The Kuroshio Shot Hole Borer in the Tijuana River Valley in 2017-18 (Year Three): Infestation Rates, Forest Recovery, and a New Model

Final Report

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and

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1. ABSTRACT

This report presents the results of my research on the invasive Kuroshio Shot Hole Borer (KSHB) in the Tijuana River Valley during 2017-18, i.e., year three of the KSHB infestation in the valley. I detail the status of the KSHB infestation and forest recovery in the riparian habitats, and I present a new hypothesis to explain the observed patterns in KSHB impacts in San Diego County.

The status of the KSHB infestation and forest recovery is as follows:

A. **The wet forests along the main channels are recovering.** These are the sites that were heavily infested with KSHB and severely impacted in years one and two. Now many KSHB-damaged willows have resprouted vigorously from their stumps, and seedlings have established in large patches. By late 2017, the developing canopy was about 5 m tall. Infestation rates decreased in all 12 of the Wet Forest survey units, and the median infestation rate was only 6%, down dramatically from its initial 97% in 2015-16. The stems of individual resprouts were up to 10 cm in diameter and KSHB-free; of 316 tagged resprouts examined, none had any signs of KSHB infestation. This result is especially encouraging because a year earlier a small proportion of resprouts was infested (9%), and there was concern that more would be attacked as they grew. Fortunately, that was not the case – the KSHB did not continue to attack resprouts and, as I document in one case, several KSHB holes have actually healed.

B. **The dry forests are becoming more infested.** Infestation rates increased in seven of ten Dry Forest survey units, and the median infestation rate was 78%, up dramatically from its 9% in 2015-16. As of late 2017, some trees had damaged limbs but few had died – the median mortality rate was only 6%. With little damage and few deaths in the Dry Forests, the original tall canopy formed by the large, old trees was generally intact.

C. **The riparian scrub, dominated by mule fat, is not being affected by the KSHB.** Mule fat had median infestation rates of 0%, and the sparse willows growing alone or in small stands in the scrub had an infestation rate of only 2%. These willow outliers are living under harsh conditions by willow standards, which is why many have misshapen crowns, broken limbs, snags and other symptoms of drought stress. They are at the opposite end of the water/nutrient spectrum from willows in the Wet Forests.

In this report I ask “*Why were the Wet Forests in the Tijuana River Valley the first natural forests to be heavily infested by the KSHB and the only ones to be severely impacted in San Diego County?*” and I explain why I think the reason has to do with sewage pollution. I call this explanation the **Soft Tree Hypothesis**, and it goes like this:

1) When abundant sewage (or fertilizer and water) flows into a site it stimulates the growth of the trees, in this case willows. The willows grow quickly and become extremely tall, and their wood has relatively low density and high water content,
i.e. they are ‘soft’ trees.

2) The KSHB prefers soft trees because it is easy for them to tunnel through and good for their fungal symbionts. When the KSHB finds a stand of soft trees its population increases rapidly and infested trees are heavily damaged.

3) At other sites not influenced by abundant sewage, willows grow more normally and have denser wood with lower water content, i.e., they are ‘hard’ trees. The KSHB generally ignores, or has low abundances in, these hard trees.

To test this hypothesis, I compared tree height, wood density, wood water content, and infestation rates at sites near and far from the Tijuana River flows. The results of these comparisons supported the hypothesis. The Tijuana River Valley trees were significantly taller than the same-aged trees growing outside the valley. Wood samples from willow trees had significantly lower densities and higher water contents at sites near the Tijuana River flow, indicating that the Tijuana River trees were ‘softer’ in comparison to sites far from the polluted flows. With these and other results, I conclude that the Tijuana River Valley is a special case, or an exception, and that the heavy KSHB impacts seen in the valley should not be expected to occur in natural riparian habitats elsewhere in San Diego County. From this hypothesis, I develop a model that encompasses my current thinking on the KSHB in the Tijuana River Valley and makes predictions about future KSHB spread in San Diego County.

Many of the findings in this report are new and need to be incorporated into our thinking about the invasion of shot hole borers in southern California. They can inform riparian habitat risk assessments, riparian restoration practices, and management actions in natural riparian habitats. In particular, we can update these old notions:

- An infested tree is as good as dead. Not true. It is now clear that not all KSHB-infested individuals die. Many survive a heavy infestation and send up resprouts from their damaged stumps.

- Other sites are going to be attacked as severely as the Tijuana River forests. Not likely. The extreme sewage pollution and softness of the trees make the Wet Forests in the Tijuana River unique in the region.

- The KSHB destroyed the Tijuana River forests. Not true. Ecologically, the KSHB impacts in the Wet Forests can be likened to a wildfire in chaparral, with the post-disturbance recovery now well underway.

- All individuals of a species at all sites are equally susceptible to infestation. Not likely. Trees growing in excessively wet, nutrient-rich conditions are most at risk, whereas others growing elsewhere are at much lower risk.

Overall, the findings in this report should ratchet down the level of risk of KSHB infestation at riparian sites outside the Tijuana River Valley.
2. INTRODUCTION
This report presents the results of research on the invasive Kuroshio Shot Hole Borer (KSHB) in the Tijuana River Valley during 2017-18, i.e., year three of the KSHB infestation in the valley. The report is organized into five main sections:

- **Background.** Here I provide an overview of the Tijuana River Valley and the KSHB, and a summary of my earlier work during 2015-16 and 2016-17, i.e., years one and two of the KSHB infestation in the valley.

- **KSHB infestation in the valley: 2017-18 (Year 3).** Here I provide the most current rates of infestation within four riparian habitats in the valley: dry forests, wet forests, riparian scrub, and ‘willow outlier’ stands, and compare the rates to the previous years. I also provide an estimate of how much willow canopy overall has been lost in the valley due to the KSHB infestation.

- **Recovery of the damaged forests: 2017-18 (Year 3).** Here I describe the strong recovery of the willow forest via regrowth, or resprouting, of KSHB-damaged willows and the recruitment of seedlings. I also document the distribution and abundance of native and non-native species in the recovering forest.

- **Does pollution drive the KSHB infestation?** Here I explain why I think the Tijuana River Valley was the first and most severely infested natural riparian area in southern California, and why I do not expect other, less polluted natural riparian sites to be similarly affected. I put forth the *Soft Tree Hypothesis* and provide supporting data.

- **The Soft Tree Model.** Here I discuss how the *Soft Tree Hypothesis* can be turned into a model that helps us understand the patterns of KSHB infestation, damage and mortality observed in the Tijuana River Valley, and helps us predict the likely extent of infestation at other riparian areas.

My work is focused on the ecological aspects of the KSHB’s impact, behavior, and spread in the Tijuana River Valley, in contrast to most others who focus on determining how to control or eradicate the KSHB, especially in agricultural or urban settings. Not much is known about the ecology of the KSHB or other ambrosia beetles in natural habitats (Hulcr and Dunn 2011) or about forest recovery after an infestation, so most of my findings are new and add to our understanding. On a personal note, I have been studying forest ecology in the Tijuana River Valley for more than a decade (e.g., Boland 2008, 2014a), and I want to understand what is happening to the trees I have been following for years, some since they first recruited as seedlings. My findings will, I hope, be used by other scientists and land managers to make informed decisions regarding the KSHB in natural habitats.
3. BACKGROUND

3.1. THE TIJUANA RIVER VALLEY

The Tijuana River Valley (32° 33.080'N, 117° 4.971'W) in San Diego County, California, is a coastal floodplain of approximately 3,700 acres at the end of a 1,730 square mile watershed (Figure 1). The river is an intermittent stream that typically flows strongly in winter and spring and is mostly dry in summer (Boland 2014a). The channel bottom is not armored and trees growing in the streambed are often inundated. Before entering the valley the river flows through the City of Tijuana, Mexico, where it is frequently loaded with sewage and other forms of pollution.

The riparian forests in the valley are a mosaic of forests of different ages – many were established in the massive flood years of 1980 and 1993 making them 38 and 25 years old respectively – young by riparian forest standards (Faber et al. 1989). At the time of the KSHB invasion, the riparian forests along the river were dominated by two species: arroyo willow (Salix lasiolepis, SALA) and black willow (Salix gooddingii, SAGO), and the surrounding riparian scrub woodlands were dominated by the perennial shrub, mule fat (Baccharis salicifolia, BASA; Boland 2014a). Each of these three species is most abundant in a particular zone around the river and the factors that govern their zonation were described in Boland (2014a). These young forests are of low diversity and do not have some of the species seen in older forests; there are no oaks (Quercus spp.) and only a few sycamores (Platanus racemosa) and cottonwoods (Populus fremontii).

The riparian forest and scrub habitats are preserved within three adjoining parks: the San Diego County Tijuana River Valley Regional Park, the Border Field State Park, and the Federal Tijuana Slough National Wildlife Refuge. The riparian habitats are relatively undisturbed and support numerous reptile, mammal and bird species, most notably the endangered least Bell's vireo (Vireo bellii pusillus) for which most of the riparian habitats are designated critical habitat (U.S. Fish and Wildlife Service 1994).

For my work on the KSHB in the valley, I divided the riparian habitats into 29 survey units so that the vegetation within each unit was relatively homogenous in terms of plant species composition, age and density (Boland 2016, 2017b). This resulted in 22 forest units dominated by willows, and seven scrub units dominated by mule fat (Figure 1).

3.2. THE KUROSHIO SHOT HOLE BORER (KSHB)

The Kuroshio Shot Hole Borer (KSHB, Euwallacea sp. near fornicatus; Eskalen 2018) is an ambrosia beetle native to Asia that has recently invaded southern California. Until 2015 it had been found in avocado groves and landscape trees only (Eskalen et al. 2013, Umeda et al. 2016). But in 2015, it was found in the native riparian forests in the Tijuana River Valley and has since caused extensive damage to those forests (Boland 2016, 2017b). Now the KSHB has been found in several other sites in southern
Figure 1. The location of the riparian forest and riparian scrub habitats within the Tijuana River Valley (from Boland 2016). Riparian forests units are numbered 1-22 and riparian scrub units are numbered 23-29.

California, including several parks and a few native forests (Eskalen 2018) causing managers and other authorities to be extremely concerned.

The KSHB is one of two ambrosia beetles currently attacking live trees in southern California. The other is the Polyphagous Shot Hole Borer (PSHB; *Euwallacea* sp. near *fornicatus*; Eskalen 2018). The two species are morphologically identical and are distinguished by their DNA sequences and by their associated fungi (Eskalen 2018). They are part of a species complex that also includes the Tea Shot Hole Borer (*Euwallacea fornicatus*), which has caused devastating damage to tea (*Camelia sinesis*) in at least ten countries, including India and Sri Lanka. The PSHB was first documented in Los Angeles County in 2003, and the KSHB was first observed in San Diego County in 2012 (Eskalen et al. 2013; Eskalen 2018; Umeda, Eskalen & Paine 2016). Both beetles attack many tree species in southern California, including native species, landscape trees, and the economically important avocado (*Persea americana*; Freeman et al. 2013; Eskalen et al. 2013). The ever-increasing list of reproductive host plants used by these two species currently stands at 63 host species (Eskalen 2018). Some people are starting to refer to the two species as the Invasive Shot Hole Borers (ISHB),
however for consistency with my other work in the valley I will continue to refer to the Tijuana River Valley species as the KSHB.

Both beetles damage or kill trees through their tunneling activities and their associated fungal pathogens (Freeman et al. 2013). Females drill into tree trunks, create galleries of tunnels in the xylem, inoculate the tunnels with a fungus (e.g., Fusarium sp.), and live in the tunnels eating the fungus and reproducing (Biedermann et al. 2009). Within a few weeks new females emerge, fly to new trees, and perpetuate the infestation (Rudinsky 1962). The beetles are tiny (~2 mm in length) and seldom seen, however their burrowing activities and impacts are easily seen (Eskalen 2018, Boland 2016).

3.3. KSHB INFESTATION AND FOREST RECOVERY IN 2015-16 and 2016-17 (YEARS 1 and 2)

Below is a brief list of findings from my first two years of work on the KSHB in the Tijuana River Valley (Boland 2016, 2017b).

- The KSHB infestation was more severe in some parts of the valley than in others (Figure 2). The wetter willow forests had higher rates of infestation and mortality than the drier forests; the mule fat-dominated riparian scrub had very low rates of infestation and was not substantially affected by the KSHB. Early infestation and mortality rates were significantly correlated with nearness to the river flow.

- Many infested and badly damaged willow trees resprouted in spring 2016 (Figure 3). In the wetter forests, where the tall willow canopy was extensively weakened by the KSHB and mostly felled by winter storms, willow resprouts formed an extensive, shrubby canopy up to 4 m tall. The average density of resprouting trees was 258 trees per acre, which is greater than the density of plants typically planted in a riparian restoration site, indicating that the forest was “restoring itself.” The new low-canopy that the resprouts created was suitable breeding habitat for many species, including the endangered least Bell's vireo (Vireo bellii pusillus).

- The resprouting of so many infested willows was noteworthy because it showed that the KSHB and its associated fungi did not kill all of the trees it infested.

- In late 2016, some of the larger-diameter willow resprouts were infested by the KSHB (9%).

- The KSHB infestation progressed differently in wet and dry willow forests (Figure 2):
  - Wetter forests went relatively quickly from heavy infestation of trees, to extensive damage of trees, to forest recovery via regrowth and recruitment. After two years, most of the trees had been attacked by the KSHB, many trees had been killed, the original tall willow canopy was
mostly gone, and willow resprouts were growing vigorously and creating an extensive new, shrubby canopy.

- **Drier forests went more slowly** from light infestation to just mild damage. After two years, only some of the trees had been attacked, most of the original tall willow trees were still standing, and their tall canopy remained intact. Resprouts were rare because few trees were damaged.

- Of the 23 common Tijuana River Valley plant species examined, **14 species** showed evidence of KSHB attack. The four species with the highest rates of infestation (arroyo willow, black willow, red willow and western cottonwood) were all **native riparian trees** in the Salicaceae (willow) family. These four species were usually heavily damaged when infested.

- The three species considered to be the **worst invasive plants** in the valley – arundo (Arundo donax), castor bean (Ricinus communis), and tamarisk (Tamarix ramosissima) – have benefited from the KSHB infestation. They all had low rates of KSHB infestation and, because the willow canopy was so reduced by the KSHB, they received more light, which increased their growth.

*Figure 2. The status of the vegetation within the riparian survey units as of February 2017, two years after the initial KSHB attack. Wet Forests = all dark green forest units; Dry Forests = yellow and red forest units; and Riparian Scrub = light green units.*
Figure 3. A typical resprouting arroyo willow. The original trunk is large, broken and riddled with KSHB holes. At the time of the photo, the four vertical resprouts were growing strongly and had no KSHB holes.

- I have estimated that during the first two years of the KSHB infestation:
  - 88% of the willows in the valley were infested, or a total of 355,510 trees;
  - 24% of the willows in the valley were killed, or a total of 95,791 trees;
  - 71,280 willow trees resprouted; and
  - Nearly all of the infested, killed and resprouting trees were in the Wet Forests.

- I have estimated that more than two billion KSHB were produced in the valley during the first year of infestation (2015-16), likely the single largest production of offspring by the KSHB in California so far.
4. KSHB INFESTATION IN THE VALLEY: 2017-18 (Year 3)

In this section, I report on the surveys of infestation I conducted in the Wet Forest, Dry Forest, and Riparian Scrub units, and on the surveys I conducted of individual plants that I had tagged in previous years. Surveys in the units provide an overall rate of KSHB infestation, and surveys of tagged individuals provide annual survivorship and growth rates and a detailed look at how the infestation is impacting individuals. I also report on a new survey I conducted this year of the isolated willows growing in the riparian scrub units. I called these trees “Willow Outliers” because they live alone or in small stands surrounded by mule fat. At the end I provide an estimate of the overall canopy loss in the valley due to the infestation. Figure 4 shows typical views of each habitat and Table 1 shows the number of units and tagged individuals surveyed this year.

Figure 4. Typical views of the habitats surveyed in the Tijuana River Valley during 2017-18. (A) Wet Forest showing the damaged but resprouting willow trees, (B) Dry Forest showing the original willow trees still standing, (C) Riparian Scrub showing the abundant mule fat, and (D) occasional Willow Outliers in the Riparian Scrub.
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4.1. KSHB IN THE WET FORESTS

By early 2017 the KSHB had already swept through the Wet Forests. The original tall willow canopy had been heavily-damaged, and a new canopy was growing composed mainly of willow resprouts. Because some of the larger-diameter resprouts were being infested (9%), concerns were voiced that all resprouts larger than one inch would be attacked by the KSHB (Eskalen in Sahagun 2017). This year, the questions I aimed to answer were:

- Is the KSHB still attacking the willows in the Wet Forests?
- Is the KSHB continuing to attack willow resprouts?
- Are the larger resprouts (>1 inch) being infested?

Methods

The Wet Forests total 245 acres and are Units 2-13 (Figure 2). To determine the KSHB infestation rates in the Wet Forests, I conducted the same type of surveys as in previous years, using the same survey units and the same survey points (Figure 1; Boland 2016, 2017b). In each Wet Forest unit, I did two surveys starting at the survey point and focusing on arroyo willow and black willow. I examined as many live willow trees as I could in two hours and classified each as either ‘currently infested’ or ‘not currently infested’. A tree was counted as ‘currently infested’ if it showed evidence of active tunneling by the KSHB, i.e., extrusion of sawdust or recent gumming out of sap from KSHB holes, or as ‘not currently infested’ if it had no evidence of KSHB attack or had only old, non-active KSHB holes. This year, I also categorized each tree encountered in the survey as either a seedling (<3 years old), young tree (3-5 years old), Big Tree (relatively undamaged adult tree >5 years old), or damaged, resprouting adult tree. Surveys were conducted November-December 2017.

To determine infestation rates specifically in resprouts, I reexamined the 302 resprouts on 34 individual willow trees that I had tagged in November 2016. The tagged trees were scattered throughout the Wet Forest units. [Some of the tagged resprouts were
In October-November 2017, I examined each resprout for signs of infestation and measured each resprout diameter. [I made additional measurements (resprout lengths and overall tree characteristics) that I will discuss in Section 5.2.]

Results

Survey in Units

- In late 2017 the KSHB was rare in the Wet Forests; the median infestation rates were 0% for willow seedlings, 3% for young trees, and 0% for resprouting adult trees (Table 2).
- Only the scattered Big Trees showed a moderate rate of current infestation; the median infestation rate for Big Trees was 42% (Table 2).
- Comparison of the infestation rates for 2015-16 and 2017-18 show that infestation rates have decreased in all of the Wet Forest units; the median infestation rate went from 97% to only 6% (Figure 5).

Survey of Tagged Individuals

- Survivorship of the 34 tagged resprouting trees was 100%.
- The resprouts on the tagged trees grew during the year; the resprouts in 2017 were significantly larger in diameter than the resprouts in 2016 (Figure 6; t-test, t-value = -8.87, p < 0.001).
- None of the 316 resprouts on the 34 tagged trees showed signs of KSHB infestation, and none had been killed by the KSHB (Figure 6).
- Even the larger-diameter resprouts were not infested. Of the 316 resprouts, 171 resprouts had diameters greater than one inch (2.54 cm; 54% of all the resprouts) and, again, none was infested (Figure 6).
- A close look at one of the tagged resprouts, in photographs taken one year apart, shows that the previously-infested resprout had healed and grown (Figure 7). Resprout B had several active KSHB holes in November 2016 and 15 months later the resprout had healed and had no active KSHB holes (Figure 7).

Discussion

Although the KSHB is still active in the rare Big Trees, it is virtually absent from the willows that make up the new developing canopy of the Wet Forests. This is important as it indicates that KSHB does not necessarily remain in areas previously infested, at least not in large numbers, and that the resprouts are not – so far – being immediately reinfested.

The survey of tagged individual resprouts showed that, while there was low-level infestation of some larger-diameter resprouts last year, there was no evidence of active infestation on any of the resprouts this year, even the larger ones. This means that the KSHB has not continued to attack willow resprouts. In fact, as yet I have seen no evidence of a resprout being killed by the KSHB. It is possible that the KSHB is waiting for the developing forest to mature before reinfesting. It is also possible that the resprouting willows have altered their chemistry to better resist infestation; many plants...
have been found to produce toxins and defensive proteins that target physiological processes in herbivorous insects after being attacked and thereby become immune to further attacks (see review in Howe and Jander 2008). Whatever the reason, resprouts were not being infested in late 2017.

The survey of tagged individual resprouts also led to the surprising and encouraging finding that an individual resprout can be infested with KSHB one year but not the next, i.e., an infested plant can heal (Figure 7). To my knowledge, this is the first documented evidence of such post-KSHB-infestation healing in willows.

Table 2. Current willow infestation rates in the Wet Forests of the Tijuana River Valley, as surveyed in winter 2017-18. The willow seedlings, young trees, Big Trees and resprouting trees were surveyed separately. % INF = percent of willows currently infested with KSHB.

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<th>RESPROUTING TREES</th>
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<td>10</td>
<td>56.9</td>
<td>7</td>
<td>0%</td>
<td>0</td>
<td>0</td>
<td>62</td>
</tr>
<tr>
<td>11</td>
<td>11.6</td>
<td>7</td>
<td>0%</td>
<td>0</td>
<td>0</td>
<td>33</td>
</tr>
<tr>
<td>12</td>
<td>7.8</td>
<td>136</td>
<td>0%</td>
<td>0</td>
<td>0</td>
<td>149</td>
</tr>
<tr>
<td>13</td>
<td>37.1</td>
<td>0</td>
<td>0%</td>
<td>17</td>
<td>12%</td>
<td>26</td>
</tr>
<tr>
<td>TOTAL</td>
<td>245.3</td>
<td>238</td>
<td>0%</td>
<td>140</td>
<td>0%</td>
<td>324</td>
</tr>
</tbody>
</table>

Figure 5. Changes in willow infestation rates in the Wet Forests from 2015-16 to 2017-18. Wet Forests are units 2-13. The median infestation rate for these units went from 97% to 6%.
Figure 6. The size frequency of willow resprouts in November 2016 and November 2017 growing on tagged resprouting trees in the Wet Forests. The median diameters of the resprouts was 1.9 cm in 2016 and 2.8 cm in 2017. Only a few resprouts were infested in 2016 and not one was infested in 2017. The resprouts in 2017 were significantly larger in diameter than they were in 2016 (t-test, t-value = -8.87, p < 0.001).
Figure 7. Survival and healing of arroyo willow resprouts. This is one of my tagged resprouts (R22) photographed on November 11, 2016 (top) and February 20, 2018 (bottom). TOP: In 2016 the resprouts (A-E) were alive and there was active KSHB in B at several places – two active KSHB holes are circled in yellow. [This resprouting tree was examined and sampled by Eskalen on November 10, 2016, and confirmed to have KSHB.] BOTTOM: In 2018 all of the resprouts (A-E) are still alive, they have grown and there is no sign of active KSHB in any of them. All of the KSHB holes in B are now healed – the two circled in black are the same ones circled in yellow in the top photo.
4.2. KSHB IN THE DRY FORESTS

My two previous annual surveys in the Dry Forests showed that KSHB infestation rates and impacts were low, so it appeared that these areas were not being substantially attacked and were perhaps acting as vital refuges for the willows from the beetle (Boland 2017b). This year, the questions I aimed to answer were:

- Is the KSHB continuing to invade the Dry Forests?
- What are the current rates of willow infestation and mortality?
- How long does it take a typical Dry Forest tree to go from ‘not infested’ to ‘infested’ to ‘dead’?

**Methods**

The Dry Forests total 352 acres and are Units 1 and 14-22 (Figure 2). To determine the KSHB infestation rates in the Dry Forests, I conducted the same kind of surveys as in previous years (Boland 2016, 2017b). I used the same survey units and survey points (Figure 1). During December 2017, I did two surveys in each Dry Forest unit, starting at the survey point and focusing on arroyo willow and black willow. To determine infestation rates within each unit, I examined as many live willow trees as I could in two hours and classified each as either: ‘not currently infested’ if I saw no signs of attack or only old, non-active KSHB holes; or ‘currently infested’ if I saw evidence of active tunneling by the KSHB, such as extrusion of sawdust or recent gumming out of sap from holes. To determine mortality rates within each unit, I examined as many willows as I could in two hours and classified each as either ‘alive’, ‘recently dead from KSHB attack’, or ‘dead from some other cause’. The estimated number of trees killed was extrapolated for each forest unit from the mortality rate and the estimated number of willow trees in each unit (Boland 2016, 2017b).

To follow the course of the KSHB infestation in specific trees, I had tagged more than 250 willows during February 2016 and revisited them several times to see how the infestation was progressing in those individuals. The tagged trees were scattered in Units 13 – 21, i.e., mainly Dry Forest units. When revisiting the trees I classified each as either: ‘not infested–alive’; ‘not infested–dead’; ‘infested–alive’; or ‘infested–dead’. Infested–alive included trees that had been heavily damaged by the KSHB and were resprouting as well as undamaged live trees that had signs of active KSHB infestation. Here I report on the December 2017 survey, which was completed almost two years after the trees were initially tagged.

**Results**

*Survey in Units*

- In December 2017, willows in all ten Dry Forest units were infested with KSHB, with rates ranging from 6% to 93%. Five units had infestation rates greater than 80%, and the median infestation rate was 78% (Table 3).
- Comparison of the infestation rates for 2015-16 and 2017-18 show that, while the rates in three units went down, overall the infestation rates in Dry Forests increased substantially; the median infestation rate went from 9% in 2015-16 to 78% in 2017-18 (Figure 8).
Mortality rates in most of the Dry Forest units remained low, however, with rates ranging from 0% to 41%. Six units had mortality rates less than 10%; and the median mortality rate was only 6% (Table 3).

The estimated number of willows killed by the KSHB in the Dry Forests is now at 44,839, which is 19% of the total number of trees in the Dry Forests (Table 3).

Table 3. Current willow infestation and mortality rates in the Dry Forests in the Tijuana River Valley, as surveyed in winter 2017-18.

<table>
<thead>
<tr>
<th>SITE UNIT</th>
<th>AREA (acres)</th>
<th>WILLOWS</th>
<th>WILLOW TREE INFESTATION</th>
<th>WILLOW TREE MORTALITY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>#</td>
<td># SURVEYED</td>
<td>% INFESTED</td>
<td># SURVEYED</td>
</tr>
<tr>
<td>1</td>
<td>36.2</td>
<td>7,319</td>
<td>48</td>
<td>6%</td>
</tr>
<tr>
<td>14</td>
<td>44.1</td>
<td>84,717</td>
<td>42</td>
<td>45%</td>
</tr>
<tr>
<td>15</td>
<td>45.8</td>
<td>16,204</td>
<td>69</td>
<td>17%</td>
</tr>
<tr>
<td>16</td>
<td>51.3</td>
<td>25,936</td>
<td>78</td>
<td>77%</td>
</tr>
<tr>
<td>17</td>
<td>52.9</td>
<td>16,069</td>
<td>75</td>
<td>93%</td>
</tr>
<tr>
<td>18</td>
<td>17.5</td>
<td>7,062</td>
<td>47</td>
<td>88%</td>
</tr>
<tr>
<td>19</td>
<td>16.9</td>
<td>8,524</td>
<td>30</td>
<td>83%</td>
</tr>
<tr>
<td>20</td>
<td>31.8</td>
<td>9,543</td>
<td>25</td>
<td>80%</td>
</tr>
<tr>
<td>21</td>
<td>23.0</td>
<td>7,172</td>
<td>76</td>
<td>86%</td>
</tr>
<tr>
<td>22</td>
<td>31.7</td>
<td>48,124</td>
<td>86</td>
<td>92%</td>
</tr>
<tr>
<td>TOTAL</td>
<td>351.6</td>
<td>230,770</td>
<td>576</td>
<td>78%</td>
</tr>
<tr>
<td>MEDIAN</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 8. Changes in willow infestation rates in the Dry Forests from 2015-16 to 2017-18. Dry Forests are units 1 and 14-22. The median infestation rate for these units went from 9% to 78%.
Survey of Tagged Individuals

- Of the 182 tagged willows that were not infested at the start in February 2016, 139 trees, or 76%, were ‘infested–alive’ in December 2017 (Figure 9). This means they became infested during the nearly two year period but did not die. Only a few initially uninfested trees died (7 individuals, 4%).

- Of the 75 tagged willow trees that were infested at the start in February 2016, 62 trees, or 83%, were still ‘infested–alive’ in December 2017 (Figure 9). This means they continued to live, even though infested, throughout the nearly two year period. Only a few initially infested trees died (13 individuals, 17%).

- Putting the timelines together to approximate a hypothetical four year period, the results suggest that an uninfested tree at the beginning of Year 1 had an 76% chance of becoming infested by the end of Year 2, and that an infested tree at the start of Year 3 had an 83% chance of surviving until the end of Year 4.

Figure 9. The change in condition of tagged trees from early 2016 to December 2017. One set of trees started as ‘not infested’ (n = 182), another set started out ‘infested’ (n = 75).

Discussion

KSHB infestation rates in the Dry Forests jumped dramatically in 2017-18. This means the KSHB is still spreading in the Tijuana River Valley and is now attacking trees not attacked earlier, i.e., the larger, older trees in the Dry Forests.

Mortality rates remained low, however, with the median rate of only 6%. This rate is particularly low in comparison to the mortality rates in the Wet Forests, where the median mortality rate was 48% during the initial invasion (Boland 2017).

The results from the units and the tagged trees showed that, although Dry Forest trees are being infested, only a small percent have been killed by the infestation. The low mortality rates mean that, at the moment, the Dry Forests – from Hollister down the southern arm of the river – continue to look generally sound (Figure 4B).
As for the total number of individual willows killed by the KSHB, my estimate can now be updated. The estimated total number of willows killed in the Dry Forests was 19,292 (Boland 2017b) and now is 44,839 (Table 3). Added to the 76,498 killed in the Wet Forests (Boland 2017b) the total number of willows killed in the valley is now estimated to be 121,337, which is 30% of the total that were present in 2015.

4.3. KSHB IN THE RIPARIAN SCRUB – MULE FAT

My two previous annual surveys found low KSHB infestation rates (<10%) of mule fat in the extensive riparian scrub surrounding the willow forests (Boland 2016, 2017b). Because a few mule fat had been infested, and because mule fat is listed as a reproductive host (Eskalen 2018), there was concern that the KSHB might attack more mule fat and severely impact the riparian scrub as it did the Wet Forests. This year, the question I aimed to answer was:

- Is the beetle continuing to attack the mule fat in the riparian scrub?

Methods

To determine the KSHB infestation rates in the Riparian Scrub units I did the same kind of surveys I had conducted in 2015 and 2016 (Boland 2016, 2017b). In December 2017 I examined as many live mule fat as I could in two hours within each unit and classified a shrub as either: ‘currently infested’ or ‘not infested’. A shrub was counted as ‘currently infested’ if it showed evidence of active tunneling by the KSHB, i.e., extrusion of sawdust or recent gummi out of sap from KSHB holes.

In addition to these general surveys, during January 2018 I revisited the 15 mule fat individuals that I had tagged in November 2015, examined them for signs of KSHB infestation, and remeasured the diameter of their live branches. These tagged individuals were scattered in units 23, 24 and 25 (Figure 1). When last examined, in November 2016, just three of the 15 individuals and nine of their 208 branches were infested with KSHB (Boland 2017b).

Results

Survey in Units

- Mule fat infestation rates in the scrub units were 0% (Table 4). None of the 326 mule fat examined in the scrub units showed any signs of being infested by the KSHB this year.
- Comparison of the infestation rates for 2015-16 and 2017-18 show that infestation rates have decreased in the scrub sites. The median infestation rate (and range) went from 2% (0% - 33%) in 2015-16 to only 0% (all 0%) in 2017-18.

Survey of Tagged Individuals

- None of the 229 mule fat branches on the 15 tagged mule fat examined in January 2018 showed signs of infestation. The stem-like branches of a typical, tagged mule fat looked like the photographs in Figure 10. In the years since they
had been first tagged, a few branches had died, a few branches had grown and, although nine branches showed signs of infestation in November 2016, none of the branches showed any signs of being infested in early 2018.

- Many of the branches that had been gumming out in 2015 were healed and growing in 2018 (e.g., branch A in Figure 10).
- The branches on all of the tagged mule fat individuals were growing, dying and being replaced by new branches; the 229 alive in January 2018 were not significantly different in diameter to the 208 that had been alive in November 2016 (Figure 11; t-test, t-value = 1.53, p > 0.05).

Table 4. Mule fat infestation rates in the scrub units of the Tijuana River Valley, as surveyed in winter 2017-18.

<table>
<thead>
<tr>
<th>Unit #</th>
<th>Area (ac)</th>
<th>Percent infested</th>
<th>Number surveyed</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>189.3</td>
<td>0%</td>
<td>60</td>
</tr>
<tr>
<td>24</td>
<td>94.0</td>
<td>0%</td>
<td>42</td>
</tr>
<tr>
<td>25</td>
<td>97.9</td>
<td>0%</td>
<td>43</td>
</tr>
<tr>
<td>26</td>
<td>78.3</td>
<td>0%</td>
<td>30</td>
</tr>
<tr>
<td>27</td>
<td>262.7</td>
<td>0%</td>
<td>54</td>
</tr>
<tr>
<td>28</td>
<td>169.6</td>
<td>0%</td>
<td>45</td>
</tr>
<tr>
<td>29</td>
<td>142.9</td>
<td>0%</td>
<td>52</td>
</tr>
<tr>
<td>TOTAL</td>
<td>1,034.8</td>
<td>0%</td>
<td>326</td>
</tr>
</tbody>
</table>

Discussion
The KSHB is not continuing to infest mule fat in the riparian scrub. The fact that there was no infestation of the mule fat in any of the unit surveys or the individual surveys in 2017-18 is good news. It means that the riparian scrub that borders the forests is not being affected by the KSHB.

Mule fat does not appear to be harmed by the KSHB. A branch appears to gum out when attacked, and then that branch either heals and survives or dies. The shrub will produce new branches to replace any dying ones. The mild KSHB infestation is therefore relatively easy for a multi-stemmed shrub like mule fat to 'work around.'

The size frequency of the mule fat branches was similar from year-to-year because large branches are constantly dying and being replaced by smaller ones (Figure 11). This situation is very different to the size frequency of the willow resprouts, which are getting significantly larger each year (Figure 6).
Figure 10. Growth, healing, and survivorship of mule fat branches on a tagged mule fat. Photographs taken on 11/30/2015 (above) and 1/19/2018 (below). In 2015 the branches A-D were alive and A-C were gumming out from an apparent KSHB attack (yellow circles). In 2018, there had been some branch deaths (of B and C), some branch growth (of A and D) and none of the branches showed signs of a KSHB attack.
Figure 11. The size frequency of live mule fat branches in November 2016 and January 2018 on tagged mule fat shrubs growing in the riparian scrub. The ones alive in 2018 were not significantly different in diameter to the ones that had been alive in 2016 (t-test, t-value = 1.53, ns, p > 0.05).
4.4. KSHB IN THE RIPARIAN SCRUB – WILLOW OUTLIERS

The riparian scrub surrounding the willow forests is composed mainly of mule fat and other shrubs but there are also a few arroyo willow and black willows growing in among them. These sites rarely, if ever, receive water from the main river channels, and these willows generally look shorter and dryer than the ones growing close to the river. I have not surveyed these willow outliers in the past but in 2017-18 I wanted to know:

- Is the KSHB attacking the willow outliers in the riparian scrub?

Methods
In February 2018 I walked through each riparian scrub unit and examined as many live willow trees as I could in two hours. I classified a tree as either ‘currently infested’ or ‘not currently infested’. A tree was counted as ‘currently infested’ if it showed evidence of active tunneling by the KSHB, i.e., extrusion of sawdust or recent gumming out of sap from KSHB holes, and as ‘not currently infested’ if it had no evidence of KSHB attack or had only old, non-active KSHB holes. I also noted whether or not the tree appeared to be drought-stressed.

Results
- Most of the willow outliers were not infested with KSHB the median infestation rate was 0% (Table 5).
- Only three willows in Unit 26 showed signs of KSHB infestation, or 2% of the total 150 willows examined.
- Many of the willow outliers appeared drought-stressed (Table 5); a typical outlying willow had a misshapen crown because of repeated dieback of terminal and lateral branches as a result of several years of severe moisture stress (Figure 12).

Discussion
Willow outliers largely have not been infested. The fact that only 2% of the willow outliers were infested is noteworthy because these trees are growing in close proximity to heavily-infested forests where billions of KSHB have been produced (Boland 2017b), and there is no known barrier to dispersal of the winged beetles. In Section 6, I discuss why I think the outlying trees are not as infested as the forest trees. Specifically, I suggest that the wood of outlying trees is unattractive to the KSHB because it has relatively high density and low water content.
Table 5. KSHB infestation rates in willows outliers growing in mule fat-dominated riparian scrub.

<table>
<thead>
<tr>
<th>UNIT</th>
<th># SURVEYED</th>
<th>INFESTED with KSHB</th>
<th>KILLED by KSHB</th>
<th>DROUGHT-STRESSED</th>
</tr>
</thead>
<tbody>
<tr>
<td>23</td>
<td>11</td>
<td>0%</td>
<td>0%</td>
<td>73%</td>
</tr>
<tr>
<td>24</td>
<td>15</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>25</td>
<td>22</td>
<td>0%</td>
<td>0%</td>
<td>23%</td>
</tr>
<tr>
<td>26</td>
<td>30</td>
<td>10%</td>
<td>0%</td>
<td>100%</td>
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<td>27</td>
<td>48</td>
<td>0%</td>
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<td>13</td>
<td>0%</td>
<td>0%</td>
<td>100%</td>
</tr>
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<td>29</td>
<td>11</td>
<td>0%</td>
<td>0%</td>
<td>100%</td>
</tr>
<tr>
<td>TOTAL</td>
<td>150</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

| MEDIAN |            | 0%                | 0%             | 87%              |

Figure 12. A typical willow outlier growing in the mule fat-dominated riparian scrub. Notice that the tree has a misshapen crown with broken limbs, dead branches, and snags due to severe moisture stress.
4.5. ESTIMATE OF OVERALL FOREST CANOPY LOST

The KSHB has damaged and killed many trees in the Tijuana River Valley forests in the last three years. To show the amount and distribution of the structural damage in the valley, I conducted a valley-wide survey to answer the question:

- **How much of the original willow canopy has been lost due to the KSHB infestation?**

**Methods**

During winter 2017-18, I observed each unit from as many places as possible and estimated the amount of canopy lost since the start of the KSHB-attack. I drew on my 16 years of working in these sites, and some of my ‘before’ photos and data.

**Results**

- In the past three years, 100% of the original willow canopy has been lost in many units, and a median of 79% of the original canopy has been lost in the entire valley. Higher losses were seen in the Wet Forest units between Dairy Mart and Hollister (Units 2-12), and lower losses were seen in the Dry Forest units west of Hollister (Units 15-21; Figure 13).

Figure 13. Distribution of canopy damage in the riparian habitats, as of winter 2017-18.
Discussion
Many of the forests in the valley have been substantially altered by the KSHB attack. Extensive areas that once supported willow forests with trees 20 m tall now support dense, recovering willow 'shrubs' 3-5 m tall. I think that the Wet Forests were infested first and most severely because they contained trees most preferred by the KSHB, and that Dry Forests were infested later and less severely because they contained trees less attractive to the KSHB. I test these ideas and discuss them further in Section 6.

4.6. INFESTATION CONCLUSION
The KSHB has generally moved out of the Wet Forests and into the Dry Forests, which means the KSHB is still spreading in the Tijuana River Valley and is now attacking the larger, older trees in the Dry Forests. However, the speed of the attack has slowed and so far the mortality rates in the Dry Forests are low. Whether the mortality rates stay low will need to be determined by future monitoring. The KSHB is not impacting the mule fat or willows in the Riparian Scrub.

One positive lesson learned from the Tijuana River Valley is that trees can recover, i.e., the old notion that an infested tree is as good as dead is not correct. While some trees do die as a result of KSHB infestation, many do not. Some trees can live with the infestation for several years, some show direct healing of holes, and some can be damaged but recover via resprouting of their broken stumps. This is important to keep in mind when deciding whether or not to cut an infested tree down.

5. RECOVERY OF THE HEAVILY-DAMAGED WET FORESTS: 2017-18 (Year 3)
The initial KSHB infestation in the Tijuana River Valley in 2015 was alarming, as it caused the dramatic collapse of the tall willow canopy. I published before and after photos of the forest at Dairy Mart bridge to illustrate what had happened in just a few months in the Wet Forests (Figure 14A and B; Boland 2016). Now I have added a third photo to the series to show the remarkable forest recovery (Figure 14C). The latest photo shows four aspects of the recovery that I am about to discuss – resprouting willows, recruitment of seedlings, abundant arundo, and polluted water.

In this section I explain how the most heavily-damaged forests in the Tijuana River Valley, the Wet Forests, have responded to the KSHB infestation. First, I describe the plant species now growing in the damaged forests. Second, I describe the growth and survivorship of the willow resprouts in the damaged forests. Third, I describe the distribution and abundance of the worst invasive plant species in the valley overall.
Figure 14. The Wet Forest at Dairy Mart bridge: before the KSHB infestation (A, May 2015); after the KSHB infestation (B, February 2016); and recently, showing the current forest recovery (C, March 2018).
5.1. PLANT SPECIES GROWING IN THE DAMAGED FORESTS

When walking through a KSHB-damaged forest, one can’t help but notice the abundant new growth both on the ground and in the tree stumps. Here I address the questions:

- **What plants are growing in these heavily-damaged sites?**
- **Are they mostly native or non-native species?**

**Methods**

In winter 2017-18, I conducted surveys to determine plant species composition in each of the Wet Forest units (Units 2-13) using the same methods as in my earlier annual surveys, i.e., percent cover measurement of species inside belt transects (20 m x 2 m = 40 m²; Boland 2016, 2017b). I then assigned each species present to one of the following categories: willow seedlings, willow Big Trees, willow resprouting trees, native annuals, and non-native plants. I also walked through the accessible parts of each unit to record species presence outside the belt transects.

**Results**

**Inside the belt transects:**

- Native species were more abundant than non-native species; the median percent cover of natives was 76% and of non-natives was 31% (Table 6).
- Resprouting willow trees and native annuals were the most abundant native plant categories, with median percent covers of 39% and 19%, respectively (Table 6).
- Castor bean was the most abundant non-native species, with a median percent cover of 14% (Table 6).
- Fifteen native species and 12 non-native species were present (Table 7).
- Three native species were found that had not been previously recorded in the Tijuana River Valley – sticktight (*Bidens frondosa*), false daisy (*Eclipta prostrata*) and dotted smartweed (*Persicaria punctata*; Table 7).
- Willow seedlings were patchy in the transects – 34% cover in the Unit 3 transect but rare or absent in the other transects (Table 6).

**Outside the belt transects:**

- Outside the transects, willow seedlings were present in large patches in three units – Unit 2 (arroyo willow), Unit 3 (black willow), and Unit 12 (black willow; Figure 15).
- The native bulrushes, *Schoenoplectus americanus* and *S. californicus*, are becoming common in sites where there is plenty of light and perennial water.
Table 6. The percent cover of plants along the belt transects within the 12 Wet Forest units, as surveyed in winter 2017-18.

<table>
<thead>
<tr>
<th>UNIT</th>
<th>willow seedlings</th>
<th>willow Big Trees</th>
<th>willow regrowth trees</th>
<th>native annuals</th>
<th>other natives</th>
<th>TOTAL NATIVES</th>
<th>Tamarisk</th>
<th>Castor Bean</th>
<th>Arundo</th>
<th>other non-natives</th>
<th>TOTAL NON-NATIVES</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>0%</td>
<td>0%</td>
<td>36%</td>
<td>58%</td>
<td>1%</td>
<td>95%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>0%</td>
<td>1%</td>
</tr>
<tr>
<td>3</td>
<td>34%</td>
<td>0%</td>
<td>0%</td>
<td>37%</td>
<td>0%</td>
<td>71%</td>
<td>1%</td>
<td>23%</td>
<td>0%</td>
<td>0%</td>
<td>24%</td>
</tr>
<tr>
<td>4</td>
<td>0%</td>
<td>9%</td>
<td>0%</td>
<td>5%</td>
<td>0%</td>
<td>14%</td>
<td>0%</td>
<td>71%</td>
<td>29%</td>
<td>0%</td>
<td>100%</td>
</tr>
<tr>
<td>5</td>
<td>0%</td>
<td>20%</td>
<td>53%</td>
<td>0%</td>
<td>13%</td>
<td>60%</td>
<td>0%</td>
<td>13%</td>
<td>24%</td>
<td>0%</td>
<td>37%</td>
</tr>
<tr>
<td>6</td>
<td>0%</td>
<td>12%</td>
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<td>16%</td>
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<td>39%</td>
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<td>14%</td>
<td>0%</td>
<td>0%</td>
<td>31%</td>
</tr>
</tbody>
</table>

Table 7. Plant species that occurred in the belt transects in winter 2017-18.

*** indicates a species that has not been recorded in the Tijuana River Valley before.

<table>
<thead>
<tr>
<th>NATIVE SPECIES</th>
<th>NON-NATIVE SPECIES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Willows: Gooddingia oblonga</td>
<td>Goodding’s black willow</td>
</tr>
<tr>
<td>Salix lasiolepis</td>
<td>Arroyo willow</td>
</tr>
<tr>
<td>Native annuals: Bidens frondosa***</td>
<td>Sticktight</td>
</tr>
<tr>
<td>Echtha prostrata***</td>
<td>False daisy</td>
</tr>
<tr>
<td>Helianthus annuus</td>
<td>Western sunflower</td>
</tr>
<tr>
<td>Persicaria lapathifolia</td>
<td>Willow weed</td>
</tr>
<tr>
<td>Persicaria punctata***</td>
<td>Dotted smartweed</td>
</tr>
<tr>
<td>Puccia orobiflora</td>
<td>Salt marsh fleabane</td>
</tr>
<tr>
<td>Solanum americanum</td>
<td>White nightshade</td>
</tr>
<tr>
<td>Stephanothenia sp</td>
<td>Wreath plant</td>
</tr>
<tr>
<td>Xanthium strumarium</td>
<td>Cocklebur</td>
</tr>
<tr>
<td>Other natives: Baccharis salicifolia</td>
<td>Mule fat</td>
</tr>
<tr>
<td>Ocimum americanus</td>
<td>American tule</td>
</tr>
<tr>
<td>Schoenoplectus californicus</td>
<td>Southern bulrush</td>
</tr>
<tr>
<td>NON-NATIVE SPECIES: Araujoa sericifera</td>
<td>Cruel vine</td>
</tr>
<tr>
<td>Arundo donax</td>
<td>Giant reed</td>
</tr>
<tr>
<td>Ampelopsis prostrata</td>
<td>Spearscale</td>
</tr>
<tr>
<td>Chenopodium sp (album)</td>
<td>Lamb's quarters</td>
</tr>
<tr>
<td>Ficus carica</td>
<td>Edible fig</td>
</tr>
<tr>
<td>grasses, e.g. Pennisetum clandestinum</td>
<td>Kikuyu grass</td>
</tr>
<tr>
<td>Phyllolaena kopsandra</td>
<td>Tropical pokeweed</td>
</tr>
<tr>
<td>Ricinus communis</td>
<td>Castor bean</td>
</tr>
<tr>
<td>Rumex conglomeratus</td>
<td>Whored dock</td>
</tr>
<tr>
<td>Schinus terebinthifolius</td>
<td>Brazilian pepper tree</td>
</tr>
<tr>
<td>Tamarix ramosissima</td>
<td>Tamarisk</td>
</tr>
<tr>
<td>Urtica urens</td>
<td>Dwarf nettle</td>
</tr>
</tbody>
</table>
Figure 15. Three stands of willow seedlings in the Wet Forests during 2017. 
TOP: arroyo willows (9 months old, Unit 2). MIDDLE: black willows (1.3 years old, Unit 3). 
BOTTOM: black willows (2 years old, Unit 12). There is a person in each photo to show scale.
Discussion
In winter of 2017-18, native plants dominated the regrowth in the heavily-damaged sites. Native species, particularly willows, flourished in light gaps created by the loss of the tall willow canopy. Before the KSHB invasion, the willow canopy was so tall and dense that little light penetrated to the ground and few plants were in the understory (Boland 2014a). After the KSHB invasion, the willow canopy was almost completely lost and light reached the ground, allowing for regrowth of willow stumps and recruitment of new plants, including three native species that had never been recorded from the Tijuana River Valley before.

Willow seedlings were abundant as dense patches in some areas. The main reason for their patchy distribution is that the conditions necessary for their establishment were also patchy in 2017. Willow seeds are wind-dispersed and germinate immediately upon landing in a suitable site, a suitable site being one with full sun, moist sediment, and no vegetation or debris. One final requirement has to do with timing; the moist, sunny sediment needs to be available when the willows are producing their wind-dispersed seeds, i.e., March to June (Boland 2014b). Where these conditions were met, seedlings established abundantly (Figure 15). But these conditions were not met in most moist sites because a layer of woody debris from fallen KSHB-damaged limbs interfered. As I recommended last year, clearing debris at the correct time would enhance the establishment of willow seedlings in moist, open areas (Boland 2017b).

Several non-native species have invaded the heavily-damaged sites. **Arundo** is by far the most damaging invasive in the Tijuana River Valley (Boland 2006, 2008) and its control in these heavily-damaged sites should be the highest priority. **Tamarisk** is rare in these parts of the valley and not a big concern; it is more common in the saline areas to the west where it is abundant in and around salt marshes (Whitcraft et al 2007). **Castor bean** is abundant but not really a big concern. It is killed by flooding so, in wet sites, it is an annual that produces few seeds. It grows abundantly in these sites because its seeds are washed in by flows (Boland 2017a) and there is sufficient water and light, but it will eventually be outcompeted by the more flood-tolerant, perennial plants like willows and arundo. Castor bean is less abundant just out of the streambed, and in these sites it is a perennial that produces many, long-lived seeds; these dryer castor bean should be treated. With arundo as the highest priority, managers should try to spray the invasives with herbicides in these heavily-damaged forests to improve the habitat value and stimulate native plant recovery.

The young, shrubby canopy developing in the recovering Wet Forests appears to provide reasonable breeding habitat for the endangered least Bell's vireo. In April 2017, I mapped vireos in approximately 40 acres of the Wet Forests with a qualified vireo consultant (Monica Alfaro) and we found seven males setting up territories in the heavily-damaged forests. In addition, during spring-summer 2017, Barbara Kus conducted more extensive surveys of the valley. She found 28 vireos breeding in the Wet Forests and concluded that “They certainly haven't been extirpated” (Kus personal communications 29 September 2017, and 22 March 2018). This vireo is known to require dense, young forests for breeding (Kus 2002) and the valley, including the Wet Forests, appears to be meeting this requirement at the moment.
5.2. SURVIVORSHIP AND GROWTH OF WILLOW RESPROUTS

In Section 4.4, I reported that none of the willow resprouts in the Wet Forests showed signs of KSHB infestation, even though a year earlier some had been infested. Here I give details of the survivorship and growth of individual resprouts to address the question:

- What are the survivorship and growth rates of willow resprouts in areas that were previously heavily infested by KSHB?

Methods

In March 2016 I noticed that many of the heavily-infested tree stumps were starting to resprout (Figure 16 A). In October–November 2016, I tagged 34 resprouting willow trees for close examination over time. These tree stumps were scattered throughout the heavily-damaged Wet Forest units (Units 2, 8, 10, 11, 12 and 13). All of the tagged stumps had been heavily-infested with KSHB and had many KSHB holes per 45 cm² (Table 8). At that time, I examined all the resprouts on each tagged tree for signs of KSHB infestation, and I measured the diameter of each resprout; in total, I examined and measured 302 resprouts, 27 of which were infested (Table 8). I also measured the length of the largest resprout on each tree, tagged it and named it the focal resprout.

A year later, in October–November 2017, I revisited the 34 tagged trees and again examined their resprouts; I looked for signs of KSHB infestation, measured the diameter of all of the live resprouts (including any new ones that had grown), and measured the length of the focal resprouts. In addition, I measured the total height and width of the ‘new’ tree created by the stump and its resprouts, and calculated its volume (as a cone).

Results

- All 34 of the resprouting willows tagged in 2016 were alive and growing in 2017. One-year survivorship of these tagged, recovering trees was therefore 100%.
- The resprouting willows exhibited vigorous growth. For example, in 2016 one arroyo willow stump had eight resprouts and was 3.6 m tall, and in 2017 it had 15 resprouts and was 5.5 m tall (Figure 16B and 16C).
- All 34 of the focal resprouts tagged in 2016 were alive and growing in 2017. These focal resprouts increased in length by an average of 47%, from 3.0 m to 4.4 m, and increased in diameter by an average of 90%, from 3.1 cm to 5.9 cm (Table 8).
- As a group, total resprouts were significantly larger in 2017 than in 2016 (t-test, T-stat = 8.871, p < 0.001). They increased in diameter by an average of 58%, from 2.2 cm to 3.4 cm (Table 8).
- By November 2017, the resprouting willows were large and shrubby (Figure 16C). The average ‘new’ tree had 9.3 resprouts, was 4 m tall and 5.2 m wide, and occupied a total volume of approximately 21.8 m³ (Table 8).
- As reported in Section 4.1, none of the resprouts showed signs of KSHB infestation in November 2017 (Table 2 and Figure 6). In fact, KSHB holes in a previously-infested resprout were found to have healed, and the resprout had recovered from the infestation (Figure 7).
Figure 16. The rapid growth of a resprouting arroyo willow (Unit 13, tagged individual R1). The resprouting tree was 1m tall on March 8, 2016 (A), 3.6m tall on October 7, 2016 (B), and 5.5m tall on November 7, 2017 (C). For scale, I’m standing in the same place in each photo.

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Oct-Nov 2016</th>
<th>Oct-Nov 2017</th>
<th>% change</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>ORIGINAL TREES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Number of labeled resprouting trees</td>
<td></td>
<td>34</td>
<td></td>
</tr>
<tr>
<td>Labeled trees location -- Units</td>
<td></td>
<td>2, 8, 10, 11 and 13</td>
<td></td>
</tr>
<tr>
<td>Stump height in m -- mean (std dev)</td>
<td></td>
<td>4.1 (2.1)</td>
<td></td>
</tr>
<tr>
<td>Stump circumference in cm -- mean (std dev)</td>
<td></td>
<td>92.3 (43.0)</td>
<td></td>
</tr>
<tr>
<td>Number of KSHB holes per 45 cm² on stump -- mean (std dev)</td>
<td></td>
<td>27.4 (12.0)</td>
<td></td>
</tr>
<tr>
<td><strong>FOCAL RESPROOTS</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Number of labeled focal resprouts</td>
<td>34</td>
<td>34</td>
<td>no change</td>
</tr>
<tr>
<td>Resprout length in m -- mean (std dev)</td>
<td>3.0 (0.7)</td>
<td>4.4 (1.3)</td>
<td>47% increase</td>
</tr>
<tr>
<td>Resprout diameter in cm -- mean (std dev)</td>
<td>3.1 (1.0)</td>
<td>5.9 (1.9)</td>
<td>90% increase</td>
</tr>
<tr>
<td><strong>ALL RESPROOTS - SIZE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total number of resprouts</td>
<td>302</td>
<td>316</td>
<td>5% increase</td>
</tr>
<tr>
<td>Resprout diameter in cm -- mean (std dev)</td>
<td>2.2 (1.2)</td>
<td>3.4 (2.2)</td>
<td>58% increase</td>
</tr>
<tr>
<td>t-test of resprout diameter 2016 v 2017 -- T stat. (p value)</td>
<td>8.871 (&lt;0.001)</td>
<td></td>
<td></td>
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<tr>
<td><strong>ALL RESPROOTS - INFESTATION BY KSHB</strong></td>
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<td></td>
</tr>
<tr>
<td>Number of resprouts infested with KSHB</td>
<td>27</td>
<td>0</td>
<td>100% decrease</td>
</tr>
<tr>
<td>Percent of resprouts infested with KSHB</td>
<td>9%</td>
<td>0%</td>
<td>100% decrease</td>
</tr>
<tr>
<td>Number of resprouts killed by KSHB</td>
<td>0</td>
<td>0</td>
<td>no change</td>
</tr>
<tr>
<td><strong>NEW TREE - SIZE</strong></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Number of resprouts per tree -- mean</td>
<td>8.9</td>
<td>9.3</td>
<td>5% increase</td>
</tr>
<tr>
<td>Width of new tree in m -- mean</td>
<td>nd</td>
<td>4.0</td>
<td></td>
</tr>
<tr>
<td>Height of new tree in m -- mean</td>
<td>nd</td>
<td>5.2</td>
<td></td>
</tr>
<tr>
<td>Volume of new tree in m³ -- mean</td>
<td>nd</td>
<td>21.8</td>
<td></td>
</tr>
</tbody>
</table>

**Discussion**

Documenting the continued survival and rapid growth of resprouting willows is informative for several reasons. First, it underscores the fact that a KSHB-infested tree is not necessarily a dead tree. A heavily-infested, heavily-damaged tree may at first appear to be dead, but it may still be alive and able to recover via resprouting from its stump. This means that the KSHB’s fungal symbionts are not necessarily highly pathogenic, as they do not appear to affect or inhibit regrowth of the stump.

Second, the rapid growth of resprouts shows how quickly the heavily-damaged willow trees in the Wet Forests of the Tijuana River Valley are recovering. They went from dead-looking stumps riddled with old KSHB holes to voluminous, 5-m-tall shrubs in less than two years. It therefore appears that the KSHB-damaged forests are rapidly restoring themselves. Last year I estimated that the average density of resprouting willow trees was 258 plants per acre (Boland 2016), and this is greater than the number of plants typically planted in a riparian restoration site (usually ~200 plants per acre; Boland 2017b, River Partners 2007).

Third, resprouting is the main way the damaged forests are recovering. Resprouting from a tree’s base is a common phenomenon. Foresters call it ‘coppicing’ when done intentionally in a harvesting context (Figure 17). In late 2015 and early 2016, the KSHB
infestation effectively coppiced the willows growing in the Wet Forests; the trees were structurally weakened by KSHB tunneling and then were snapped by high winds in winter (Boland 2017b). Being felled in this way was, in effect, similar to being cut by a lumberjack and left to sprout from the still-living stump.

As of November 2017, resprouting trees in the Wet Forests were recovering and not being reinfested by KSHB. It is not known how long that fortunate circumstance will last; it is not known if or when the KSHB will return to these areas, attack the resprouts, and interrupt the forest recovery. But, for now, the willows are growing vigorously and providing essential habitat.

Figure 17. A typical forestry book’s guide to coppicing. In the Tijuana River Valley Wet Forests, the KSHB acted like a lumberjack and ‘cut’ the willows down to stumps. Now the willows are growing back from those stumps.

5.3. OVERALL ABUNDANCES OF THE WORST INVASIVE SPECIES

The invasive species of greatest concern in the valley are arundo, castor bean and tamarisk. They have been the focus of a treatment program in the valley (SWIA 2002) and of several ecological studies in the valley (Boland 2006, 2008; Whitcraft et al. 2007). Arundo and castor bean were particularly abundant in the riparian forests (Boland 2017b). I conducted a survey of the valley to answer the question:

- What is current distribution and abundance of the worst invasive species in the valley?

Methods

In winter 2017-18, I estimated the percent cover of the invasives in each of my survey units, making observations from as many accessible places as possible. For arundo, which can be identified on the latest Google Earth aerial photos, I also estimated percent cover based on those aerial photos then averaged the estimates from the two sources (field surveys and Google Earth surveys).
Results

- Arundo and castor bean were abundant in the riparian forests and rare in the riparian scrub habitats (Figures 18 and 19).
- Arundo and castor bean were most abundant in the heavily-damaged eastern forests, particularly in Units 4 – 9, where arundo reached up to 60% cover and castor bean reached up to 70% cover. In some units these two species together dominated the vegetation (Figures 18 and 19).
- Tamarisk was rare in all survey units – less than 5% cover. [It is most abundant along the main channel just west of Unit 14, where the salt marshes begin.]

Discussion

Arundo and castor bean are the invasive species of greatest concern in the recovering, KSHB-damaged forests. Both species benefited from the increased light that followed the KSHB-induced loss of high willow canopy, and both species are now growing strongly. Arundo is spread mainly by bulldozers, which break-up rhizomes and make them available for downstream spread by water flows (Boland 2008), and that is why arundo is most abundant in the eastern forests immediately downstream of where the International Boundary and Water Commission (IBWC) has been bulldozing, disking, and mowing the arundo on its property for decades (Figure 1). As mentioned in Section 5.1, treatment of arundo in particular would assist the recovery of the native forests and should be a park manager’s highest priority.

Figure 18. Percent cover values of arundo in the riparian survey units, as of winter 2017-18.
5.4. RECOVERY CONCLUSION

The ecological impact of the KSHB in the Wet Forests and the subsequent recovery of the vegetation were similar to the ecological impact of a wildfire in chaparral and the subsequent recovery of the chaparral vegetation (Rundel and Gustafson 2005). The KSHB quickly ‘consumed’ most of the trees within the Wet Forests and then moved on to the other units in the valley. Now there is recovery of the damaged vegetation via resprouting of stumps and establishment of new seedlings, including seedlings of native species never before seen in the valley.

The fire analogy reminds us that the KSHB-impacted habitats have not been ‘destroyed’ or ‘lost’. By attacking the willows the KSHB has set back the competitive dominant trees, opened up the forests and let sunlight in for other species. The valley used to be a continuous willow forest (Boland 2014a) but now is a mosaic of willow forests at different stages of infestation and recovery. The KSHB has therefore increased the habitat diversity and plant diversity within the valley. New plant species have established (Table 7), new bird species have become more abundant (e.g., woodpeckers), and the ‘new forest’ is being used by breeding least Bell’s vireos.

The fire analogy can suggest new ways to think about components of the KSHB attack. For instance, ‘fuel load’ and ‘return interval’ are important concepts in fire ecology that may also be applied to the KSHB invasion. The KSHB infestation and
subsequent extensive damage to the willows in the Wet Forests has resulted in those forests becoming largely unsuitable for the KSHB and the KSHB is now mostly absent (Figure 5). One might say the fuel load is now too low for the KSHB and the developing trees are being left to grow without attack from the KSHB. I suspect that the KSHB will return when the trees have become large again and there is a lot of 'fuel' for another attack. Just how long this return interval is in the willow forest remains to be seen. For fire in chaparral it is approximately 15 years (Rundel and Gustafson 2005).

If and when the KSHB do return in high numbers they will find a changed Wet Forest. Previously the willows were densely-packed in single-aged stands (Boland 2014a) but now, in the developing forest, willows are more spread-out and mixed with other species, particularly reeds and shrubs (compare Figures 14A and 14C). The change in forest structure brought about by the KSHB is the kind of change that forest entomologists recommend in order to make any forest less susceptible to an insect outbreak – mixed age-classes, mixed species, and lowered densities; forest entomologists refer to these changes as ‘preventive control by silvicultural practices’ (Knight and Heikkenen 1980). Ironically, it is possible that the change in forest structure brought about by the KSHB will make the forest less susceptible to a future KSHB outbreak.

Arundo and castor bean are thriving in the recovering wet forests in the Tijuana River Valley. These invasive species have benefited from the canopy damage done to the willows, because the collapse of the original high canopy increased the light available to them. These two species, particularly arundo, degrade the forest and reduce the value of the habitat for other native species. The best way for a manager in one of the parks in the Tijuana River Valley to manage the KSHB problem is to focus on these invasives and treat them with herbicides. This action would greatly assist the recovery of the native forests in the valley.
6. DOES POLLUTION DRIVE THE KSHB INFESTATION?

To date, the Tijuana River Valley is the natural riparian area most hard-hit by the KSHB. None of the neighboring natural riparian areas have been similarly infested and damaged, nor to my knowledge have any others in southern California. Other sites in San Diego County that have been infested with the KSHB include patchy areas along the San Luis Rey River, Escondido Creek and Sweetwater River, but none has been as severely hit as the Tijuana River Valley (Eric Porter, USFWS personal communication 6 March 2018). So I have asked:

- What makes the forests of the Tijuana River Valley different?
- Why were they the first natural forests to be infested by the KSHB?
- Why were healthy trees so rapidly and severely impacted?

The most obvious factor that sets the Tijuana River forests apart from just about all others is that they are exceedingly well fertilized by enormous amounts of sewage that enters the river from cross border flows. This fertilizer has been pouring in for decades, and the forests have flourished.

In this section, I present a hypothesis that explains why the KSHB infestation has been severe in the Tijuana River Valley but not in other places. I then present a series of studies that serve to examine various components of the hypothesis.

6.1. THE SOFT TREE HYPOTHESIS

I hypothesize that sewage spills and KSHB abundances are biologically linked in the following way. I call it the Soft Tree Hypothesis and illustrate it in Figure 20.

1) When abundant sewage (or fertilizer and water) flows into a site it stimulates the growth of the trees, in this case willows. The willows grow quickly and become extremely tall, and their wood has relatively low density and high water content, i.e. they are ‘soft’ trees.

2) The KSHB prefers soft trees because it is easy for them to tunnel through and good for their fungal symbionts. When the KSHB finds a stand of soft trees its population increases rapidly and infested trees are heavily damaged.

3) At other sites not influenced by abundant sewage, willows grow more normally and have denser wood with lower water content, i.e., they are ‘hard’ trees. The KSHB generally ignores, or has low abundances in, these hard trees.
Figure 20. The Soft Tree Hypothesis illustrated. When excessive sewage (or fertilizer and water) flows into a site it stimulates the growth of trees, and this rapid growth leads to ‘soft’ wood and greater susceptibility to mass attack by Shot Hole Borers (SHBs). At other sites not influenced by excessive sewage (or fertilizer and water), trees grow more normally, they are ‘hard’ and are not abundantly attacked by SHBs. The brown circles show the density of wood inside the trunk. SHB = KSHB, PSHB, or ISHB.

6.2. SAN DIEGO COUNTY – A COMPARISON OF SEWAGE FLOWS

High sewage inputs into the Tijuana River Valley are an important component of the Soft Tree Hypothesis. Here I compare sewage spill data for San Diego County and the Tijuana River Valley to answer the question:

- How does the level of sewage pollution in the Tijuana River compare to that in other rivers in San Diego County?

Methods

I compiled sewage spill data for a three-year period, January 1, 2015 to December 31, 2017. The Tijuana River spill data comes from the International Boundary and Water Commission’s spill reports that are available on the San Diego Regional Board’s web site (San Diego Regional Board 2018). These spill reports document “dry weather transboundary wastewater” flows that contain raw sewage, partially treated sewage and/or other wastewaters “that creates, or threatens to create, pollution or nuisance conditions in waters of the United States.” I examined each spill report for the period, and compiled the spills into the Tijuana River, Goat Canyon and Yogurt Canyon separately. Spills into Yogurt Canyon, which go directly into the Tijuana Estuary, were not included here. The San Diego County spill data comes from the California State Water Resources Control Board sanitary sewer overflow incident map web site (State Water Board 2018). The filters I used were: area (San Diego County south of
Oceanside); and spill volume (>10,000 gallons). I examined each incident report and recorded the spill volume minus the recovered volume.

Results

- There were 55 cross border flows from Tijuana into the Tijuana River during the three years (Figure 21A). The flow events were spread over the entire three years and totaled more than 220 million gallons. During the same period, there were only seven sewage spills totaling less than 8 million gallons within the rest of San Diego County (Figure 21B).

- The largest cross border flows into the Tijuana River Valley were of 143 and 27 million gallons (off the scale on Figure 21A). The largest spills in San Diego County outside of the Tijuana River Valley were of seven million gallons into Tecolote Canyon and less than one million gallons into a residential area in El Cajon (Figure 21B).

- Overall, the Tijuana River Valley received almost 30 times the total spill volume than the rest of San Diego County.

- Goat Canyon in the Tijuana River Valley received two major cross border flows totaling 0.8 million gallons during the three years.

- These cross border flows into the Tijuana River are called “dry weather” flows because they occurred when there was no accompanying rain. This means they often occurred during the dry season when the river was usually not flowing; at such times (e.g., July – November 2015) the only flows in the river were the sewage-polluted cross border flows during the willow growing season.

Discussion

Clearly, the Tijuana River Valley experiences more sewage spills and spills of greater magnitude than any other site in San Diego County. The end result is that willow trees along the Tijuana River were frequently inundated with abundant fertilizer in the form of sewage, whereas those in other parts of San Diego County were not.

The data presented here confirm what most people already know – the Tijuana River is polluted compared to other rivers in the County. But the data show that the Tijuana River is orders of magnitude more polluted than other rivers. Furthermore, the data presented here are only part of the total for the Tijuana River, i.e., the reported “dry weather flows.” Additional discharges into the Tijuana River Valley occurred during wet weather, and these add a further 313 discharges into the river during the three year period (City of Imperial Beach et al 2017). When it comes to sewage contamination, the Tijuana River Valley is the hottest hot spot in San Diego County, at least an order of magnitude, and possibly 2-5 orders of magnitude, worse than any other site in San Diego County.
Figure 21. Sewage spills into the Tijuana River (above) and the rest of San Diego County (below) during the three years (2015-17).
Sewage contamination has an impact on the aquatic and riparian habitats, and also on the estuarine habitats farther downstream. In a comparison of 27 estuaries in the Southern California Bight, the Tijuana Estuary was found to have the highest total nitrogen load leading to unusually large macroalgal biomass and phytoplankton blooms, and many low dissolved oxygen events (McLaughlin et al. 2014). This finding is consistent with the idea that plants along the Tijuana River receive the most nutrient-enriched water.

The San Diego Regional Water Quality Control Board has recognized the “decades-long history of water quality issues” and has developed a Tijuana River Valley Recovery Strategy with the goal of producing “a healthy Valley, free of pollutants, where plants and animals can thrive and residents, visitors, and landowners can enjoy the unique jewel that is the Tijuana River Valley” (Tijuana River Valley Recovery Team 2012). The cities of Imperial Beach and Chula Vista and the San Diego Unified Port District are trying to use a lawsuit to compel cleanup efforts (City of Imperial Beach et al 2017).

6.3. SAN DIEGO COUNTY – A COMPARISON OF WILLOW HEIGHTS

According to the Soft Tree Hypothesis, trees growing in the Tijuana River Valley under high nutrient conditions will grow taller than those growing under normal conditions. Here I show a simple comparison of tree height at two sites. I ask:

- Do trees in Tijuana River Valley grow taller than trees outside the valley?

Methods

I compared the height of black willows growing in Unit 2 in the valley, with the height of black willows growing within the Otay River watershed. The willows at both sites were the same age – five years old. The trees in the valley were growing next to the Dairy Mart bridge, and I know their age because I have been following them since they first recruited as seedlings (Boland 2014a). I estimated the height of eight trees from a photograph taken on May 15, 2015, when the trees were five-years old, using the known height of the bridge in the photo (26 ft to the top of the railing; Figure 22). The trees outside the valley were growing in the Otay Delta Habitat Restoration Project on the Otay River, and I know when they were first planted. I measured the heights of 12 of these trees with a stiff tape measure on March 24, 2017, when the trees were also five-years old.

Results

- Five-year old black willows were 10.0 ± 0.5 m (n = 8) in the Tijuana River Valley and 6.7 ± 1.0 m (n = 12) in the Otay Delta Habitat Restoration Project, i.e., 33 ft tall and 22 feet tall, respectively (Figure 22). Although the same age, the Tijuana River willows were significantly taller than the Otay willows (Mann-Whitney U-test; Z-Score = -3.6647; p < 0.01).
Discussion
This simple comparison shows that the conditions within the Tijuana River Valley are such that willows grow taller there than in a neighboring riparian habitat on a different river. This result is consistent with the Soft Tree Hypothesis – the trees in the site receiving more water and pollution are taller than the trees in the site receiving less water and pollution (Figure 20).

Incidentally, the Tijuana River Valley willows measured here were all heavily-infested with KSHB in 2015 and many died (Figure 14B), whereas the slower growing Otay River trees have not been infested (as of March 2, 2018).

Figure 22. Five-year old black willows at Dairy Mart Bridge in the Tijuana River Valley (photo taken May 2015). Arrows indicate the average height of these trees and trees of the same species and age at the nearby Otay Delta Habitat Restoration Project on the Otay River. The Tijuana River Valley trees were considerably taller despite being the same age as those in Otay.
6.4. SAN DIEGO COUNTY – WILLOW WOOD CHARACTERISTICS

A key part of the Soft Tree Hypothesis is that willows growing in the Tijuana River Valley under high nutrient, wet conditions should have "soft" wood, and greater KSHB infestation rates than willows at other sites. Here I test this idea by asking:

- Do willows at sewage-polluted sites have lower-density wood compared to willows at less-polluted sites?
- Do willows at sewage-polluted sites have wood with higher water content compared to willows at less-polluted sites?
- Do wood density and water content correlate with KSHB infestation rate?

Methods

I chose 18 sites for comparison of polluted and less-polluted sites (Figure 23). The nine polluted sites were inside the main channels of the Tijuana River, within both Wet Forest and Dry Forest survey units. The nine less-polluted sites were outside the main channels of the Tijuana River – two were in the Tijuana River watershed and seven were in other San Diego County watersheds. Each site was in a public park with an established native riparian habitat (Table 9). I visited each at least twice during fall 2017.

At each site, I collected branch samples from live arroyo and black willow trees. Branch samples were 2.3 – 3.0 cm in diameter and approximately 23 cm long, estimated to be three to five years old, and were not damaged or infested (Figure 24). [Note: I developed this method because increment cores could not be used as few large willows were still standing in the Wet Forests and most of those were filled with KSHB tunnels.] On a walk through the forest at each site, I collected one sample per tree until I had samples from 10 arroyo willows and 10 black willows with three exceptions: I collected more samples at one site; no arroyo willows at one site because none were present; and no black willows at one site because none were present (Table 9). Branches were cut with a small pruning saw, and cut ends on the trees were immediately sprayed with TreeKote Tree Wound Dressing to reduce the risk of subsequent infection or infestation at the cut. The saw was cleaned between samples with a disinfectant wet wipe.

Branch samples were taken to the lab and stripped of their bark. I recorded the stripped weight (wet weight) and measured the volume of each sample using the water displacement method (Chave 2005, Osazuwa-Peters et al 2018). Samples were then placed in a drying oven for three days at 212–225 degrees F. After drying, I measured the dry weight of each sample, and calculated two values:

\[
\text{Density of wood (g/ml) = dry weight (g) / volume (ml)}
\]

\[
\text{Moisture content of wood (%) = [wet weight (g) – dry weight (g)] x 100 / wet weight (g)}
\]

Differences between the polluted and less-polluted sites were tested separately on the density of the wood samples and the moisture content of the wood samples for both willows species via a two-level nested ANOVA for unequal sample sizes (McDonald
2009). The null hypothesis was that there were no differences in the wood characteristics of the two sets of sites.

On a second visit to each of the less-polluted sites, willow trees were examined for KSHB infestation and KSHB-induced mortality. For the polluted sites, infestation data comes from Tables 2 and 3, and mortality data comes from Table 3 and Boland (2017b).

In addition, I collected branch samples from arroyo willows at two Orange County sites on 28 August 2017. The sites were Fairview Park and Talbert Regional Park. Fairview Park is a constructed, treatment wetland and therefore should be considered somewhat nutrient-enriched and well-watered. I am not familiar with the nutrient inputs to Talbert Regional Park, but it is downstream of the Fairview Park and appears to receive water from Fairview Park. At each site, I collected 20 branch samples in the same size range as described above and processed the samples as described above, except I determined only wood density, and not water content. During collection I noted whether or not the sampled tree was infested.

![Figure 23. Location of the Tijuana River Valley and San Diego County sites where willow branch samples were collected for analysis of wood density and water content.](image-url)
Table 9. Details of the sites used in the comparison of willow wood characteristics inside and outside the Tijuana River. An * = unit numbers; ** = arranged according to distance from the Tijuana River Valley. SALA = *Salix lasiolepis* (arroyo willow), and SAGO = *Salix gooddingii* (black willow).

<table>
<thead>
<tr>
<th>Site name</th>
<th>Watershed</th>
<th>Preserve Name</th>
<th>Dominant trees</th>
<th>Samples collected</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>INSIDE MAIN Tijuana River CHANNELS</strong>*</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Tijuana River</td>
<td>Tijuana River Valley Regional Park</td>
<td>willows</td>
<td>20</td>
</tr>
<tr>
<td>3</td>
<td>Tijuana River</td>
<td>Tijuana River Valley Regional Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>9</td>
<td>Tijuana River</td>
<td>Tijuana River Valley Regional Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>12</td>
<td>Tijuana River</td>
<td>Tijuana River Valley Regional Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>13</td>
<td>Tijuana River</td>
<td>Tijuana River Valley Regional Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
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<td>willows</td>
<td>20</td>
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</tr>
<tr>
<td>21</td>
<td>Tijuana River</td>
<td>Tijuana River Valley Regional Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td><strong>OUTSIDE MAIN Tijuana River CHANNELS</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OUT-1</td>
<td>Tijuana River</td>
<td>Border Field State Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>OUT-2</td>
<td>Otay River</td>
<td>Otay Valley Regional Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>OUT-3</td>
<td>Tijuana River</td>
<td>Pacific Gateway Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>OUT-4</td>
<td>Flordia Canyon</td>
<td>Balboa Park</td>
<td>willows</td>
<td>10</td>
</tr>
<tr>
<td>OUT-5</td>
<td>Sweetwater River</td>
<td>San Diego National Wildlife Refuge</td>
<td>Old diverse stand</td>
<td>10</td>
</tr>
<tr>
<td>OUT-6</td>
<td>San Diego River</td>
<td>Mission Valley Preserve</td>
<td>willows + cotton</td>
<td>10</td>
</tr>
<tr>
<td>OUT-7</td>
<td>San Diego River</td>
<td>Mission Trails Regional Park</td>
<td>Old diverse stand</td>
<td>10</td>
</tr>
<tr>
<td>OUT-8</td>
<td>Penasquitos Creek</td>
<td>Torrey Pines State Natural Reserve</td>
<td>willows + cotton</td>
<td>10</td>
</tr>
<tr>
<td>OUT-9</td>
<td>Penasquitos Creek</td>
<td>Los Penasquitos Canyon Preserve</td>
<td>Young diverse stand</td>
<td>10</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td></td>
<td></td>
<td></td>
<td>190</td>
</tr>
</tbody>
</table>

Figure 24. A typical collection of willow branch samples before their bark was removed. These were from arroyo willows in the Otay River Valley (OUT-2). Each sample was from a different tree and their average dimensions when the bark was removed were: diameter 2.4 cm, and length 23.2 cm.
Results

- Overall, willow wood densities ranged from 0.30 to 0.56 g/ml and water content ranged from 42% to 67%.

- **Densities of wood** samples from polluted Tijuana River and less-polluted San Diego County sites were significantly different; for both arroyo willow and black willow, wood densities were significantly lower at sites inside the Tijuana River (Figure 25; ANOVA F = 21.5; p< 0.001; and ANOVA F = 16.8; p< 0.001, respectively).

- **Water content of wood** samples from polluted Tijuana River and less-polluted San Diego County sites were significantly different; for both arroyo willow and black willow, water content was significantly higher at sites inside the Tijuana River (Figure 26; ANOVA F = 35.8, p< 0.001; and ANOVA F = 17.1, p< 0.005, respectively).

- **Black willows and arroyo willows varied in similar ways** among the sites (Figure 27); their wood densities were significantly correlated ($r = 0.886$, p < 0.01), and their wood water contents were significantly correlated ($r = 0.682$, p < 0.01). This means that the two species co-vary – at sites where SAGO had high wood density, SALA also had high wood density, and at sites where SAGO had low wood density, SALA also had low wood density. Separation of the polluted and less-polluted sites is also evident in these graphs (Figure 27).

- **KSHB infestation rates** and **KSHB-induced mortality rates** were high at the polluted sites and zero or low at the less-polluted sites (Table 10). Only one outside site showed any KSHB infestation, and that was OUT- 4 (Florida Canyon in Balboa Park), where the infestation rate was 9%.

- **Densities of wood samples from arroyo willows at the two Orange County sites** were low; they were the lowest densities measured outside the Tijuana River polluted sites (Figure 28). Infestation rates at the Orange County sites were moderate; the arroyo willows at Fairview Park were 70% infested (n = 20) and the arroyo willows at South Talbert were 55% infested (n = 20).
Figure 25. The density (g/ml) of wood samples collected at sites inside (left) and outside (right) the main Tijuana River channels. The sites are described in Table 9 and mapped in Figure 23. SALA = *Salix lasiolepis* (arroyo willow), and SAGO = *Salix gooddingii* (black willow). Data are mean ± 1 std. dev.
Figure 26. The percent water content of wood samples collected at sites inside (left) and outside (right) the main Tijuana River channels. The sites are described in Table 9 and mapped in Figure 23. SALA = Salix lasiolepis (arroyo willow), and SAGO = Salix gooddingii (black willow). Data are mean ± 1 std. dev.
Figure 27. A comparison of SAGO and SALA wood characteristics among sites. SALA = *Salix lasiolepis* (arroyo willow), and SAGO = *Salix gooddingii* (black willow).
Table 10. KSHB infestation rates and KSHB-induced mortality rates at sites where branch samples were collected. Infestation rates source = these surveys; mortality rates source = Boland (2017b) and these surveys.

<table>
<thead>
<tr>
<th>Site</th>
<th>WILLOWS</th>
<th># examined</th>
<th>% INFESTED IN 2017</th>
<th>% MORTALITY SINCE 2015</th>
</tr>
</thead>
<tbody>
<tr>
<td>INSIDE MAIN TIJUANA RIVER CHANNELS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>127</td>
<td>5%</td>
<td>67%</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>79</td>
<td>0%</td>
<td>97%</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>44</td>
<td>7%</td>
<td>42%</td>
</tr>
<tr>
<td>12</td>
<td></td>
<td>149</td>
<td>1%</td>
<td>78%</td>
</tr>
<tr>
<td>13</td>
<td></td>
<td>58</td>
<td>16%</td>
<td>41%</td>
</tr>
<tr>
<td>15</td>
<td></td>
<td>69</td>
<td>17%</td>
<td>0%</td>
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<td>17</td>
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<td>0%</td>
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<td>19</td>
<td></td>
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<td>21</td>
<td></td>
<td>76</td>
<td>86%</td>
<td>0%</td>
</tr>
<tr>
<td>MEDIAN</td>
<td></td>
<td>75</td>
<td>16%</td>
<td>41%</td>
</tr>
<tr>
<td>OUTSIDE MAIN TIJUANA RIVER CHANNELS</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>OUT-1</td>
<td></td>
<td>48</td>
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</tr>
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<td>OUT-2</td>
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<td>OUT-3</td>
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<td>79</td>
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</tr>
<tr>
<td>OUT-4</td>
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<td>82</td>
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</tr>
<tr>
<td>OUT-5</td>
<td></td>
<td>58</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>OUT-6</td>
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<td>42</td>
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<td>0%</td>
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<tr>
<td>OUT-9</td>
<td></td>
<td>72</td>
<td>0%</td>
<td>0%</td>
</tr>
<tr>
<td>MEDIAN</td>
<td></td>
<td>63</td>
<td>0%</td>
<td>0%</td>
</tr>
</tbody>
</table>

Figure 28. The density (g/ml) of arroyo wood samples collected at the two Orange County sites compared to densities collected from sites inside the Tijuana River channels (left) and outside the Tijuana River channels (right). OC-FV = Fairview Park, OC-ST = South Talbert Regional Park, and SALA = *Salix lasiolepis* (arroyo willow). Data are mean ± 1 std. dev.
Discussion
The willow wood results support the Soft Tree Hypothesis. Both arroyo willows and black willows within the sewage-polluted Tijuana River Valley forests had wood with significantly lower density and significantly higher water content than the wood at other, less-polluted sites in San Diego County. That is, trees in the Tijuana River were 'soft' compared to those at the other San Diego County sites. In addition, trees in the Tijuana River were infested with KSHB whereas those at the other San Diego County sites were not at all, or only minimally infested.

The two Orange County sites provided an additional test of the Soft Tree Hypothesis. Both sites appeared to receive urban runoff (one, Fairview Park, was a constructed treatment wetland), and both sites had moderate PSHB infestations. To be consistent with the hypothesis, wood densities of willows at these sites would have to be low, and this was the case – wood densities were similar to the Tijuana River polluted sites and lower than any of the other San Diego County sites. The Orange County results are therefore consistent with the hypothesis.

Wood density is known to vary from species to species, and willows are considered to have medium density wood, along with sycamores, pines and cottonwoods (Table 11). The willow wood densities I measured are similar to the willow wood densities given in the literature, i.e., within the 0.4 – 0.6 g/ml range. However, many of the willow wood densities, particularly from the polluted sites inside the Tijuana River Valley, were lower than the reported range in the literature.

I have added three species to Table 11 – tamarisk, mule fat and castor bean – and of these, tamarisk had the hardest wood and castor bean the softest. All three are on the list of plant hosts used by the KSHB (Eskalen 2018), however I have noticed that the KSHB infests the softer castor bean more than the harder tamarisk.

Table 11. Wood densities from the literature and this study. LIT 1* = Engineering Tool Box (2018); LIT 2** = SiMetric (2018); TRV = Tijuana River Valley; *** = Boland (unpublished data, n = 10 samples for each species).

<table>
<thead>
<tr>
<th>SPECIES</th>
<th>WOOD DENSITY (g/ml)</th>
</tr>
</thead>
<tbody>
<tr>
<td>common name</td>
<td>LIT 1*</td>
</tr>
<tr>
<td>Lignum vitae</td>
<td>Gualacum spp.</td>
</tr>
<tr>
<td>Ebony</td>
<td>Diospyros spp.</td>
</tr>
<tr>
<td>African Teak</td>
<td>Pterocarpus angolensis</td>
</tr>
<tr>
<td>Oak</td>
<td>Quercus spp.</td>
</tr>
<tr>
<td>Tamarisk</td>
<td>Tamarix ramosissima</td>
</tr>
<tr>
<td>Sycamore</td>
<td>Platanus spp.</td>
</tr>
<tr>
<td>Mule fat</td>
<td>Baccharis salicifolia</td>
</tr>
<tr>
<td>Willow</td>
<td>Salix spp.</td>
</tr>
<tr>
<td>Arroyo willow</td>
<td>Salix lasioloapis</td>
</tr>
<tr>
<td>Black willow</td>
<td>Salix gooddingii</td>
</tr>
<tr>
<td>Yellow pine</td>
<td>Pinus spp.</td>
</tr>
<tr>
<td>Cottonwood</td>
<td>Populus spp.</td>
</tr>
<tr>
<td>Bamboo</td>
<td>many genera</td>
</tr>
<tr>
<td>Castor bean</td>
<td>Ricinus communis</td>
</tr>
<tr>
<td>Balsa</td>
<td>Ochroma pyramidale</td>
</tr>
</tbody>
</table>

Table 11 consists of three parts: a list of plant species, their wood density measurements from various sources, and their general classification as soft, medium or hard, based on their wood density.
6.5. WITHIN THE TIJUANA RIVER VALLEY – WILLOW MORTALITY AND WOOD CHARACTERISTICS

The Soft Tree Hypothesis can be tested in another way. The hypothesis predicts that the forests that receive the most sewage should have the ‘softest’ trees and the most KSHB damage. Here I examine the small-scale patterns in KSHB-induced mortalities and wood structure and ask:

- What is the route of polluted flow through the Tijuana River Valley?
- Are the sites with the most KSHB damage located along this route?
- Are trees with the softest wood along this route?

Methods

Route of polluted flows. From many years of observations I can state that most of the polluted flows enter from Tijuana, go through the main forests, take the northern route through the valley, then go through the estuary to the ocean. This route is shown in red in Figure 29. The currently most polluted forests are therefore along this main route. Slightly less polluted is the forest in the southwest (Unit 22) on the Goat Canyon tributary which receives less polluted water from Goat Canyon. Forests currently receiving the least amount of pollution are those along the southern route shown in green in Figure 29. This southern route is frequently blocked by annual deposition of sediment into the Pilot Channel from Smuggler’s Gulch, and it has received only modest flows since October 22, 2004, when the river breached the berm at Hollister Bridge and flowed into the northern route.

Figure 29. The main routes taken by the polluted flows through the Tijuana River Valley. The sizes of the arrows are proportional to the volume of polluted flows.
Willow mortality and wood characteristics. For each of the survey units, I compiled willow mortality data from Tables 3 and 10, and Boland (2017b), and measured the distance from the center of the unit to the nearest main polluted flows (Figure 29). For each of the sampled trees, I used wood density and water content from Section 6.4 above, and measured the tree’s distance to the nearest main polluted flows. This distance is a rough estimate of the amount of pollution reaching each sampled tree – the greater the distance from the flow the less pollution the tree was likely exposed to.

Results

- **KSHB-induced willow mortality rates were highest** at the main pollution-carrying channels and declined significantly away from the channels ($r = 0.650$, $n = 29$, $p < 0.01$; Figure 30). Many of the units closest to the main pollution-carrying channel had KSHB-induced willow mortality rates greater than 50%, whereas all of the units farther than 200 m from the main pollution-carrying channels had rates lower than 10%.

- **Most willow deaths were near the polluted flow.** Of the 121,337 willows trees that I have estimated have been killed by the KSHB in the Tijuana River Valley since 2015 (Section 4.2), 92% (111,361) were in units that were less than 50 m from the polluted flows.

- **The density of the willow wood was lowest** at the main pollution-carrying channels and increased significantly away from the channels (Figure 31; $r = 0.267$, $n = 207$, $p < 0.01$).

- **Water content of the willow wood was highest** at the main pollution-carrying channels and declined significantly away from the channels (Figure 32; $r = 0.316$, $n = 159$, $p < 0.01$).

![Figure 30. The relationship between willow mortality within a unit and that unit’s distance from polluted flows. Each unit is represented by a single data point. The fitted line is a second-order polynomial. All data are from within the Tijuana River Valley.](image)
Figure 31. The relationship between a willow tree’s wood density and its distance from polluted flows. Both arroyo willows and black willows are included. All data are from within the Tijuana River Valley.

Figure 32. The relationship between a willow tree’s water content and its distance from polluted flows. Both arroyo willows and black willows are included. All data are from within the Tijuana River Valley.
Discussion
These within-Tijuana River Valley results support the Soft Tree Hypothesis. Forest units with the highest mortality and trees with the softest wood were in, or close to, the route of polluted river flow. Also the route through the valley taken by cross border flows from Tijuana (Figure 29) is almost identical to the maps of extensive canopy damage (Figure 13) and infestation status of each unit (Figure 2). The similarity of the maps is consistent with the idea that pollution is correlated with the KSHB attack and willow damage.

Because they receive so much polluted input, the Tijuana River Valley riparian forests are unintentionally acting as ‘treatment wetlands’, i.e., they assimilate, filter, and/or trap pollutants such as nutrients, organic matter, pathogens, heavy metals, sediment and trash from the river, thereby reducing the pollutant loads that reach the estuary and ocean. In this respect, they are unlike any other natural riparian forests in San Diego County.

It is occasionally claimed that the recent drought has stressed the trees and that is why they are susceptible to KSHB attack. This is absolutely not the case for willows in the Tijuana River Valley. Here the fastest-growing, healthiest and wettest trees that were growing in the main river channels were the most quickly infested and most quickly killed by the KSHB (Figure 30). It was actually the slowest-growing, most drought-stressed and driest trees that were growing far from the main channel that were infested the least. Therefore, the drought has not increased the likelihood of a KSHB attack, but – on the contrary – the drought has decreased the possibility of a KSHB attack on willow trees.

6.6. WITHIN A TREE –THE ORIENTATION OF TUNNELS IN A TRUNK
One component of the Soft Tree Hypothesis is that KSHB prefer ‘soft’ trees. As part of a separate study of KSHB gallery formation, I examined KSHB tunnels in an infested tree trunk. Here I present some of the results of that study to ask:

- When KSHBs tunnel into a tree do they prefer to tunnel through soft wood?

Methods
With permission of the Border Field State Park, I obtained a six-foot section of trunk from a living black willow tree that was actively infested with KSHB and cut the trunk into many slices. The tree was growing in Border Field State Park (Unit 22), 21 cm in diameter and estimated to be 12 years old. I then examined the KSHB tunnels on the faces of 19 of these slices. I used tweezers to clean out the tunnels exposed on each slice, and traced the tunnels onto an overlain sheet of transparent polypropylene film. I recorded the lengths and orientations of those tunnels, categorized them as either following the curvature of annual rings or crossing annual rings, and tallied the tunnel lengths in each of the two categories.
Results

- Figure 33 shows a typical slice of trunk and the exposed KSHB tunnels. On this face, the tunnels totaled 49.8 cm in length and 85% followed the curvature of the annual rings.
- Of the total 630 cm of tunnels measured on the 19 faces, most followed the curvature of the annual rings (median 71%); the remainder crossed annual rings (median 29%).

![Figure 33](image)

*Figure 33. A typical slice of trunk showing KSHB tunnels. The three pins indicate the KSHB holes to the exterior.*

Discussion

KSHB galleries were mainly oriented along the curvature of annual rings. This means that the beetles tended to tunnel through the softest wood, as the wood cells in the light band of an annual ring are large and thin walled (less dense), while cells in the darker band of an annual ring are smaller and thick-walled (more dense; Thomas 2014).
Therefore a typical KSHB gallery crosses only a few dark bands (Figure 34-1), while a hypothetical gallery of the same length but in a different orientation would cross many more (Figure 34-2). These observations of KSHB tunnels suggest that KSHB prefer the soft wood within a tree trunk and therefore support the Soft Tree Hypothesis even at the cellular scale.

![Figure 34. The orientation of the KSHB tunnels in wood. #1 illustrates the way KSHB tunnels usually appear, i.e., they run parallel to the annual rings and cross few annual rings (two in this example). #2 illustrates the way KSHB tunnels seldom appear, i.e., running perpendicular to the annual rings and crossing many annual rings (twelve in this hypothetical example).]
### 6.7. POLLUTION CONCLUSION

I have summarized my findings below (Table 12); all of the results are consistent with and support the Soft Tree Hypothesis.

**Table 12. Summary of support for Soft Tree Hypothesis.**

<table>
<thead>
<tr>
<th>Hypothesis component</th>
<th>Support</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>1</strong></td>
<td>When abundant sewage (or fertilizer and water) flows into a site it stimulates the growth of the trees, in this case willows. The willows grow quickly and become extremely tall, and their wood has relatively low density and high water content, i.e. they are ‘soft’ trees.</td>
</tr>
<tr>
<td>1a.</td>
<td>Sewage flows into the Tijuana River Valley were extremely large and frequent (Figure 21).</td>
</tr>
<tr>
<td>1b.</td>
<td>Five-year old black willows in the Tijuana River Valley were significantly taller than five-year old black willows in the Otay Delta Habitat Restoration Project (Figure 22).</td>
</tr>
<tr>
<td>1c.</td>
<td>Arroyo willows and black willows within the Tijuana River Valley forests had wood that was significantly less dense and of higher water content than those at other sites in San Diego County (Figures 25 and 26).</td>
</tr>
<tr>
<td>1d.</td>
<td>The two Orange County sites are considered to have high nutrient input, and the arroyo willows at these sites had the lowest densities measured outside the Tijuana River (Figure 28).</td>
</tr>
<tr>
<td><strong>2</strong></td>
<td>The KSHB prefers soft trees because it is easy for them to tunnel through and good for their fungal symbionts. When the KSHB finds a stand of soft trees its population increases rapidly and infested trees are heavily damaged.</td>
</tr>
<tr>
<td>2a.</td>
<td>Most KSHB tunnels followed the contours of annual rings rather than crossing annual rings, suggesting that the beetles prefer to tunnel through the softer wood in a trunk (Figure 33).</td>
</tr>
<tr>
<td>2b.</td>
<td>Tijuana River Valley had the softest trees and I have estimated that the KSHB population in the valley in 2015-16 was more than two billion (Boland 2017b).</td>
</tr>
<tr>
<td>2c.</td>
<td>As an indication of heavy infestation in a Tijuana River Valley tree, I determined that there were more than 26,900 KSHB holes in a single willow killed by mass attack in 2015-16 (Boland 2017b).</td>
</tr>
<tr>
<td><strong>3</strong></td>
<td>At other sites not influenced by abundant sewage, willows grow more normally and have denser wood with lower water content, i.e., they are ‘hard’ trees. The KSHB generally ignores, or has low abundances in, these hard trees.</td>
</tr>
<tr>
<td>3a.</td>
<td>Sewage spills into other rivers in San Diego County were rare (Figure 21).</td>
</tr>
<tr>
<td>3b.</td>
<td>Arroyo willows and black willows growing in other San Diego County watersheds had wood that was significantly denser and of lower water content than those growing inside the Tijuana River Valley (Figures 25 and 26).</td>
</tr>
<tr>
<td>3c.</td>
<td>KSHB was not abundant in any of the other San Diego County watersheds (Table 10).</td>
</tr>
<tr>
<td>3d.</td>
<td>KSHB was not abundant in the willow outliers growing in the dry riparian scrub of the Tijuana River Valley (Table 5).</td>
</tr>
</tbody>
</table>
There is support in the literature for components of the Soft Tree Hypothesis. Support for the “high nutrients leads to faster growth and softer wood” component comes from Hacke et al. (2010) who found that heavy fertilization led to fast-growing trees with less dense wood. Support for the idea that KSHB could show a preference for soft wood with high water content comes from Rudinsky (1962) who, in his review of the ecology of the Scolytidae, reported that growth rates of the fungi and larvae of ambrosia beetles were positively correlated with the moisture content of the host plants, and from Coyle et al (2005) who found that the eastern cottonwood, Populus deltoides, was attacked by ambrosia beetles significantly more frequently when the trees received liquid fertilizer than when they received control treatments.

Based on my findings and support in the literature I conclude that sewage pollution and KSHB abundances are linked and I have proposed the Soft Tree Hypothesis as the mechanism by which they are linked. I have focused on ‘sewage as fertilizer’ because it makes sense and the tests I have done support it. However, I recognize that there may be alternative hypotheses that link sewage pollution and KSHB abundances. Here I suggest two possibilities. **The first alternate hypothesis involves ethanol.** Waterlogged trees emit ethanol as a by-product of anaerobic respiration (Pezeshki and DeLaune 2012) and ethanol is known to be an attractant to some ambrosia beetles (Hulcr et al. 2011, Kelsey 1994). It is therefore possible that the most waterlogged and polluted trees in the Wet Forests were producing the most ethanol and were consequently the most attractive to the KSHB. But researchers have found that both PSHB and KSHB have an aversion to ethanol, at least the ultrahigh release ethanol used in their experimental traps, and they have recommended against using ethanol as a lure (Dodge et al 2017). **The second alternative hypothesis involves a chemical attractant associated with sewage.** It is possible that the KSHB are attracted to trees that have taken up a chemical from the sewage but I do not know what this chemical attractant would be. The Tijuana River flows contain a host of industrial wastes, pesticides and metals, including: Aldrin, Lindane, Chloroform, DDT, Dieldrin, Heptachlor, Benzene, Chlorobenzene, Toluene, 2-4-dinitrotoluene, Nitrophenol and Phenol (City of Imperial Beach et al 2017). Both alternative hypotheses are possible and worth thinking about, but I have no evidence to support either.
7. A PREDICTIVE MODEL OF KSHB INFESTATION

Here I expand the Soft Tree Hypothesis into the Soft Tree Model and show that it can explain the observed patterns within the Tijuana River Valley and can be used to make predictions about the likely impacts of the KSHB in other sites.

7.1. THE SOFT TREE MODEL – WITHIN THE TIJUANA RIVER VALLEY

When viewed through the lens of the Soft Tree Model, the progression of the KSHB infestation in different parts of the Tijuana River Valley make sense (Figure 35).

According to the Soft Tree Model:

**Wet Forests.** The Wet Forests were infested first, fastest, and most severely because they received plentiful nutrients from polluted flows and therefore had soft wood, i.e., their wood had low density and high water content. Now recovery is underway but I would expect the KSHB to return to these forests when the trees are larger because they have soft wood.
Dry Forests. The Dry Forests were attacked later, more slowly, and less severely than wet forests because they received infrequent polluted flows and therefore had intermediate density wood. It remains to be seen how the infestation will play out in the Dry Forests.

Outlier Willows. Willows in the drier Riparian Scrub habitat were only lightly attacked because they received very little water and no nutrients from polluted flows, and therefore had relatively hard, dry wood. The same rationale applies to mule fat, which is abundant in the Riparian Scrub. I expect outlier willows and mule fat to remain largely unaffected by the KSHB.

In short, the Soft Tree Model helps to make sense of the spatial and temporal variation in KSHB-infestation rates seen among different sites within the Tijuana River Valley.

7.2. THE SOFT TREE MODEL – PREDICTIONS IN SAN DIEGO COUNTY

Here I apply the reasoning from the Soft Tree Model to make predictions about the KSHB infestation in other natural riparian habitats in San Diego County (Figure 36).

Sites similar to the Wet Forests in the Tijuana River Valley. As far as I know there are no other super-polluted riparian sites in San Diego County – the Wet Forests in the Tijuana River Valley are uniquely well fertilized. I predict that no other site will experience the fast, destructive KSHB mass attack that resulted in many willow deaths, and the fast vegetation recovery that followed.

Sites similar to the Dry Forests in the Tijuana River Valley. Forests that receive infrequent polluted flows or whose wood has intermediate density and moisture content could fall into this category. In these sites a KSHB infestation is likely and the infestation is likely to be slow and drawn out, and it may not result in much structural damage to trees or extensive mortality. I expect the sites where the KSHB already occurs to fall into this category, i.e., “patchy areas along the San Luis Rey River, Escondido Creek and Sweetwater River” (Eric Porter, USFWS personal communication 6 March 2018). Furthermore, I suggest examining these coastal riparian sites:

- Peñasquitos Creek in Torrey Pines State Nature Reserve (OUT-8) because the arroyo willows collected there had wood characteristics most similar to wood from within the Tijuana River Valley (Figure 25 and 26); and
- Florida Canyon (OUT-4) because the KSHB infestation rate was 9% (Table 10).

Sites similar to the Outlier Willows in the Tijuana River Valley. I expect that most of the riparian habitats in San Diego County will fall into this category; the trees rarely receive polluted flows, their wood is relatively dense and dry, and they are unlikely to be attacked substantially by the KSHB. The information that is currently available suggests that these lower-risk sites are all of the main riparian areas along:

- Otay River;
- Sweetwater River;
- Mission Trails Park on the San Diego River;
- Los Peñasquitos Canyon Preserve;
- High elevation rivers and streams; and
- Riparian trees that are outliers, i.e., growing in drier conditions away from main river flows.

![Figure 36: The Soft Tree Model predicting the likely course of events in the natural riparian sites of San Diego County.](image)

**New restoration sites.** Some restoration professionals are so concerned that their willows will be attacked by the KSHB that they are not planting willows in riparian restoration sites. The research described in this report suggests that this approach is misguided – their concern should be less about willows and more about nutrient conditions at their restoration location. It is perfectly acceptable for managers to plant willows in restoration sites in any part of San Diego County so long as the water quality at that location is known to be good. The Otay Delta Habitat Restoration Project is an example of a thriving restoration project. It was started in 2012, it is less than 4 km from the heavily-infested Tijuana River Valley, and it has many willows that are all growing well and appear to be uninfested.
The Soft Tree Model is a simple representation of what I consider the most important processes at play. I present the model because it helps us understand the patterns seen in Tijuana River Valley and allows us to predict the likely course of events in other sites. The model will require further testing and improvement as new data comes to light, but it is a good initial framework to build upon.

7.3. RISK ASSESSMENT – LOCATION, LOCATION, LOCATION

Here I take a slightly different approach to understanding the threat posed by the KSHB to trees in San Diego County, and the threat posed by the SHB infestation in general.

Up to now, risk of SHB infestation has been based on a list of plant species that the KSHB and PSHB have been found to use as hosts (Eskalen 2018). The logic has been that: if a given tree species is on that list, then all individuals of that species, at all locations are at risk of being killed by a SHB infestation. McPherson (2016) used this logic to determine that 26.8 million urban trees were at risk in southern California and Ekalen and Lynch (2017) repeated this number in their LA Times op-ed article. Many common native species are on the list, therefore park and wildland managers are concerned because, by this reckoning, all riparian sites in southern California are at risk, and they all have the same high risk.

But now with the results from this report we can refine that risk (Figure 37). In this new refinement, not all locations have the same high risk. The first component of risk – layer one – is the presence of a susceptible plant species, e.g., arroyo willow. Now we add a second component of risk – layer two – which is the distribution of sewage pollution or overwatering and over-fertilization in the same area. Tijuana River would be a big red spot on this layer because of excessive sewage pollution, and perhaps one or two other small areas would be included. Together the layers define the areas of highest risk – only those small areas of overlap of the two layers.

This refinement ratchets down the threat level for most riparian sites. Now only the areas that have both susceptible plant species and excessive sewage spills are at high risk of infestation; all of the other areas are at lower risk. This refinement also suggests places to look to for new KSHB attacks – the subset of sites with susceptible plant species and excessive sewage spills or excessive overwatering and over-fertilizing.
Figure 37. A Risk Diagram illustrating KSHB-risk in a hypothetical region of San Diego County. The first layer is the hypothetical distribution of a susceptible plant species, e.g., arroyo willow. The second layer is the hypothetical distribution of sewage pollution or overwatering and over-fertilization in the same area. Together the layers define areas of highest risk, i.e., the small area of overlap of the two layers.

There may be no other natural area in southern California like the Tijuana River because it is so severely polluted, but other trees growing in artificially wet, high-nutrient conditions are also at high risk of infestation. Such conditions might possibly be found at treatment wetlands, golf courses, and urban parks.

Pollution or high nutrient conditions may also occur on a small scale, such as at the outfall of a storm drain. The patchy distribution of KSHB-infested trees in San Diego County may be because there is high-nutrient input at those patchy sites. In Florida Canyon, willows with signs of infestation were within 200 m of a storm drain outfall whereas trees farther away had no signs of infestation (as of 4 January 2018). In the San Luis Rey River, infested willows were immediately downstream of a storm drain and a nursery (personal observations). The possible links between KSHB infestations and high-nutrient sources need to be further considered and investigated.
As for even further refinement of risk level, I think two more factors that increase the risk of KSHB infestation could be added: (1) perennialization of stream flows in naturally intermittent sites, and (2) presence of a high “fuel load” at a site, or the amount of suitable wood per unit area. These factors may eventually be added as third and fourth layers on Figure 37, further refining the identification of locations likely to be at high risk of heavy KSHB infestation. I am continuing to look into these factors.

8. CONCLUSIONS
This report offers a broad ecological perspective on the KSHB infestation in the Tijuana River Valley. It documents the progression of the infestation in the riparian habitats and the recovery of vegetation in the heavily KSHB-damaged units. It also introduces a new hypothesis for why the Tijuana River Valley has been more impacted than other sites, and turns that hypothesis into a predictive model for other natural riparian habitats in San Diego County.

The research reported here can serve to update our thinking about the KSHB infestation in southern California, particularly along the lines described below.

- **The Tijuana River Valley is a special case.** We can update the notion that other sites are going to be attacked as severely as the Tijuana River forests. The extreme sewage pollution and softness of the trees make the Wet Forests in the Tijuana River unique in the region. The fast invasion by the KSHB, the collapse of the willow canopy and the many willow deaths seen in the valley should not be expected to occur elsewhere.

- **Post-infestation survival.** We can update the old notion that an infested tree is as good as dead. For arroyo willow, black willow, and mule fat, it is now clear that not all KSHB-infested individuals die. Many persist with low-level infestation (e.g., Dry Forest willows), and many survive a heavy infestation and send up resprouts from their damaged stumps (Wet Forest willows). Some individuals, as documented here, can survive an infestation and heal KSHB wounds (willows, mule fat).

- **Infestation as a disturbance.** We can end the sometimes-expressed old notion that the KSHB destroyed the Tijuana River forests. This characterization is an inaccurate exaggeration. Ecologically, the KSHB impacts in the wet forests can be likened to a disturbance such as wildfire, after which there is post-disturbance recovery. The post-disturbance succession and recovery is now well underway and the recovering habitats provide many ecological benefits.

- **Reduced level of risk.** When assessing risk, it no longer makes sense to assume that all individuals of a given tree species are equally susceptible to infestation at all locations. The correlation between sewage pollution and infestation reported here allows a more refined assessment of risk and more focused predictions as to
where infestations are most likely to occur. Now, trees growing in excessively wet, nutrient-rich conditions are most at risk, whereas others growing elsewhere are at much lower risk. High-risk sites might include treatment wetlands or small, localized forest stands exposed to high-nutrient runoff. This more refined assessment of risk should allow for more effective management and distribution of limited resources.

The research reported here supports the following management actions.

- **Continue to plant willows in new riparian restoration sites if the water quality is good.** The correlation of infestation with sewage pollution detailed in this report suggests that willows can and should be planted in restoration sites so long as the water quality is known to be good.

- **Treat invasives.** Arundo and castor bean are the invasive species of greatest concern in the Wet Forests of the Tijuana River Valley. Both have benefited from the KSHB-induced damage to the willow canopy and are abundant in the recovering forest. Both, particularly arundo, degrade the forest and reduce the value of the habitat for other native species. The best way for managers of parks in the valley to manage the KSHB problem is to focus on these invasives and treat them with herbicides.

- **Do not over-fertilize or overwater.** I have based the Soft Tree Model on my work on the KSHB in willows in natural riparian habitats. But the concept of increased KSHB-infestation risk with over-fertilizing and overwatering should apply to KSHB in other tree species in urban and agricultural settings as well. Park managers and city managers can lower the risk of KSHB infestation by not over-fertilizing or overwatering their landscape ornamentals, particularly during summer.

9. ACKNOWLEDGEMENTS

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10. LITERATURE CITED


