.

267 Although the Sacramento River floristic dataset is $\sim 250 \text{ km}^2$ in area, we choose to address it at
268 this scale because the diversity is examined within a continuous river reach.

269

270 The intra-riverine scale analysis of the native Cosumnes River riparian flora was based on the
271 collection of Tu (2000). We examined data from four sites representative of successional
272 gradients and passive restoration techniques, created by levee breaches, on the Cosumnes River
273 Preserve. The sites are within 2 km of each other and represent $\sim 5 \text{ km}$ of river. Tu (2000)
274 effectively captured four successional habitats within CRP, grading from a sand splay complex
275 ripe for plant recruitment created by intentional breaching in 1997 (Florsheim & Mount 2002) to
276 one of the largest remaining stands of late-successional riparian valley oak forest in California
277 (Meyer 2002). Intermediate between them is a willow-cottonwood stand, the “accidental forest”,
278 created through heavy tree recruitment following an accidental levee break in 1985. Today the
279 largest cottonwoods are 27m tall (Viers, unpublished data). Adjacent to these habitats is a mixed
280 riparian forest (Tu 2000).

281

282 For both studies, we filtered all observed species using CalJep riparian designates and tabulated
283 α diversity and complementarity (DI_j , as above) among all sites, and across native, woody or
284 herbaceous designations. For the Sacramento River study, we also calculated mean DI_j – our β
285 diversity measure – to examine ‘turnover’ along a riverine gradient. We correlated mean DI_j with
286 interplot distance (a measure of isolation) and river position (RKM) to determine if intra-riverine
287 gradients could explain patterns in observed plant diversity.

288

289 **(A) Results**

290 (B) *Riverscape Analysis*

291 CalJep riparian species distributions based on species defined in the California Rivers
292 Assessment, were developed for 1245 species. We calculated the number of riparian plant
293 species within each study unit and examined geographic patterns of α diversity and similarity. Of
294 the 24 Central Valley study units (total area = 40,234 km²; mean area = 1676 km²; sd area =
295 1359 km²), riparian α diversity ranged from 143 to 210 (mean = 181.8; sd = 17.6), as shown in
296 Table 1. Native riparian species – our species pool – represented on average 24.6% of all
297 probable species and 29.5% of all probable native species assigned to each study unit. Native
298 riparian herbs formed the largest portion of riparian species within the study units (mean = 163.2;
299 sd = 16.8), with an average of 89.8% being herbaceous species in life form. Native riparian
300 species with a woody life form represented a considerably smaller portion of α diversity in each
301 unit (mean = 18.6; sd = 1.61).

302
303 The native riparian taxonomic richness assigned to each study unit is area dependent ($r = 0.51$; p
304 = 0.01). We fitted a log-log function of native riparian richness to study unit area (mean = 1676
305 km²; sd = 1389 km²) that explained 30.7% of the variance (LN Native Riparian Richness = 4.79
306 + 0.057 LN Area km²; $R^2 = 0.307$; $p = 0.0058$). Fitted estimates and 95% confidence intervals
307 for native riparian taxonomic richness are shown in Figure 1. There is a marked difference
308 between woody and herbaceous components of this function. The native riparian woody species
309 did not show similar log-area dependency ($R^2 = 0.00$; $p = 0.93$), which is understandable given
310 the depauperate levels of richness. Therefore, we focused on the herbaceous component, which
311 showed stronger trends overall (LN Native Riparian Richness = 4.64 + 0.064 LN Area km²; $R^2 =$
312 0.335; $p = 0.0039$). The residuals from this area adjustment to native riparian richness

313 subsequently showed strong latitudinal trends. There is a unimodal peak centered on the
314 California Bay-Delta, suggesting that both the flora changes in this area and that herbaceous
315 riparian obligate species are concentrated in this area. We fitted a 2nd degree polynomial of these
316 residuals to latitude to capture additional variance (Adj $R^2 = 0.28$; $p = 0.013$). A combined model
317 to predict log native riparian herb richness, using log area and a latitudinal quadratic, results in
318 an overall adjusted R^2 of 0.48, which was highly significant ($p=0.0009$).

319
320 Jaccard dissimilarity index for all probable CalJep species ranged from 0.06 to 0.64 across all
321 pairwise comparisons (Table 2). Mean DI_j for different subsets generally decreased with greater
322 specificity in taxonomic grouping (e.g., native riparian woody species showed the lowest DI_j).
323 Mean dissimilarity increases with increasing distance between study units ($p < 0.0001$), for all
324 taxonomic groupings. Comparatively, however, there was less turnover of native riparian woody
325 species as a function of distance than for native riparian herbs (Figure 3). Overall mean DI_j
326 decreased with increasing northerly latitude of the study unit centroid for both native riparian
327 herbaceous ($r = -0.57$; $p = 0.004$) and woody taxa ($r = -0.62$; $p = 0.001$). Longitudinal trends
328 were also evident with DI_j values increasing easterly for both subsets of native riparian species,
329 herbaceous ($r = 0.39$; $p = 0.061$) and woody ($r = 0.58$; $p = 0.003$). Considering all native riparian
330 species, the spatial distance between the most ($n_s = 210$) and least ($n_s = 143$) speciose was
331 116km; the distance between the two study units with the most dissimilarity ($DI_j = 0.54$) was
332 300km.

333

334 (B) *Inter-riverine Analysis*

335 We examined observed plant richness and complementarity for six rivers and creeks in the
336 Central Valley as determined by seven published studies. The watersheds from north to south
337 comprise Sacramento River, Putah Creek, Cosumnes River, Stanislaus River, Tuolumne River
338 and San Joaquin River. Although each of these studies was conducted with different objectives
339 and methods, and over different areas, they all provide a suitable estimate of respective floral
340 diversity. There are considerable differences in observed plant richness, however; total plant
341 species ranged from 66 in the Putah Creek study to 215 on the Stanislaus River (Table 3). There
342 are also considerable differences in native species, ranging from 40 (Putah Creek) to 113 (San
343 Joaquin River). This disparity lessens when considering only native riparian herbaceous and
344 woody species. Two study sites, Putah Creek and the Tuolumne River have lows of 17 native
345 riparian herbaceous species, whereas two study sites have highs of 56 (Stanislaus River and San
346 Joaquin River). Native riparian plant species with woody lifeforms were fewer still, with Putah
347 Creek having a low of 11 and Sacramento River and Tuolumne River each having 19 such
348 species.

349
350 Pairwise dissimilarity (DI_j) values, shown in Table 4, confirm the relatively depauperate nature
351 of native riparian woody species in the Central Valley; DI_j values ranged between 0.16 and 0.50,
352 suggesting that riparian trees and vines are largely cosmopolitan, though limited in number.
353 Pairwise dissimilarity for native riparian herbaceous taxa was markedly greater, with DI_j values
354 ranging from 0.56 to 0.94. Although similar in number of native riparian herbs observed at each
355 site, the Cosumnes River ($n_s = 18$) and Tuolumne River ($n_s = 17$) have highly different flora (DI_j
356 = 0.94). For the Tuolumne River, mean DI_j values were highest for herbaceous species (0.87),
357 while Putah Creek was highest for woody species (0.40) (Table 4). Latitude was not correlated

358 with DI_j values; however, herbaceous dissimilarity generally increased from north to south when
359 examining species turnover between adjacent study units (e.g., Sacramento to Putah, Putah to
360 Cosumnes) while it decreased for woody species. When examining drainages separated by an
361 intervening drainage (e.g., Sacramento to Cosumnes), it becomes apparent that the Stanislaus and
362 San Joaquin riparian flora are quite similar, although one site removed. Putah and Tuolumne
363 sites have the most dissimilar native riparian flora among the drainages that are two sites
364 removed from each other ($DI_j = 0.50, 0.90$ for woody and herbaceous respectively) suggesting
365 that maximum turnover is centered between these two sites which are $\sim 200\text{km}$ apart (Table 4).

366

367 *(B) Intra-riverine Analysis*

368 *(C) Sacramento River*

369 To conduct the intra-riverine scale analysis, we examined trends in plant diversity along a middle
370 reach of the Sacramento River. Vaghti (2003) observed 98 species in 91 plots located from River
371 Kilometer (RKM) 230 to RKM 352 on the middle reach of the Sacramento River. Of these
372 sampled species, 94 were cataloged in CalJep and 59 were considered riparian obligates.
373 Considering only the species cataloged in CalJep, Vaghti (2003) found on average 12.9 species
374 per site ($sd = 4.7$), ranging from 3 – 25 species. There was a positive upriver trend in richness,
375 gaining 3 species per 100km of river ($\alpha = 3.63 + 0.03 \text{ RKM}$; $F_{1,89} = 4.68$; $p = 0.0331$). When
376 narrowing records to riparian obligates, on average 9.4 species were observed ($sd = 3.6$) with a
377 range of 3 – 24. The same positive upriver trend in α diversity was evident ($\alpha = 2.55 + 0.02$
378 RKM ; $F_{1,89} = 3.46$; $p = 0.0663$); however, the gain of 2 riparian obligate species per 100km of
379 river is proportionally much higher than the full complement of observations.

380

381 We correlated dissimilarity (DI_j) for all plant species, as well as for native, riparian, native
382 riparian woody and native riparian herbaceous species against interplot distance (i.e., km
383 between sample plots) and river position (RKM). Mean DI_j was significantly higher for sample
384 plots further from other plots when focusing on riparian herbs ($r = 0.25$; $p < 0.05$); other
385 taxonomic sets did not show a similar trend. River position was standardized (0 – 1) to represent
386 a downriver to upriver continuum (~121 km), with mean DI_j for riparian herbs decreasing
387 upriver ($r = -0.24$; $p < 0.05$). River position was not significantly correlated with mean DI_j in
388 other taxonomic subsets.

389

390 (C) *Cosumnes River*

391 Our finest scale intra-riverine analysis is an examination of observational data from the
392 Cosumnes River Preserve, which has no large dams and thus represents the dynamism of a
393 largely unimpaired flow hydrograph on a restored floodplain. We examined richness for all
394 observed plant species, as well as native, native riparian, and native riparian herbaceous and
395 woody subsets, and we tabulated DI_j for all study sites and taxonomic groups (Table 5). As
396 shown in Table 5, the sand splay had the highest observed richness ($n_s = 50$) and the mixed
397 riparian site the lowest ($n_s = 23$) for all observed species. When reducing the pooled observations
398 to native species, however, the ‘Accidental Forest’ is most speciose in native ($n_s = 22$) and
399 riparian ($n_s = 18$) floral richness. The sand splay had the most non-native species by absolute (n_s
400 = 29) and relative (58%) scores. The valley oak forest showed the highest percent floral
401 composition of native (67%) and native riparian (57%) species. Considering only native
402 composition, the mixed riparian site had the highest percentage of riparian obligates (87%). The
403 disturbance related successional gradient between Cosumnes River Preserve study locations is

404 quite evident in α diversity, where the sand splay has the fewest native riparian woody species
405 ($n_s = 4$) and Accidental Forest has the most ($n_s = 8$); these sites have the most and next most
406 flood-induced disturbance respectively.

407

408 The dissimilarity indices between Preserve sites also showed trends in regards to succession
409 (sand splay \rightarrow Accidental Forest \rightarrow mixed riparian site \rightarrow valley oak forest) as predicated by
410 flood induced disturbance (Table 5). Namely, the sand splay is most dissimilar from the valley
411 oak forest in all comparisons of native, native riparian, native riparian herbaceous, and native
412 riparian woody taxonomic groupings; this trend is progressive through Accidental Forest and the
413 mixed riparian site. The valley oak forest is most similar in composition to mixed riparian in its
414 herbaceous complement ($DI_j = 0.27$) and its native riparian woody species ($DI_j = 0.43$), although
415 mixed riparian and Accidental Forest are least dissimilar in this regard ($DI_j = 0.38$). At each level
416 of consideration, however, there is clear evidence that each of these successional sites supports
417 unique native riparian flora promoted by dynamic ecosystem processes.

418

419 (A) Discussion

420 (B) *Multi-scale Patterns of Riparian Diversity*

421 The patterns of riparian plant richness at the riverscape scale corroborate findings of others
422 (Nilsson *et al.* 1994; Pollock *et al.* 1998; Mouw & Alaback 2003); namely, larger regional
423 assessments show the cumulative effect of herbaceous species driving richness in riparian flora .
424 The effective contribution of riparian flora to the total flora of the Central Valley (~16%), whilst
425 only 5-12% of the original habitat remains, reflects the disproportionate importance of
426 understanding the underlying ecological processes promoting diversity in riparian ecosystem

427 restoration. The watersheds constituting the Central Valley originate in both the Coastal Range
428 and the Sierra Nevada mountains; thus, the riverscape patterns suggest that in addition to a peak
429 in area-adjusted richness over the Bay-Delta – the confluence of all rivers in the Valley – there
430 are predictable north-south and east-west trends in vascular plant species turnover. Floristic
431 complementarity is strongest in the southern portion of the Central Valley, with mean
432 dissimilarity increasing north to south and west to east regardless of taxonomic grouping. This
433 observed pattern in complementarity holds at the inter-riverine scale too, but with marked
434 differences between woody and herbaceous species. In effect, woody species were cosmopolitan
435 at each spatial scale of analysis.

436

437 For the tributaries at the inter-riverine scale of analysis, constituent woody species are most
438 dissimilar between Putah Creek and the Tuolumne River, again suggesting a north to south
439 change in flora over the Bay-Delta and also from west to east. Size of riverine feature appears to
440 affect complementarity, with the large Sacramento and San Joaquin Rivers sharing many of the
441 same woody and herbaceous native riparian species. The Stanislaus River study was near its
442 confluence with the San Joaquin River, hence their similarity at the inter-riverine scale.

443 Surprisingly, the ratio of native riparian herbaceous to woody species drops to 2:1 at the inter-
444 riverine scale; whereas at the riverscape scale this ratio is 8:1, suggesting that there is within unit
445 turnover between networked tributaries of different stream orders at a scale coarser than our
446 inter-riverine samples.

447

448 Intra-riverine results indicate native riparian herbs drive overall species richness; however, north-
449 south trends on the Sacramento River are confounded by local conditions. Geomorphic

450 conditions in the upriver portions of the Sacramento River study reach are conducive to
451 increased herbaceous richness; these conditions include set back levees that allow for greater
452 river meander and the formation of exposed substrates viable for colonization. The levee
453 constriction in the downriver portions of the Sacramento River promotes β diversity by creating a
454 dynamic environment conducive to pioneering herbs. This paradox is generally observed within
455 the Cosumnes River too, wherein the Accidental Forest (i.e., a moderately disturbed habitat), has
456 the highest richness for native species and bridges the composition between the newly disturbed
457 sand splay adjacent to the intentional levee breach and the late-seral stage valley oak forest.
458 Thus, mosaics of disturbance and successional gradients are promoting diverse riparian
459 communities within and across river systems; these observations are similar those of others
460 investigating intermediate disturbance as a working hypothesis for elevated riparian richness
461 (e.g., Lite *et al.* 2005).

462

463 Consistent patterns emerge across all scales of analysis. As a nested set of observations, it is
464 clear that regional restoration and conservation goals for riparian habitats need to acknowledge
465 the differences in floristic composition and hydrological conditions across the region. For
466 example, the San Joaquin River contains higher levels of riverscape β diversity and inter-riverine
467 herbaceous richness; however, it is also one of the most hydrologically modified rivers in the
468 study area and has depauperate levels of riparian habitat. We find that a mosaic of geomorphic
469 conditions provides for both increased richness and complementarity across different habitats
470 within specific river systems. In the Sacramento River, we find that herbaceous species richness
471 generally increases upriver (i.e., northward) at the intra-riverine scale, in the opposite direction
472 of the general riverscape scale trend, which is downriver toward the Bay-Delta confluence. Our

473 observations reinforce the need for a multi-scale biogeographic framework to guide ecosystem
474 conservation and restoration efforts (Whittaker *et al.* 2005).

475

476 *(B) Considerations*

477 At each scale of analysis there exist inherent potential sources of error. At the riverscape scale,
478 CalJep represents the most comprehensive geographic database of California flora, but has
479 limitations (Viers *et al.* 2006). The inter-riverine comparison represents data from several studies
480 that were initiated for different purposes; in some cases they are represented as complete floras
481 (Sutter & Dawson 1986; Quinn 1993), and in others comprehensive surveys within distinct
482 riparian habitat (McBain & Trush 2000; Tu 2000; Moise & Hendrickson 2002; Vaghti 2003).
483 Further, the relative position of comparative studies was not taken into account and represents
484 one source of error. At the intra-riverine scale, individual studies used different field methods
485 and the species pools are limited by the choice of study location. For example, Cosumnes River
486 data purposefully cover a successional gradient and Sacramento River data purposefully sample
487 known riparian communities, irrespective of successional trend.

488

489 We appreciate the complexity and uncertainty involved in determining which patterns are
490 ecologically meaningful (Miller *et al.* 2004) given the limitations above; however, our approach
491 was to examine patterns at different scales in parallel to determine if similar patterns emerge from
492 disparate datasets. Furthermore, we have not addressed the temporal component of species
493 turnover in dynamic riparian systems (i.e., succession), but we do know that at the intra-riverine
494 scale species composition can change dramatically over annual and seasonal cycles (Tu 2000;
495 Lite *et al.* 2005). Thus, gauging long term restoration success will require monitoring

496 frameworks sensitive to not only the spatiotemporal dynamic (Rood *et al.* 2003; Aguiar &
497 Ferreira 2005), but also inherent riverscape processes and instability (Ward *et al.* 2001). Lastly,
498 we reassert the observations of Lamb *et al.* (2005); namely, the effectiveness of our efforts to
499 conserve biodiversity and restore key ecological functions depends on the complementarity of
500 our actions within the riverscape mosaic, which at present is not well planned nor understood.

501
502 Long term watershed-scale restoration is an overarching goal for the Central Valley (CALFED
503 2000); in implementation, however, funded restoration projects are often localized actions to
504 improve native fish and avian habitats and reestablish native vegetation in the shorter term.
505 Active CBDA restoration projects to date have mostly involved converting orchards, row crops
506 or pasture to riparian plantings supported by irrigation and weed control (e.g., Alpert *et al.* 1999;
507 Holl & Crone 2004). Passive riparian restoration is not immune to the establishment of weeds,
508 where invasibility is promoted by the general productivity of sites (Stohlgren *et al.* 1998) and
509 flood-induced disturbance (Renofalt *et al.* 2005). At each scale of our analysis, while not an
510 explicit goal of the study, we found proportionately high numbers of exotic plants, as did Planty-
511 Tabacchi *et al.* (1996). Therefore, gauging restoration success regardless of restoration
512 technique should explicitly acknowledge levels of invasion within riparian habitats as promoted
513 by both passive and active restoration.

514

515 (A) Conclusion

516 Our study examined patterns in riparian plant diversity at multiple scales across a large area; and
517 at each scale we showed that native riparian herbs drive richness and complementarity. While
518 acknowledging the importance of woody species, we reinforce the notion that restoration and

519 conservation management programs dedicated to charismatic megaflora (i.e., *Quercus lobata*
520 Née) do not necessarily meet all restoration objectives; separate actions dedicated to biodiversity
521 are also needed. Unfortunately, many restoration actions have relied on “jumpstarting” riparian
522 woody plant succession; however, it is not clear if a native herbaceous component can “catch up”
523 in comparative richness to remnant riparian forests (Holl & Crone 2004). If biodiversity is to be
524 a unifying theme for understanding riverscape ecosystems, as suggested by Ward & Tockner
525 (2001), we advocate additional experimental breaches in floodplain levees (i.e., Florsheim &
526 Mount 2002), to ensure hydrological conditions that promote ecological processes. Ecosystem
527 management planning for riverscapes in general and Central Valley restoration in particular
528 should be explicit in identifying and conserving hydrological processes that ensure habitat
529 complexity and promote biodiversity at multiple scales.

530

531 Results in this study are consistent with emerging riverscape ecological theory. Natural
532 disturbance processes, principally floods, initiate positive geomorphic feedback and the creation
533 of patterned structural heterogeneity. Resultant ecological processes operating on these dynamic
534 habitats, such as recruitment, in turn promote aquatic and terrestrial biodiversity. Thus, if
535 biodiversity is to be a goal of future ecosystem and watershed restoration efforts, our findings
536 suggest that processes promoting the diversity and distribution of native riparian herbaceous
537 flora are critical elements to any viable strategy. To be effective, large ecosystem restoration
538 efforts need multi-scale approaches, which permit assessment of baseline conditions and
539 development of desired benchmarks. The findings from this scaled analysis can serve as
540 estimates of expected riparian floral diversity and turnover for floodplain restoration efforts
541 within the Sacramento – San Joaquin Valley.

542

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554

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813

814 **Table 1.** Riverscape Scale Riparian Plant Richness. For the CalJep study units (n=24), we show
 815 mean richness for different taxonomic groupings at the ‘probable’ distribution designation.

816

	Mean Richness (α)	Std Dev	Std Err Mean	Lower 95%	Upper 95%
All CalJep Taxa	740.2	77.0	15.8	707.5	772.9
All Native Taxa	616.1	77.1	15.7	583.5	648.6
Native Riparian Taxa	181.8	17.6	3.6	174.3	189.2
Native Riparian Herbaceous Taxa	163.2	16.8	3.4	156.0	170.3
Native Riparian Woody Taxa	18.6	1.6	0.3	17.9	19.3

817

818

819
 820 **Table 2.** Pairwise dissimilarity for taxonomic comparisons between CalJep study units. At the
 821 riverscape scale, we show descriptive statistics for DI_j values for different levels of taxonomic
 822 grouping.

Taxonomic Comparison	Mean (DI_j)	Std Dev (DI_j)	Maximum (DI_j)	Minimum (DI_j)
All CalJep Taxa	0.397	0.134	0.636	0.065
All Native Taxa	0.397	0.137	0.652	0.056
Native Riparian Taxa	0.364	0.101	0.540	0.088
Native Riparian Herbaceous Taxa	0.375	0.104	0.557	0.087
Native Riparian Woody Taxa	0.255	0.103	0.480	0.000

823

824

825

826 **Table 3.** Inter-riverine scale riparian plant species richness. We show species richness across six
 827 river systems in the Central Valley by differing levels of taxonomic grouping.

828

Study System	Study	Taxa (n)	Native Taxa (n)	Native Riparian Taxa (n)	Native Riparian Herbaceous Taxa (n)	Native Riparian Woody Taxa (n)
Sacramento River	Conard et al. (1983); Vaghti (2003)	141	57	42	23	19
Putah Creek	Sutter & Dawson (1986)	66	40	28	17	11
Cosumnes River	Tu (2000)	90	43	31	18	13
Stanislaus River	Quinn (1993)	215	111	71	56	15
Tuolumne River	McBain & Trush (2000)	86	53	36	17	19
San Joaquin River	Moise & Henderson (2002)	202	113	72	56	16

829

830

831 **Table 4.** Pairwise dissimilarity values for native riparian flora at the inter-riverine scale, for
 832 herbaceous and woody lifeforms. 1st order DI_j values are noted between adjacent study
 833 watersheds; 2nd – 5th order comparisons follow on the diagonal where study watersheds are
 834 separated by 1 – 4 locations, respectively.

835

Native Riparian Woody Taxa				Native Riparian Herbaceous Taxa					
5 th Order	4 th Order	3 rd Order	2 nd Order			2 nd Order	3 rd Order	4 th Order	5 th Order
				Sacramento River					
			0.42		0.79				
			0.40	Putah Creek	0.76				
		0.30	0.40		0.79	0.64			
	0.19		0.38	Cosumnes River	0.78		0.79		
0.16		0.50	0.35		0.84	0.90		0.70	
	0.31		0.48	Stanislaus River	0.94		0.78		
		0.29	0.30		0.84	0.81			
			0.18	Tuolumne River	0.56				
			0.33		0.86				
				San Joaquin River					

836

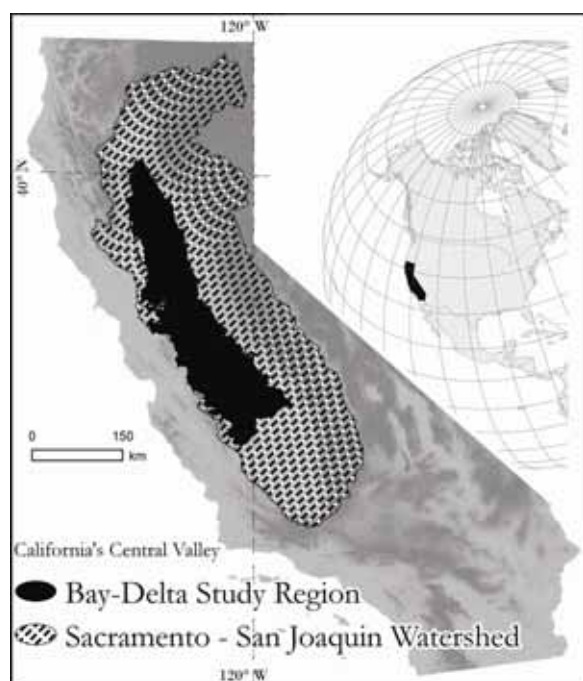
837

838 **Table 5.** Intra-riverine Cosumnes River Riparian Plant Species Dissimilarity. Four levels of
 839 taxonomic grouping are tabulated across four sites (SS = Sand Splay; AF = Accidental Forest;
 840 MR = Mixed Riparian; VO = Valley Oak) from Tu (2000). Dissimilarity coefficients (DI_j) follow
 841 study site codes; numbers of species are indicated parenthetically for each site by taxonomic
 842 grouping. The successional gradient follows from SS → AF → MR → VO as predicated by
 843 flood induced disturbance.
 844

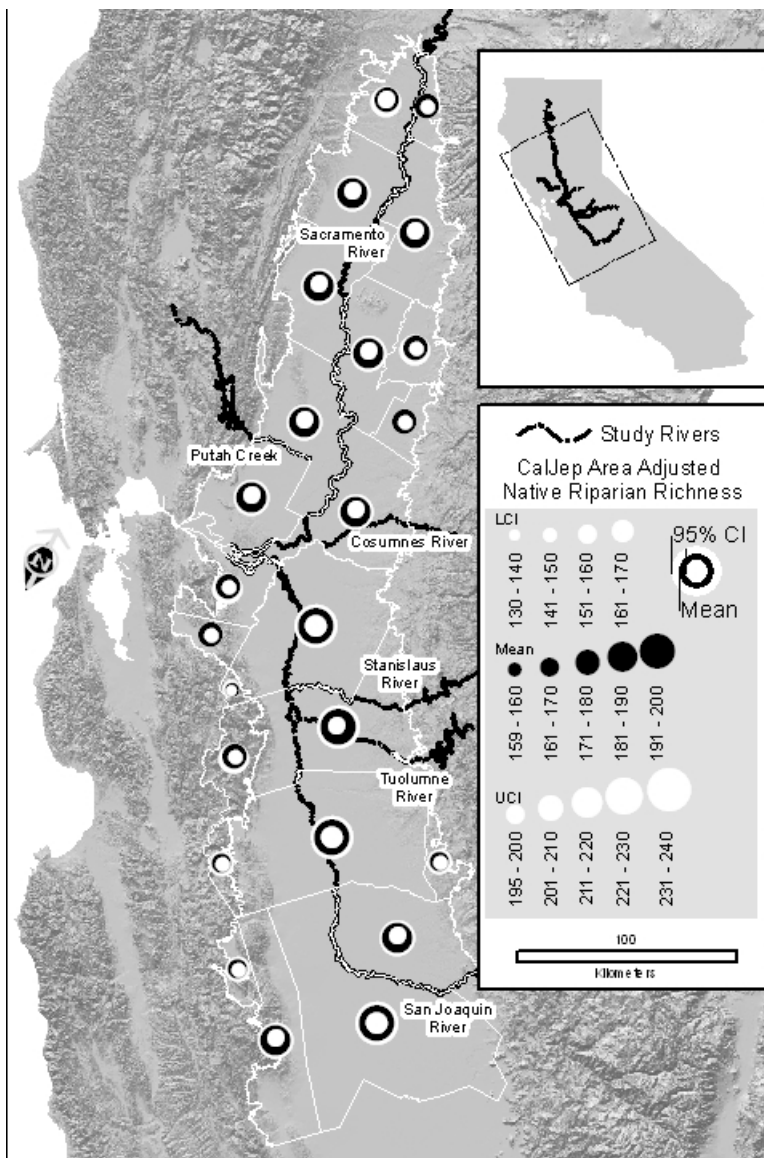
Taxonomic Grouping	Study Site (n)	SS	AF	MR
All Species	SS (50)	—		
	AF (38)	0.725	—	
	MR (23)	0.823	0.512	—
	VO (30)	0.806	0.612	0.441
All Native Species	SS (21)	—		
	AF (22)	0.697	—	
	MR (15)	0.759	0.391	—
	VO (20)	0.794	0.552	0.333
Native Riparian Species	SS (15)	—		
	AF (18)	0.625	—	
	MR (13)	0.727	0.368	—
	VO (17)	0.769	0.542	0.333
Native Riparian Herbaceous Species	SS (11)	—		
	AF (10)	0.500	—	
	MR (8)	0.643	0.364	—
	VO (11)	0.706	0.500	0.273
Native Riparian Woody Species	SS (4)	—		
	AF (8)	0.800	—	
	MR (5)	0.875	0.375	—
	VO (6)	0.889	0.600	0.429

845

846 **Figure 1.** Location of California's Central Valley in relation to the state and coverage of the
847 California Bay-Delta region of interest for this study. The state of California is approximately
848 410,000 km², with the primary tributaries of the Central Valley – the Sacramento and San
849 Joaquin Rivers – and their headwaters covering 154,000 km². The California Bay-Delta region is
850 approximately 40,234 km² in area. [Note: This is the low resolution version; a high resolution version can be
851 downloaded from <http://baydelta.ucdavis.edu/reports/ripfig1hires.jpg> 1MB]
852

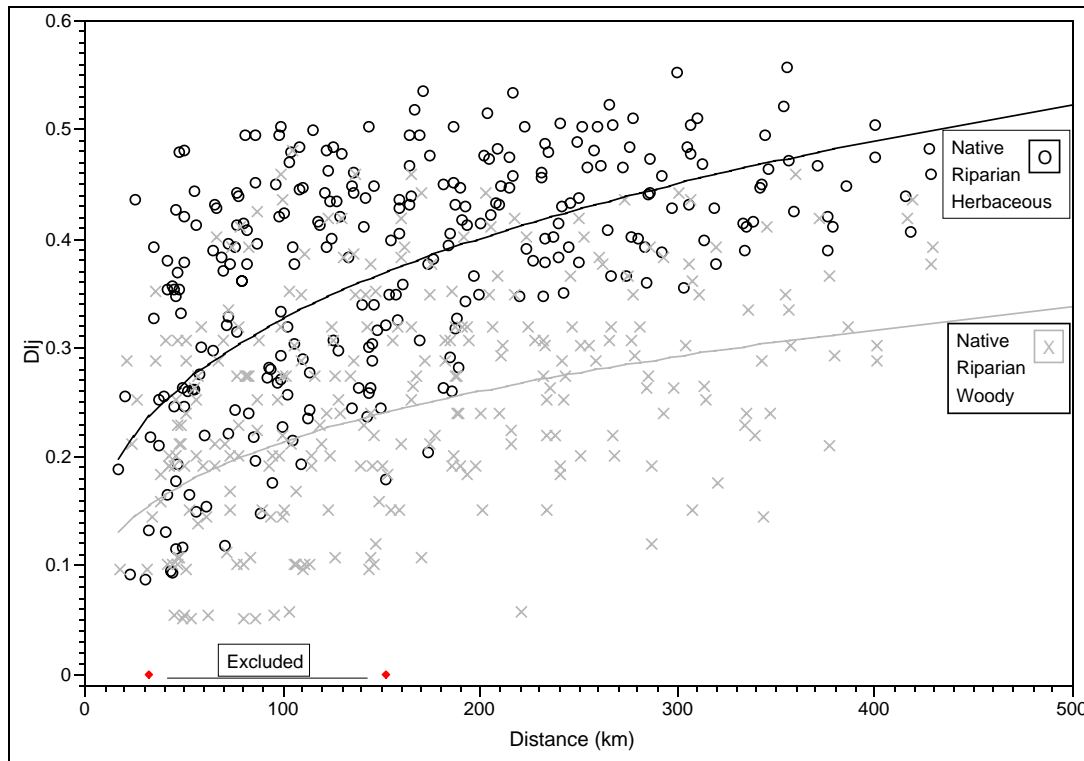


854 **Figure 2.** Location of CalJep Study Units and primary riverine features described in this study.
 855 Area adjusted estimates of native riparian richness, with 95% confidence intervals, are shown as
 856 study unit centroids. [Note: This is the low resolution version; a high resolution version can be downloaded
 857 from <http://baydelta.ucdavis.edu/reports/ripfig2hires.jpg> 5MB]
 858



859

860 **Figure 3.** Jaccard Dissimilarity Index (DI_j) values are shown for Native Riparian Herbaceous
 861 and Woody Taxa calculated between each pair of CalJep Study Units (n=24) as a function of
 862 intercentroid distance (km). Log-log functions yielded a higher coefficient of determination for
 863 herbaceous ($\text{LN}(DI_j) = -2.47 + 0.29 \text{ LN}(\text{Distance (km)})$; Adj $R^2 = 0.32$; $p < 0.0001$) than for
 864 woody species ($\text{LN}(DI_j) = -2.85 + 0.28 \text{ LN}(\text{Distance (km)})$; Adj $R^2 = 0.15$; $p < 0.0001$), which
 865 had two comparisons excluded.
 866



867