Impacts of the invasive shot hole borer (*Euwallacea kuroshio*) are linked to sewage pollution in southern California: the Enriched Tree Hypothesis

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ABSTRACT

The Kuroshio Shot Hole Borer (KSHB, *Euwallacea kuroshio*) and the Polyphagous Shot Hole
Borer (PSHB, *E. whitfordiodendrus*; Coleoptera: Curculionidae: Scolytinae) have recently
invaded southern California and are attacking live trees in commercial agriculture groves, urban
parks and native riparian forests. Among native forests the worst impacts observed to date have
been in the Tijuana River Valley in south San Diego County, where approximately 30% of the
native willows (*Salix* spp.), or 120,000 trees, have died as a result of a KSHB infestation.

This paper examines wood densities, wood moisture contents, KSHB infestation rates, and
KSHB-induced mortality rates in two willow species (*Salix lasiolepis* and *S. gooddingii*) at sites
near and far from sewage input. Comparisons were made on two spatial scales: broadly among
sites within San Diego County; and locally among sites within the Tijuana River Valley. The
results showed that, on average, willow trees growing closest to sewage pollution had
significantly lower wood density, higher wood moisture content, higher KSHB infestation rates,
and higher KSHB-induced willow mortality rates than those growing farther away.

We present the Enriched Tree Hypothesis to explain the link between sewage pollution and
KSHB impacts; it is as follows: (A) Riparian trees subject to nutrient enrichment from frequent
sewage pollution grow quickly, and their fast growth results in wood of low density and high
moisture content. If attacked by the KSHB, the trunks and branches of these nutrient-enriched
trees provide an environment conducive to the fast growth of the symbiotic fungi upon which the
KSHB feeds. With an abundant food supply, the KSHB population increases rapidly and the
trees are heavily damaged by thousands of KSHB galleries in their trunks and branches. (B)
Riparian trees not subject to frequent sewage pollution grow more slowly and have denser, drier
wood. Conditions in their trunks and branches are not conducive to the fast growth of the
KSHB's symbiotic fungi. The KSHB generally ignores, or has low abundances in, these slow
growing trees.

This new hypothesis explains current patterns of KSHB impact in San Diego County and focuses
attention on the important roles of the environment and preexisting conditions of trees in
determining the extent of KSHB impact. It highlights the Tijuana River Valley as an unusual site
due to high sewage inputs and predicts that the high KSHB-induced willow mortality seen there
should not occur in other natural riparian habitats in southern California. Most importantly, by
identifying sewage pollution (or nutrient enrichment) as a major risk factor for KSHB impacts,
the hypothesis ratchets down the KSHB-threat level for most riparian sites in southern California
and directs attention to other nutrient-enriched sites as those most at risk.

INTRODUCTION

Two closely related ambrosia beetle species have recently invaded southern California and are attacking live trees in commercial agriculture groves, urban parks and native forests (Eskalen et al. 2013; Freeman et al. 2013; Boland 2016; Eskalen 2018). They are the newly described Kuroshio Shot Hole Borer (KSHB, *Euwallacea kuroshio* Gomez and Hulcr, sp. nov.) and Polyphagous Shot Hole Borer (PSHB, *Euwallacea whitfordiodendrus* Schedl 1942, stat. rev.; Coleoptera: Curculionidae: Scolytinae; Stouthamer et al. 2017, Gomez et al. 2018). These borers are considered a serious threat because of the many important tree species they can use as reproductive hosts (Eskalen 2018) and because of the considerable impacts to the Tijuana River Valley forests, where an estimated 120,000 willows (*Salix* spp.), or approximately 30% of the native trees, died in just three years due to a KSHB infestation (Boland 2016, 2018).

The PSHB and KSHB were first observed in 2003 and 2013, respectively, and have since been caught in traps or on trees in coastal southern California and Baja California, Mexico (Eskalen 2018). They are not advancing as a diffusion-like expanding front (*sensu* Wilson et al. 2009), but instead are appearing at disjunct sites in the region (Eskalen 2018). When present they infest and impact sites to differing degrees and, because so little is known about the ecology of the borers, it has been impossible to explain their current patterns of distribution and impact, or to predict where they will impact next.

The Tijuana River Valley is unusual in two respects – it is the site where the KSHB has had its greatest impact and it appears to be the most polluted valley in southern California. As the pollution is sewage, a plant fertilizer, we suggest that there is a link between the nutrient enrichment of willows and their susceptibility to shot hole borer attack. This is not a new idea; Gadd (1944a,b) described a controlled experiment in which different fertilizers were added to tea bushes (*Camellia sinensis* L.) in Ceylon and reported that "*treatments, which improve the yielding capacity of the tea bush, also increase the liability of the bush to attack by the shot hole borer beetle*" (Gadd 1944b; page 253). The beetle was the Tea Shot Hole Borer (*Euwallacea fornicatus* Eichhoff), and Gadd went on to state, "*Why this should be so raises a question of considerable importance, to which no very exact answer can be given at present.*" Little has changed since then. The link between nutrient enrichment of the soil and the susceptibility of trees to shot hole borer attack has not been made clear and has led Hulcr and Stelinski (2017, page 296), in their recent review, to comment that "*in ambrosia beetle research, the role of the environment and preexisting conditions of the trees has not yet been well appreciated, even though it appears to determine the impact of these beetles.*"

In this study, we examined the links between the environment (i.e., sewage loading), preexisting conditions (i.e., the characteristics of willow wood), and the severity of the KSHB impacts in two species of willows growing in the Tijuana River Valley and in other sites in San Diego County. In particular, we evaluated the following hypotheses: (H$_1$) the level of sewage pollution in the Tijuana River Valley is greater than at other sites in San Diego County; (H$_2$) willow trees growing in the Tijuana River Valley have wood characteristics that are significantly different to those growing outside the valley; (H$_3$) willow trees growing in the Tijuana River Valley have KSHB infestation rates and KSHB-induced mortality rates that are significantly greater than those growing outside the valley; (H$_4$) a site with intermediate nutrient enrichment will have intermediate wood characteristics and intermediate shot hole borer impacts; and (H$_5$) the links

114   between sewage pollution level, willow wood characteristics, and KSHB impacts observed on a
115   large scale (on the order of km) will also hold on a small scale (on the order of m).
116
117   Based on the results of these tests, we have developed a general hypothesis describing the link
118   between nutrient enrichment and shot hole borer impacts. This hypothesis explains the current
119   patterns of KSHB distribution and impact, and allows one to make predictions about where the
120   KSHB will cause impacts next. While the tests focused on the KSHB in San Diego County, the
121   insights gained are likely to apply to both the KSHB and PSHB throughout southern California.
122

MATERIALS & METHODS

123

124   ***The shot hole borers.*** The KSHB and PSHB weaken or kill trees through their tunneling
125   activities and their associated fungal symbionts (Eskalen et al. 2013; Freeman et al. 2013;
126   Eskalen 2018). Females drill into tree trunks and branches, excavate galleries in the wood,
127   inoculate their gallery walls with fungi (e.g., *Fusarium* sp.), and live in their galleries eating the
128   fungi and reproducing (Biedermann, Klepzig and Taborsky 2009). Within a few weeks mated
129   females emerge and either remain on their natal tree or fly to new trees perpetuating the
130   infestation (Rudinsky 1962). The borers are small (~ 2 mm in length), but their many tunnels and
131   spreading fungal symbionts can undermine the structural integrity of the tree (Boland 2016) or
132   block the water-transporting vessels in the xylem and cause the progressive death of shoots and
133   branches (Eskalen et al. 2013). Both borers are currently rated "Q" by the California Department
134   of Food and Agriculture (CDFA), indicating that more information is needed before they can be
135   correctly rated. Most research on KSHB and PSHB to date has focused on controlling the borers,
136   especially in agricultural and urban settings (Dodge et al. 2017; Mayorquin et al. 2018) and on
137   describing their fungal symbionts (Freeman et al 2013, Na et al. 2018). The borers causing the
138   damage in the riparian habitats of the Tijuana River Valley were collected and identified as the
139   KSHB by Dr. Akif Eskalen at University of California Riverside (UCR), and specimens have
140   been stored in the UCR collection.
141
142   ***The willows.*** The arroyo willow (*Salix lasiolepis* Benth.) and black willow (*Salix gooddingii*
143   C.R. Ball) are abundant riparian trees in San Diego County. They grow to heights of 9 and 20 m
144   respectively and dominate early successional riparian forests along the coastal rivers and
145   streams. Recent research on these willows has addressed seed dispersal (Boland 2014a), seedling
146   establishment patterns (Boland 2014b, 2017a), adult tree zonation (Boland 2014b), KSHB
147   impacts (Boland 2016), and post-KSHB recovery (2018), and all has been conducted in the
148   Tijuana River Valley.
149
150   ***The main study site – the Tijuana River Valley.*** The Tijuana River Valley is a coastal floodplain
151   in San Diego County, California, of approximately 15 square kilometers at the end of a 4,480
152   square kilometer watershed (Figure 1). The Tijuana River is an intermittent stream (Boland
153   2014b) that frequently becomes polluted with sewage and other wastewater as it flows through
154   the City of Tijuana, Mexico, before entering the valley (TRNERR 2010). Its channel through the
155   valley is not armored and, because it has frequently changed course during the past 40 years
156   (Safran et al. 2017), the riparian forests in the valley are a mosaic of stands of different ages at
157   various distances from the current river flows (Boland 2016). The riparian forests are dominated
158   by arroyo and black willows (Boland 2014b) and are preserved within three adjoining open space

159   parks. The riparian habitats support many species, most notably the endangered least Bell's vireo
160   (*Vireo bellii pusillus*) for which most of the riparian habitat is designated critical habitat (U.S.
161   Fish and Wildlife Service 1994). For allowing access to their properties in the Tijuana River
162   Valley and elsewhere, we thank the US Fish & Wildlife Service (permits 19001TJS, 2017-
163   81720-R-011), State of California Parks and Recreation (17-669-01, 17-669-02), County of San
164   Diego Department of Parks and Recreation (ROE08.08.16-08.31.19, TRVRP07-2017, MP09-
165   2017), City of San Diego (07.23.2018SS), and Orange County Parks (08.04.2017CN).

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167   **(H_1) The level of sewage pollution in the Tijuana River Valley is greater than at other sites in**
168   **San Diego County.** Sewage spill data were compiled for the Tijuana River Valley and the rest of
169   San Diego County for the three-year period January 1, 2015 to December 31, 2017. Spill data for
170   the Tijuana River Valley were from the International Boundary and Water Commission's spill
171   reports, which document "dry weather transboundary wastewater" flows from Mexico that
172   contain raw sewage, partially treated sewage and other wastewaters (San Diego Regional Water
173   Quality Control Board 2018). Spill data for the rest of San Diego County were from the
174   California State Water Resources Control Board sanitary sewer overflow incident web site (State
175   Water Board 2018). Each incident report was examined, and the spill volume minus the
176   recovered volume was recorded for all spill volumes >10,000 gallons that occurred in the San
177   Diego County area south of Oceanside, an area of approximately 3,000 square kilometers.

178

179   To confirm that sewage spills were influencing the nutrient concentrations in the rivers, water
180   quality data from the California Environmental Data Exchange Network (CEDEN) website were
181   examined from the one station in the Tijuana River Valley (Tijuana River 5) and from six
182   stations in San Diego County (TWAS 1 on the Otay River, TWAS 1 on the Sweetwater River,
183   TWAS 1 and 2 on the San Diego River, TWAS 2 and 6 on Peñasquitos Creek; CEDEN 2018).
184   The maximum values for "Ammonia as N, total" and "Phosphorus as P, total" from January
185   2005 to December 2017 were recorded for each station.

186

187   **(H_2) Willow trees growing in the Tijuana River Valley have wood characteristics that are**
188   **significantly different to those growing outside the valley.** Nine sites were chosen along the
189   main river channel in the Tijuana River Valley and nine sites were chosen away from the
190   influence of the Tijuana River. When the Tijuana River Valley was first impacted by the KSHB
191   in 2015 the riparian habitats were divided for study purposes into 29 vegetation units so that each
192   unit was relatively homogenous in terms of plant density, species composition and age (Boland
193   2016). Nine of the forest units were chosen for this study in a stratified random manner and their
194   unit numbers were retained (Figure 1 and Table 1). The other nine sites, chosen to represent the
195   rest of San Diego County, were mainly in other watersheds, though one site (OUT-1) was within
196   the Tijuana River Valley but not influenced by the main river flows. All of the San Diego County
197   sites were in open space parks with established riparian forests comparable to those in the
198   Tijuana River Valley.

199

200   Wood density was determined from branch samples of live arroyo and black willow trees
201   collected between August 28 and October 10, 2017 at the 18 sites; all trees still had their leaves
202   and were actively growing. Branch samples were 2.3–3.0 cm in diameter, approximately 23 cm
203   long, not damaged or infested, and estimated to be three to five years old. Branch samples were
204   cut with a small pruning saw on a walk through the forest, one sample per tree, usually until ten

205 arroyo and ten black willows were collected. Cut ends on the trees were immediately sprayed
206 with TreeKote Tree Wound Dressing to reduce the risk of infection at the cut, and the saw was
207 cleaned between samples with a disinfectant wet wipe. There was some variation in the number
208 of samples collected (Table 2): at Sites 2 and 19 more than ten samples were collected; at Site 3
209 arroyo willows were absent so none could be collected; and at Site OUT-8 black willows were
210 absent. Branch samples were taken to the lab, stripped of their bark, and measured for wet
211 weight and volume. Volume was measured using the water displacement method (Chave 2005).
212 The dry weight of each sample was recorded after three days in a drying oven at 102–104
213 degrees C, and wood density was calculated as: *Density (g/ml) = dry weight (g) / volume (ml).* A
214 total of 372 branch samples were collected and analyzed for wood density (Table 2).

216 The moisture content of each branch sample was calculated as: *Moisture content (%) = [wet
217 weight (g) – dry weight (g)] x 100 / wet weight (g).* This is the percentage of the original green
218 weight that was water and is described as 'moisture content on a wet basis' (Hartley and
219 Marchant 1995). In total, 302 branch samples were analyzed for moisture content. [Wet weight
220 was not recorded for the first round of samples collected, resulting in fewer samples analyzed for
221 moisture content than for wood density (Table 2).]

223 Wood densities and moisture contents of the willows in the Tijuana River Valley were compared
224 to those in the San Diego County sites, and tested separately for each willow species via a two-
225 level nested ANOVA for unequal sample sizes (McDonald 2009 and the worksheets therein).
226 The null hypothesis was that there were no differences in the wood characteristics for the two
227 groups of sites.

229 ***(H₃) Willow trees growing in the Tijuana River Valley have KSHB infestation rates and***
230 ***KSHB-induced mortality rates that are significantly greater than those growing outside the***
231 ***valley.*** The impact of the KSHB was measured at the nine sites along the main Tijuana River
232 channel and the nine San Diego County sites. At each site the condition of as many willows as
233 could be examined in two hours was recorded. For infestation rate, each willow was examined
234 and classified as 'currently infested' if it had evidence of active tunneling by the KSHB, such as
235 extrusion of sawdust or recent gumming out of sap from KSHB holes. For mortality rate, each
236 willow was classified as alive, recently dead from KSHB attack if it had KSHB holes, or dead
237 from some other cause if it had no KSHB holes. KSHB infestation rates and KSHB-induced
238 mortality rates were calculated for each site as the percent of the total number of willow trees
239 examined. At 13 sites, these surveys were done during October 2017. At the other five sites
240 (Tijuana River Valley sites 2, 3, 9, 12, and 13), such surveys could not be done in 2017 because
241 of extensive willow damage caused by the KSHB in 2015-16 (Boland 2016); instead, for these
242 sites, infestation rates are from Boland (2016) and mortality rates are from Boland (2017b).
243 KSHB infestation rates and KSHB-induced mortality rates within the two groups of sites were
244 compared using the Mann-Whitney U-test (McDonald 2009).

246 ***(H₄) A site with intermediate nutrient enrichment will have intermediate wood characteristics***
247 ***and intermediate shot hole borer impacts.*** To include a nutrient-enriched site outside the
248 Tijuana River Valley, we surveyed two sites in Orange County. These were Fairview Park, a
249 constructed, treatment wetland consisting of riparian trees, and South Talbert Regional Park a
250 natural riparian habitat downstream of Fairview Park. As the water flowing into these sites is

251 nutrient-enriched (Brown 2018), these sites should have wood densities and shot hole borer
252 impacts that are intermediate between the heavily polluted Tijuana River and the less polluted
253 other San Diego County sites. We collected 20 branch samples from arroyo willows at each of
254 these sites in August 2017 and processed the samples as described above, except we determined
255 only wood density, and not moisture content. During collection we noted whether the sampled
256 tree was infested with shot hole borer (PSHB in these sites; Eskalen 2018).
257
258 **(H₅) The links between sewage pollution level, willow wood characteristics, and KSHB**
259 **impacts observed on a large scale (on the order of km) will also hold on a small scale (on the**
260 **order of m).** The ten sites within the Tijuana River Valley (Sites 2 to 21 and OUT-1; Table 1)
261 were compared with respect to the level of sewage pollution, wood density, wood moisture
262 content, KSHB infestation rate, and KSHB-induced mortality rate using correlation analysis
263 (McDonald 2009). For this small-scale comparison, data for arroyo and black willows were
264 combined. Distance from the main Tijuana River channel was used as a proxy for the amount of
265 sewage reaching each site, the assumption being that the greater the distance from the main
266 channel, the lower the exposure to sewage-polluted flows (Table 1). To present logarithmic trend
267 lines, one meter was added to all distances from the main channel to remove zero distances.
268
269

270 **RESULTS**

271 **(H₁) The level of sewage pollution in the Tijuana River Valley is higher than at other sites in**
272 **San Diego County.** The total sewage spill volume into the Tijuana River Valley was
273 approximately 30 times that of the entire rest of San Diego County during the three-year period
274 2015 through 2017. In that period, there were 55 cross border flows from Mexico into the
275 Tijuana River totaling more than 220 million gallons (Figure 2A) and only seven sewage spills
276 totaling less than 8 million gallons within the rest of San Diego County (Figure 2B). The largest
277 cross border flows into the Tijuana River Valley were of 143 and 27 million gallons (off the
278 scale on Figure 2A), whereas the largest spill in San Diego County outside the Tijuana River
279 Valley was of seven million gallons into a concrete lined channel that discharged into Mission
280 Bay (Figure 2B). CEDEN water quality measurements reflected the sewage spill data; the
281 Tijuana River values for maximum nitrogen and phosphorus were 23.40 and 9.75 mg/l
282 respectively, and were 10 to 20 times more than the maximum measured in the other San Diego
283 County rivers (1.20 and 1.01 mg/l). The hypothesis was supported: the level of sewage pollution,
284 or nutrient enrichment, was far greater in the Tijuana River Valley than elsewhere in the county.
285
286 **(H₂) Willow trees growing in the Tijuana River Valley have wood characteristics that are**
287 **significantly different to those growing outside the valley.** Wood density of branch samples
288 ranged in black willows from 0.29 to 0.53 g/ml ($n = 182$) and in arroyo willows from 0.31 to
289 0.56 g/ml ($n = 190$). For both willow species, wood density was significantly lower at the
290 polluted Tijuana River sites than at the less polluted San Diego County sites (Figure 3). For
291 black willows, the mean (± S.D.) wood densities at the polluted and less polluted sites were 0.40
292 (± 0.043) g/ml ($n = 102$) and 0.44 (± 0.038) g/ml ($n = 80$), respectively, and these densities were
293 significantly different (ANOVA F = 16.8; $p < 0.001$). For arroyo willows, the mean wood
294 densities at the polluted and less polluted sites were 0.42 (± 0.043) g/ml ($n = 100$) and 0.48 (±
295 0.042) g/ml ($n = 90$), respectively, and these densities were significantly different (ANOVA F =

296   21.5; $p < 0.001$). Wood densities of black willows and arroyo willows were significantly
297   correlated at the sites where both species were present ($r = 0.886$, $n = 15$ sites, $p < 0.0001$), i.e.,
298   where wood density was low in one species it was low in the other, and where it was high in one
299   species it was high in the other.
300
301   Wood moisture content of branch samples ranged in black willows from 42% to 67% ($n = 141$)
302   and arroyo willows from 44% to 63% ($n = 161$). For both willow species, wood moisture
303   contents from the polluted Tijuana River sites were significantly higher than those from the less
304   polluted San Diego County sites (Figure 4). For black willows, the mean wood moisture contents
305   at the polluted and less polluted sites were 54% ($\pm 4.7\%$, $n = 68$) and 49% ($\pm 3.4\%$, $n = 73$),
306   respectively, and these moisture contents were significantly different (ANOVA F = 17.1, $p <$
307   0.005). For arroyo willows, the mean moisture contents at the polluted and less polluted sites
308   were 55% ($\pm 3.7\%$, $n = 71$) and 50% ($\pm 3.2\%$, $n = 90$), respectively, and these moisture contents
309   were significantly different (ANOVA F = 35.8, $p < 0.001$). Like wood density, moisture content
310   in black willows and arroyo willows were significantly correlated at the sites where both species
311   were present ($r = 0.682$, $n = 15$ sites, $p < 0.01$), i.e., where moisture content was high in one
312   species it was high in the other, and where it was low in one species it was low in the other.
313
314   The hypothesis was supported: the wood characteristics (wood densities and moisture contents)
315   of black and arroyo willows growing in the polluted Tijuana River Valley sites were significantly
316   different to those of willows growing in the less polluted sites.
317
318   ***(H₃) Willow trees growing in the Tijuana River Valley have KSHB infestation rates and***
319   ***KSHB-induced mortality rates that are significantly greater than those growing outside the***
320   ***valley.*** KSHB infestation rates and KSHB-induced willow mortality rates ranged from 0% to
321   100% and 0% to 97% respectively, at the 18 sites (Table 3). Willows in the polluted Tijuana
322   River sites had significantly higher rates of KSHB infestation (Mann-Whitney U-test; $n = 9, 9$; U
323   $= 0$; $p < 0.001$) and significantly higher rates of KSHB-induced mortality (Mann-Whitney U-test;
324   $n = 9, 9$; U $= 4.5$; $p < 0.01$). The hypothesis was therefore supported.
325
326   Among all sites, willow mortality rates were significantly and negatively correlated with average
327   wood densities ($r = 0.903$, $n = 18$, $p < 0.0001$), and significantly and positively correlated with
328   average wood moisture content ($r = 0.908$, $n = 17$, $p < 0.0001$). That is, KSHB caused the most
329   damage at sites with trees of low wood density and high moisture content.
330
331   ***(H₄) A site with intermediate nutrient enrichment will have intermediate wood characteristics***
332   ***and intermediate shot hole borer impacts.*** Wood densities of the arroyo willow branch samples
333   ranged from 0.33 to 0.53 g/ml ($n = 40$) at the two Orange County sites that receive polluted
334   runoff. For Fairview Park, the mean wood densities were 0.43 (± 0.050) g/ml ($n = 20$) and for
335   South Talbert they were 0.44 (± 0.039) g/ml ($n = 20$). The wood characteristics of the arroyo
336   willow were therefore intermediate between the polluted Tijuana River sites and the less polluted
337   San Diego County sites (Figure 5). PSHB infestation rates at the two Orange County sites were
338   also intermediate; the arroyo willows at Fairview Park were 70% infested ($n = 20$) and the arroyo
339   willows at South Talbert were 55% infested ($n = 20$). The Orange County results are therefore
340   consistent with the hypothesis.
341

342 ***(H₅) The links between sewage pollution level, willow wood characteristics, and KSHB***
343 ***impacts observed on a large scale (on the order of km) will also hold on a small scale (on the***
344 ***order of m).*** Among the ten sites within the Tijuana River Valley there were significant patterns
345 in wood densities, wood moisture contents, KSHB infestation rates, and willow mortality rates.
346 Wood densities of willow branch samples were significantly lower near the main channel than at
347 more distant sites ($r = 0.278$, $n = 222$ trees, $p < 0.0001$). Moisture contents of branch samples
348 were significantly higher near the main channel ($r = 0.316$, $n = 159$ trees, $p < 0.0001$). KSHB
349 infestation rates were significantly higher near the main channel ($r = 0.723$, $n = 10$ sites, $p <$
350 0.05), and willow mortality rates due to the KSHB were high near the main channel and dropped
351 precipitously to zero away from the channel (the values for the logarithmic trend line were: $r =$
352 0.888, $n = 10$ sites, $p < 0.01$). On the other hand, there were no significant patterns in stand
353 structural traits with distance from the main channel; stand age ($r = 0.370$, $n = 10$ sites, $p > 0.05$),
354 median girth of willows ($r = 0.191$, $n_1 = 21 - 40$ trees per site, $n_2 = 10$ sites, $p > 0.05$), and stand
355 density of willows ($r = 0.191$, $n = 10$ sites, $p > 0.05$) showed no significant patterns among the
356 ten sites.

357

358 The hypothesis was supported: the links between pollution level, willow wood characteristics,
359 and KSHB impacts observed on a large scale (within San Diego County) also hold on a small
360 scale (within the Tijuana River Valley), i.e., willows growing in or close to the sewage-polluted
361 water had wood of lower density and higher moisture content, and suffered higher rates of KSHB
362 infestation and KSHB-induced mortality than those growing farther away.

363

DISCUSSION

364

365 In this study, high levels of sewage pollution were correlated with high rates of KSHB
366 infestation and willow mortality, as well as with willow wood of low density and high moisture
367 content. These correlations were observed both countywide and locally. We propose the
368 following new hypothesis, the Enriched Tree Hypothesis, to explain this connection between
369 sewage pollution and the KSHB:
370 • Riparian trees subject to nutrient enrichment from frequent sewage pollution grow quickly,
371   and their fast growth results in wood of low density and high moisture content. If
372   attacked by the KSHB, the trunks and branches of these nutrient-enriched trees provide
373   an environment conducive to the fast growth of the symbiotic fungi upon which the
374   KSHB feeds. With an abundant food supply, the KSHB population increases rapidly and
375   the trees are heavily damaged by thousands of KSHB galleries in their trunks and
376   branches.
377 • Riparian trees not subject to frequent sewage pollution grow more slowly and have denser,
378   drier wood. Conditions in their trunks and branches are not conducive to the fast growth
379   of the KSHB's symbiotic fungi. The KSHB generally ignores, or has low abundances in,
380   these slow-growing trees.
381 • In short, trees of the same species growing under different conditions have different wood
382   characteristics, and the most enriched trees among them are the most susceptible to an
383   abundant KSHB infestation.

384

385 Each element of the Enriched Tree Hypothesis has support in the literature. Sewage contains the
386 most important plant macronutrients – nitrogen, phosphorus and potassium (Singh and Agrawal

387   2008) – and, when used as a fertilizer, sewage is as effective as chemical fertilizers in promoting
388   tree growth (Prescott and Blevins 2005). Nutrient enrichment is known to influence wood
389   characteristics, and heavy fertilization and irrigation leads to fast growth, low density wood, and
390   high moisture content in several species of trees (Constantz and Murphy 1990; Hacke et al. 2010;
391   Drew, Downes and Evans 2011; West 2014). With respect to ambrosia beetle growth, both the
392   nutrient and moisture contents of wood are known to influence beetle growth. The standard
393   medium for growing ambrosia beetles and their symbiotic fungi in the laboratory is water-based
394   and rich in nutrients (Biedermann, Klepzig and Taborsky 2009; Cooperband et al. 2016). The
395   growth rates of the fungi and larvae of ambrosia beetles are positively correlated with the
396   moisture content of the host plants (Rudinsky 1962); and several authors, working on bark
397   beetles, have shown that low nitrogen levels adversely affect beetle development by increasing
398   development time and reducing fecundity (Kirkendall 1983; Ayers et al 2000; Raffa, Gregoire
399   and Lindgren 2015). Finally, when the KSHB find a suitable host they attack it *en masse*; one
400   black willow, killed by the KSHB in the Tijuana River Valley, had up to 40 KSHB holes per 40
401   cm^2 of bark and more than 20,000 KSHB holes over its entire surface (Boland 2017b).
402
403   The results of the tests are also corroborated by the findings of others. Several researchers have
404   found that the Tijuana River is the most polluted in San Diego County (e.g., Tetra Tech, Inc.
405   2006; McLaughlin et al. 2014) and that the KSHB's impact has been greatest in the Tijuana
406   River Valley – the U.S. Fish and Wildlife Service has conducted extensive surveys for KSHB
407   throughout San Diego County and have reported that "*nowhere has been as severely hit* (by the
408   KSHB) *as the Tijuana River Valley*" (Eric Porter, USFWS, personal communication 6 March
409   2018). Also, black willows growing in the Tijuana River Valley were found to grow 50% faster
410   than black willows growing in the Otay River watershed (Boland 2018). Finally, the measured
411   range of wood density for black and arroyo willows in this study (0.29 to 0.56 g/ml) is
412   comparable to the range in the literature for *Salix* spp. (0.4 – 0.6 g/ml; Engineering Tool Box
413   2018) except, notably, willows growing in the nutrient enriched Tijuana River Valley extend the
414   lower range by more than 0.1 g/ml.
415
416   A view commonly encountered in southern California is that the severity of a shot hole borer
417   infestation reflects the age of an infestation, i.e., a stand with many infested trees is said to be an
418   older infestation, and a stand with few infested trees is said to be a younger infestation. This 'age
419   of infestation' view presumes that all host trees of a given species are of the same condition in all
420   stands, and that the trajectory of a shot hole borer infestation will also be the same in all stands,
421   i.e., a mild infestation with little tree damage will quickly turn into a severe infestation with
422   heavy tree damage. Our results, particularly those from within the Tijuana River Valley, do not
423   support this view for two reasons. First, tree condition in terms of wood density and moisture
424   content varied significantly among willow stands in the valley. Second, the trajectory of
425   infestation varied among stands; the KSHB has been present throughout the valley since 2015
426   (Boland 2016), yet only stands close to the polluted river have been heavily infested and have
427   suffered high mortality, while those farther away have remained only lightly infested and largely
428   undamaged. These results therefore do not support the assumptions of the age of infestation
429   view, but they do support the Enriched Tree Hypothesis view, i.e., trees of the same species
430   growing under different conditions have different wood characteristics, and the most enriched
431   trees among them are the most susceptible to an abundant KSHB infestation. While age of

432   infestation must play some role, the environment and preexisting condition of the trees likely
433   determine the trajectory and ultimate severity of an infestation.
434
435   Understanding the mechanism underlying the rapid growth of ambrosia beetles in enriched trees
436   could be a promising area of future research. Fungi require sugars and nutrients (such as nitrogen
437   and phosphorus) for growth (Kendrick 1992). In enriched trees it may be as simple as the sap in
438   the tree is nutrient loaded in two ways – phloem sap is loaded with sugars from the fast-growing
439   leaves, and xylem sap is loaded with nutrients from the enriched soil – and these extremely high
440   nutrient conditions in the trunks and branches promote the fast growth of the symbiotic fungi
441   and, ultimately, the fast growth of the beetles. Measurements of the sugar and nutrient
442   concentrations and loading rates in trees subject to differing amounts of sewage, followed by
443   replicated and controlled growth rate trails with the fungal symbionts receiving various
444   appropriate sugar and nutrient concentrations and loading rates would be particularly valuable.
445
446   ***Predicting where KSHB will occur next.*** One rationale for this study was to answer the
447   questions: "Where are the shot hole borers likely to appear next? And where are they going to do
448   the most damage?" Until now, these questions have been addressed using the list of plant species
449   that the KSHB and PSHB can use as reproductive hosts (Eskalen 2018). The logic has been that
450   if a tree species is on that list, then all individuals of that species, at all sites, are at risk of being
451   killed by an infestation. McPherson et al. (2017) used this logic to predict that nearly 12 million
452   urban trees were at risk in coastal southern California and the asset value lost due to the invasive
453   shot hole borers could be greater than $9 billion over ten years. By the current logic, many
454   millions of riparian trees in southern California are at risk of being killed by the shot hole borers,
455   and all of these trees have the same high risk.
456
457   Now, using the Enriched Tree Hypothesis in a predictive manner, risk assessments can be
458   improved. By identifying sewage pollution (or nutrient enrichment) as a major risk factor for
459   KSHB impacts, predictions should now be based on the presence of a susceptible plant species
460   *plus* the presence of sewage pollution (or overfertilization). Only areas with both of these factors
461   will be at high risk of infestation; all other areas will be at lower risk. This refinement
462   immediately ratchets down the threat level for most riparian sites in San Diego County. A few
463   natural sites may have some nutrient enrichment leading to moderately enriched trees and
464   moderate infestations, but high nutrient conditions are rare in natural habitats and are more likely
465   to be found elsewhere, in treatment wetlands, agricultural fields, golf courses and urban parks.
466   This refinement also strongly suggests that the Tijuana River Valley is an unusual case, and that
467   the extreme sewage pollution in the Tijuana River makes the trees growing near the main
468   channel unique in the region. The rapid invasion by the KSHB, the subsequent collapse of the
469   willow canopy, and the many thousands of willow deaths in the valley (Boland 2016, 2017b,
470   2018) should not be expected to occur in more normal, unpolluted riparian habitats elsewhere.
471   The maximum level of impact to be expected in moderately enriched sites is likely to be similar
472   to the Orange County sites, with their intermediate pollution levels and intermediate infestation
473   rates.
474
475   The Enriched Tree Hypothesis should make one examine more closely the dire predictions others
476   have made about the future impact of the borers in southern California. For instance, according
477   to the Enriched Tree Hypothesis the predictions that the borers will (1) damage other natural

478   sites as severely as the Tijuana River Valley (Greer, Rice and Lynch 2018), (2) kill all the
479   sycamores (*Platanus racemosa* Nutt.) in California (Raver 2018), and (3) cause billions of
480   dollars worth of damage to urban trees (McPherson et al. 2017) likely overstate the threat.
481

482   The conventional way to answer the question "Where are the borers most likely to appear next?"
483   is to construct a pest risk map using host distributions, empirical measures of cold tolerance, and
484   models of climate suitability (e.g., Venette et al. 2010). Maps of this sort would predict the final
485   geographic range of the spreading insect and guide management efforts in those areas, but they
486   have two drawbacks. First, they usually do not indicate where the impacts will be greatest within
487   the range; as Venette, Coleman and Seybold (2015; page 237) state, "*the magnitude of impact*
488   *remains the most difficult component of any pest risk assessment to forecast.*" Second, these
489   maps assume that all individuals of a host tree species are the same (McPherson et al. 2017)
490   when in fact, as shown here within the Tijuana River Valley, trees of the same species growing
491   under different conditions have different wood characteristics and very different KSHB
492   infestation rates. Therefore, while a pest risk map will be useful in predicting the ultimate range
493   of the KSHB, the Enriched Tree Hypothesis can direct us to sites within the range where the
494   KSHB is likely to have the most impact.
495

496   The spread and establishment of the KSHB is likely to be similar to the microbiologist's tenet,
497   "*Everything is everywhere, but the environment selects*" (de Wit and Bouvier 2006). The KSHB
498   may disperse widely but, according to the Enriched Tree Hypothesis, they will establish and
499   thrive only where suitable enriched trees occur. The hypothesis therefore provides the underlying
500   mechanism by which the environment selects. The concept that the KSHB may be everywhere
501   but their establishment at a site depends on the characteristics of the trees at the site is especially
502   important when interpreting the results of shot hole borer trapping efforts because, although the
503   borers may be found in traps and, therefore, present at a site, the trees in the area may not be at
504   high risk of heavy infestation.
505

CONCLUSIONS
506

507   The Enriched Tree Hypothesis states that trees of the same species growing under different
508   conditions have different wood characteristics, and the most enriched trees among them are the
509   most susceptible to an abundant KSHB attack. This straightforward hypothesis can explain why
510   the Tijuana River Valley riparian forests were far more severely impacted by the KSHB than
511   other similarly forested sites in the county, and it can predict the general level of impact expected
512   at a site using nutrient enrichment as a major risk factor.
513

514   This hypothesis should focus future research on nutrients in the soils and nutrients in the trees
515   because a better understanding of these factors will be essential for predicting the outcome of
516   future shot hole borer attacks in southern California. Finally, the hypothesis can guide
517   management; realizing that nutrient enrichment is a major risk factor, the fertilization and
518   irrigation frequency of urban trees should be reduced where possible to slow tree growth and
519   make trees less attractive to shot hole borers.
520

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696

697

Figure 1

Site locations.

Locations of the 18 sampling sites in San Diego County, California. Sites influenced by polluted Tijuana River flows are in blue, and those not influenced by polluted Tijuana River flows are in yellow. Nomenclature follows Table 1. This map was created using ArcGIS® software; image source: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community.

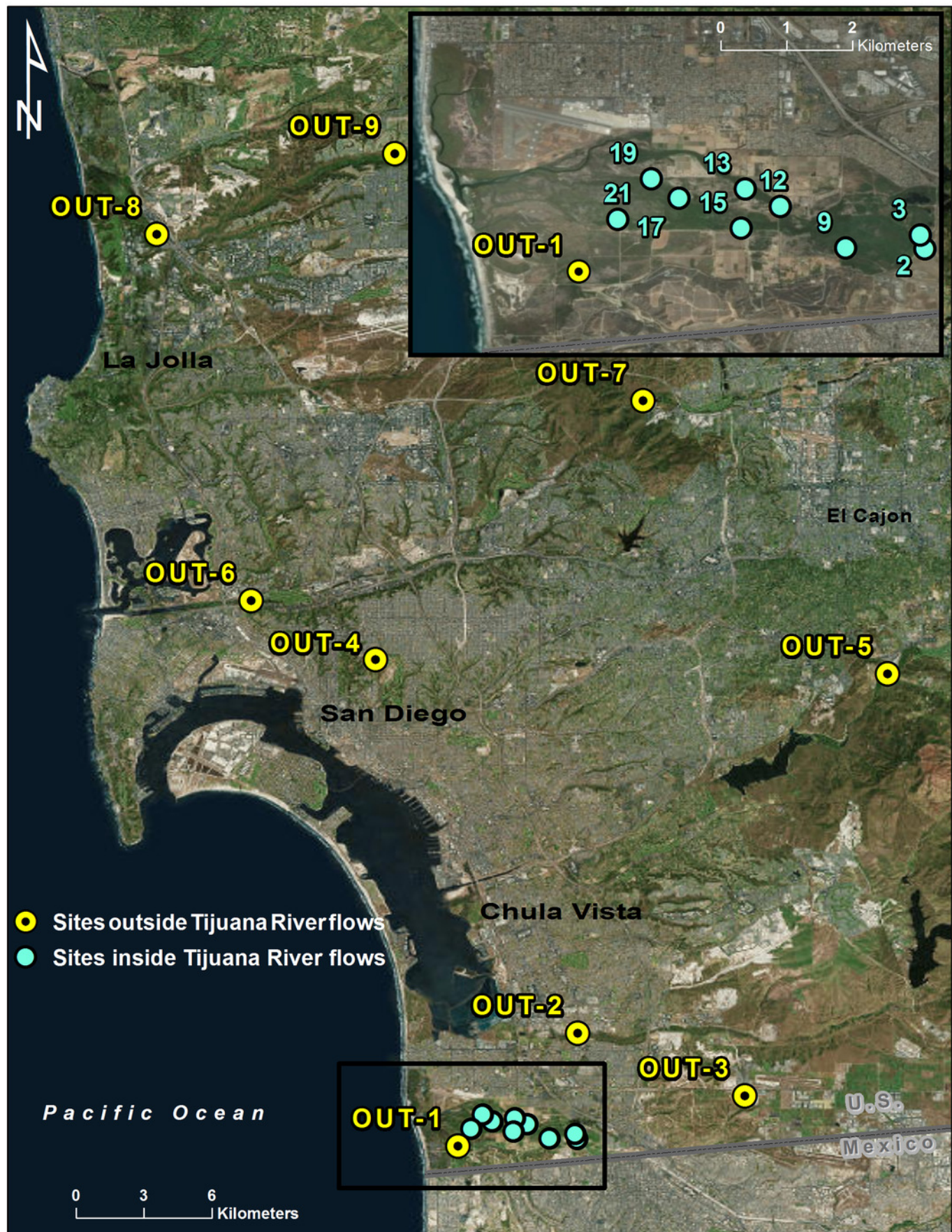



Figure 2

Sewage spill volumes.

Magnitude of sewage input during the three year period 2015 to 2017 into two areas. (A) The Tijuana River. (B) The rest of San Diego County.

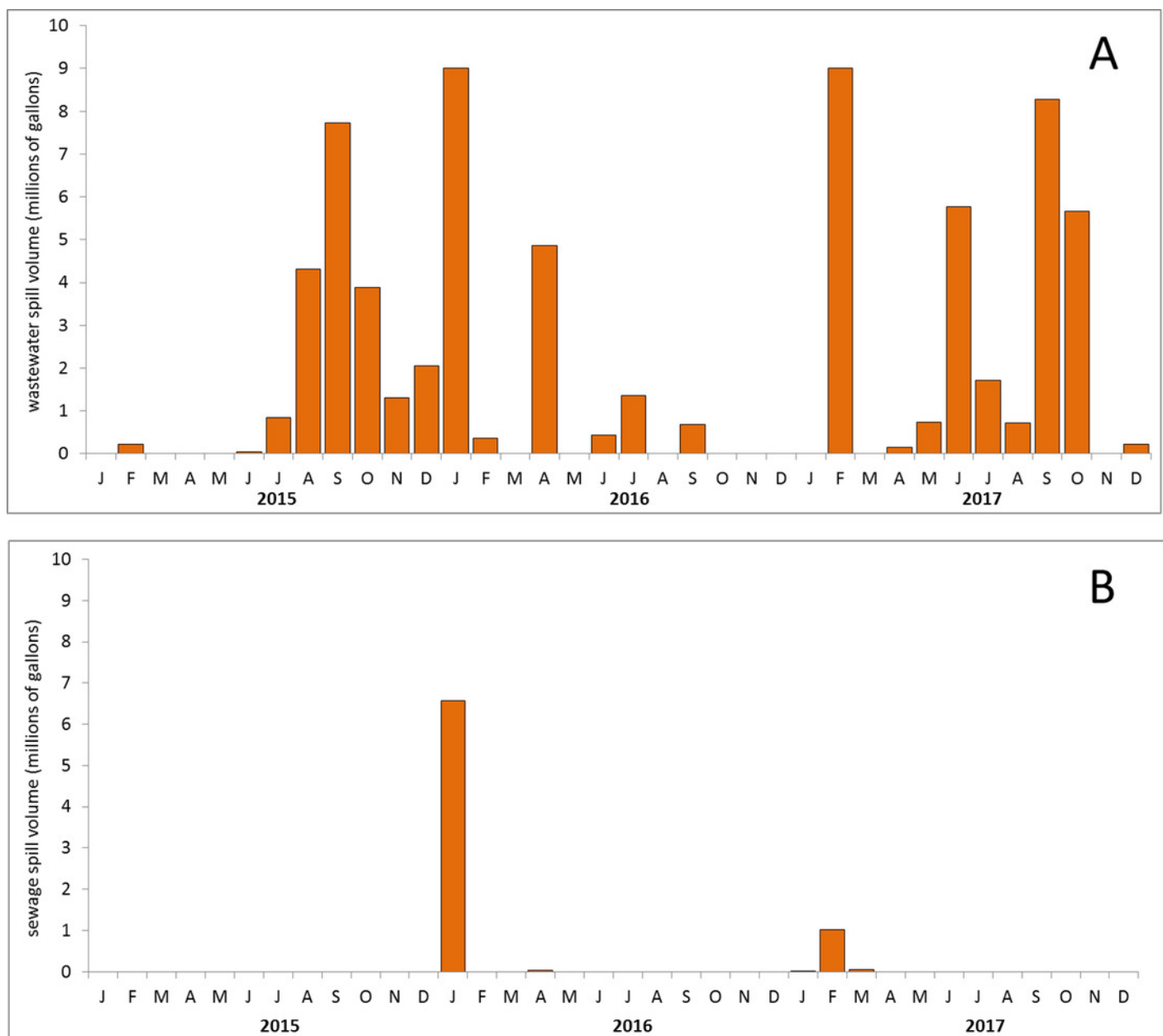



Figure 3

Willow wood densities.

Densities (g/ml) of branch samples from the two willow species collected at the polluted Tijuana River (left) and less polluted San Diego County (right) sites. (A) Black willow. (B) Arroyo willow. Data are mean ± 1 std. dev. Site nomenclature follows Table 1.

Figure 4

Willow wood moisture contents.

Moisture contents (%) of branch samples from the two willow species collected at the polluted Tijuana River (left) and less polluted San Diego County (right) sites. (A) Black willow. (B) Arroyo willow. Data are mean ± 1 std. dev. Site nomenclature follows Table 1.

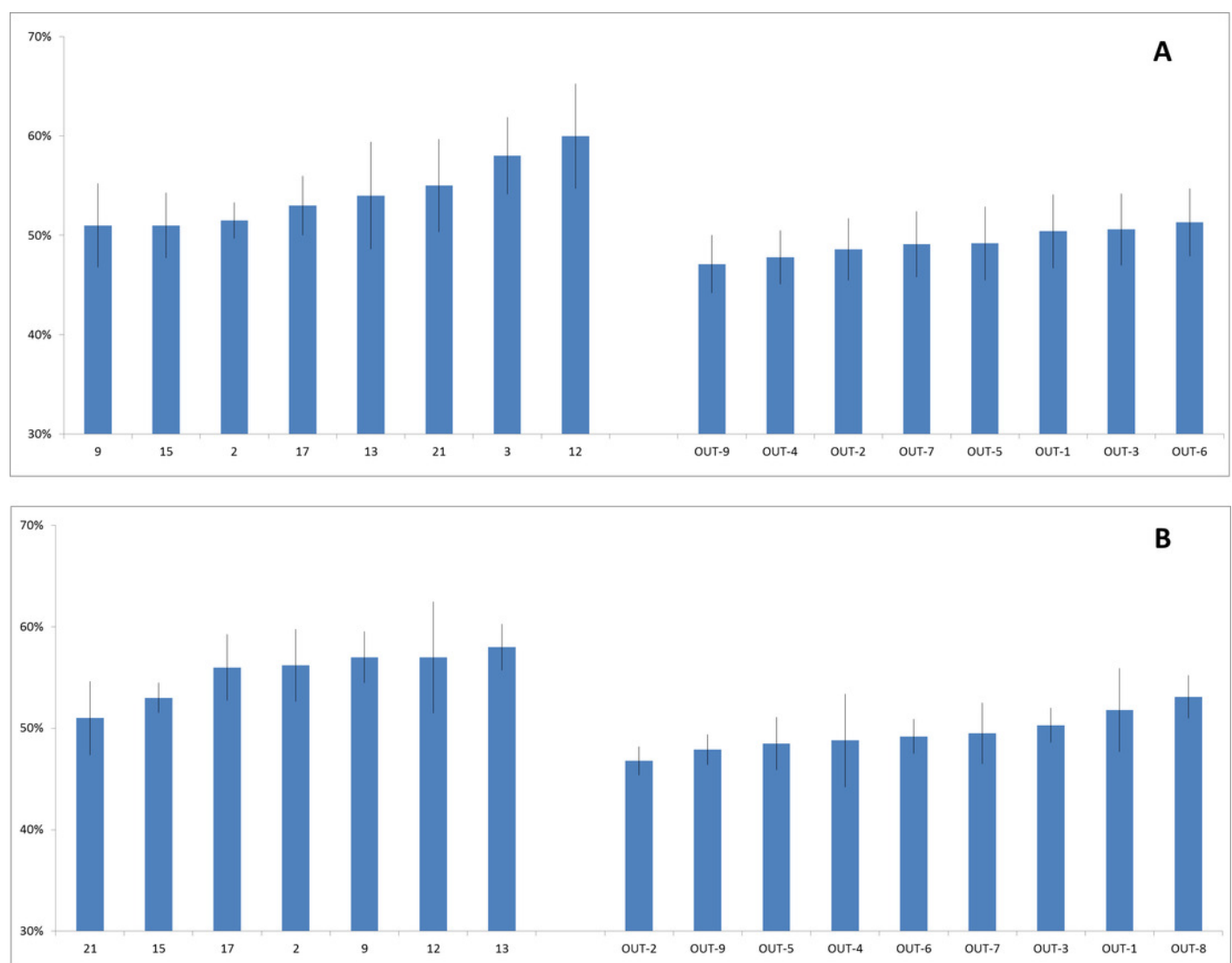
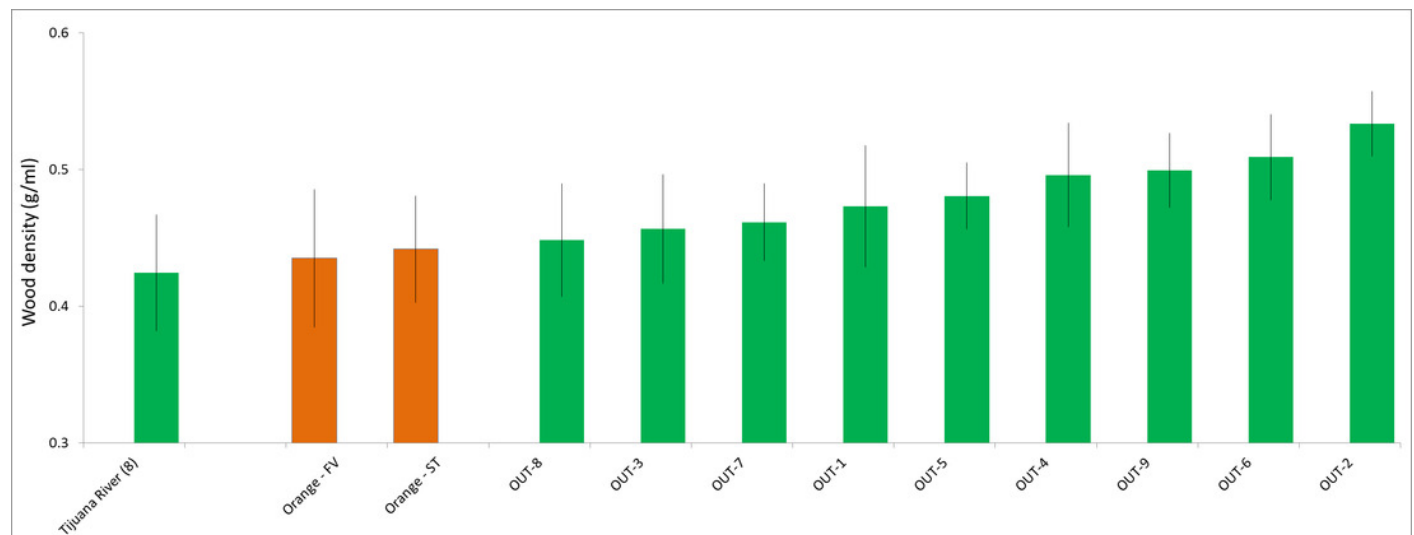



Figure 5

Inclusion of two intermediates.

The density (g/ml) of arroyo willow branch samples collected at two Orange County sites (center) compared to densities collected at the polluted Tijuana River sites (left) and the less polluted San Diego County sites (right). FV = Fairview Park, ST = South Talbert Regional Park. Data are mean ± 1 std. dev.

Site descriptions.

The park in which each site is located and its associated river. For sites within the Tijuana River Valley, the distance to the Tijuana River (TJR) main channel is given.

1 Table 1. Site descriptions. The park in which each site is located and its associated river. For
2 sites within the Tijuana River Valley, the distance to the Tijuana River (TJR) main channel is
3 given.

Site	Park	River	Distance to TJR main channel (m)
2	Tijuana River Valley Regional Park	Tijuana River	0
3	Tijuana River Valley Regional Park	Tijuana River	0
9	Tijuana River Valley Regional Park	Tijuana River	0
12	Tijuana River Valley Regional Park	Tijuana River	0
13	Tijuana River Valley Regional Park	Tijuana River	40
15	Tijuana River Valley Regional Park	Tijuana River	100
17	Tijuana River Valley Regional Park	Tijuana River	140
19	Tijuana River Valley Regional Park	Tijuana River	60
21	Tijuana Slough National Wildlife Refuge	Tijuana River	520
OUT-1	Border Field State Park	Tijuana River tributary	1,400
OUT-2	Otay Valley Regional Park	Otay River	Outside TJR Valley
OUT-3	Pacific Gateway Park	Tijuana River tributary	Outside TJR Valley
OUT-4	Balboa Park	Florida Canyon Creek	Outside TJR Valley
OUT-5	San Diego National Wildlife Refuge	Sweetwater River	Outside TJR Valley
OUT-6	Mission Valley Preserve	San Diego River	Outside TJR Valley
OUT-7	Mission Trails Regional Park	San Diego River	Outside TJR Valley
OUT-8	Torrey Pines State Natural Reserve	Peñasquitos Creek	Outside TJR Valley
OUT-9	Los Peñasquitos Canyon Preserve	Peñasquitos Creek	Outside TJR Valley

Number of samples.

The number of branch samples analyzed for wood density and wood moisture content. SALA = *Salix lasiolepis* (arroyo willow), and SAGO = *Salix gooddingii* (black willow).

1 Table 2. Number of samples. The number of branch samples analyzed for wood density and
2 wood moisture content. SALA = *Salix lasiolepis* (arroyo willow), and SAGO = *Salix gooddingii*
3 (black willow).

Site	Wood Density		Wood Moisture Content	
	SALA	SAGO	SALA	SAGO
2	20	22	20	10
3	0	10	0	10
9	10	10	10	10
12	10	10	7	7
13	10	10	7	7
15	10	10	10	7
17	10	10	10	10
19	20	10	0	0
21	10	10	7	7
OUT-1	10	10	10	10
OUT-2	10	10	10	10
OUT-3	10	10	10	5
OUT-4	10	10	10	10
OUT-5	10	10	10	8
OUT-6	10	10	10	10
OUT-7	10	10	10	10
OUT-8	10	0	10	0
OUT-9	10	10	10	10
Total	190	182	161	141
Grand Total	372		302	

Impacts of the KSHB.

KSHB infestation rates and KSHB-induced willow mortality rates at sites where branch samples were collected. An * indicates data are from Boland (2017b) and ** indicates data are from Boland (2016).

1 Table 3. Impacts of the KSHB. KSHB infestation rates and KSHB-induced willow mortality
2 rates at sites where branch samples were collected. An * indicates data are from Boland (2017b)
3 and ** indicates data are from Boland (2016).

Site	# Willows Examined	% Infested	% Mortality
A. Polluted Sites			
2	187	94%**	67%*
3	65	100%**	97%*
9	57	100%**	42%*
12	36	100%**	78%*
13	49	97%**	41%*
15	69	17%	0%
17	37	93%	3%
19	34	83%	12%
21	79	86%	4%
Median	**53**	**84%**	**41%**
B. Less Polluted Sites			
OUT-1	48	0%	0%
OUT-2	63	0%	0%
OUT-3	79	0%	0%
OUT-4	82	9%	0%
OUT-5	58	0%	0%
OUT-6	68	0%	0%
OUT-7	42	0%	0%
OUT-8	42	0%	0%
OUT-9	72	0%	0%
Median	**63**	**0%**	**0%**