If you build it, they will come: Rapid colonization by dragonflies in a new effluent-dependent river reach

Michael T Bogan [Corresp., 1] , **Drew Eppehimer** [1] , **Hamdhani Hamdhani** [1, 2] , **Kelsey Hollien** [1]

[1] School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, United States

[2] Department of Aquatic Resources Management, University of Mulawarman, Samarinda, Indonesia

Corresponding Author: Michael T Bogan
Email address: mbogan@email.arizona.edu

Background Aquatic ecosystems are greatly altered by urban development, including the complete loss of natural habitat due to water diversions or channel burial. However, novel freshwater habitats also are created in cities, such as effluent-dependent streams that rely on treated wastewater for flow. However, it is unclear how diverse these novel ecosystems are, or how quickly aquatic species are able to colonize them. In this study, we (1) quantify odonate (Insecta, Odonata) colonization of a novel effluent-dependent river reach, (2) examine how drying events affect odonates in these novel habitats, and (3) explore whether effluent-dependent streams can support diverse odonate assemblages.

Methods We conducted monthly odonate surveys at three sites along the Santa Cruz River (Tucson, Arizona, USA) between June 2019 and May 2020. One site was in a long-established effluent-dependent reach (flowing since the 1970s) that served as a reference site and two sites were in a newly-established reach that began flowing on June 24, 2019 (it was previously dry). We compared odonate species richness, assemblage composition, and colonization patterns across these reaches, and examined how these factors responded to flow cessation events in the new reach.

Results Seven odonate species were observed at the study sites in the new reach within hours of flow initiation, and species rapidly continued to arrive thereafter. Within three months, species richness and assemblage composition of adult odonates were indistinguishable in the new and reference reaches. However, drying events resulted in short-term and chronic reductions in species richness at one of the sites. Across all three sites, we found over 50 odonate species, which represent nearly 40% of species known from the state of Arizona.

Discussion Odonates were surprisingly diverse in the effluent-dependent Santa Cruz River and rapidly colonized a newly established reach. Richness levels remained high at study sites that did not experience drying events. These results suggest that consistent discharge of high-quality effluent into dry streambeds can be an important tool for promoting urban biodiversity. However, it remains to be seen how quickly and effectively less vagile taxa (e.g. mayflies, caddisflies) can colonize novel reaches. Effluent-dependent urban streams will always be highly managed systems, but collaboration between ecologists and urban planners could help to maximize aquatic biodiversity while still achieving goals of public safety and urban development.

1 If you build it, they will come: rapid colonization by
2 dragonflies in a new effluent-dependent river reach

5 Michael T. Bogan[1], Drew E. Eppehimer[1], Hamdhani[1,2], Kelsey D. Hollien[1]

7 [1] School of Natural Resources and the Environment, University of Arizona, Tucson, AZ, USA

8 [2] Department of Aquatic Resources Management, University of Mulawarman, Samarinda,

9 Indonesia

11 Corresponding Author:

12 Michael Bogan[1]

13 1064 E. Lowell Street Room N326, Tucson, AZ, 85716, USA

14 Email address: mbogan@arizona.edu

17 Abstract

18 Background

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20 natural habitat due to water diversions or channel burial. However, novel freshwater habitats also

21 are created in cities, such as effluent-dependent streams that rely on treated wastewater for flow.

22 However, it is unclear how diverse these novel ecosystems are, or how quickly aquatic species

23 are able to colonize them. In this study, we (1) quantify odonate (Insecta, Odonata) colonization

24 of a novel effluent-dependent river reach, (2) examine how drying events affect odonates in these

25 novel habitats, and (3) explore whether effluent-dependent streams can support diverse odonate

26 assemblages.

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30 Arizona, USA) between June 2019 and May 2020. One site was in a long-established effluent-

31 dependent reach (flowing since the 1970s) that served as a reference site and two sites were in a

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47   colonized a newly established reach. Richness levels remained high at study sites that did not

48   experience drying events. These results suggest that consistent discharge of high-quality effluent

49   into dry streambeds can be an important tool for promoting urban biodiversity. However, it

50   remains to be seen how quickly and effectively less vagile taxa (e.g. mayflies, caddisflies) can

51   colonize novel reaches. Effluent-dependent urban streams will always be highly managed

52   systems, but collaboration between ecologists and urban planners could help to maximize aquatic

53   biodiversity while still achieving goals of public safety and urban development.

54

55

56   **Introduction**

57   Urbanization is generally associated with dramatic alterations of natural ecosystems and

58   subsequent losses of biodiversity (Grimm et al., 2008). Urban ecosystems frequently have

59   reduced species richness and are more homogeneous when compared to natural systems (e.g.

60   McKinney, 2006; Ball-Damerow et al., 2014; Villalobos-Jimenez et al., 2016). Freshwater

61   ecosystems are particularly affected by urbanization. For example, the physical structure of water

62   bodies is often modified to allow development close to water while trying to reduce flood risk

63   (Stein et al., 2013; Steele & Heffernan, 2014). Additionally, runoff from impervious surfaces

64   alters flow regimes and hydroperiods, and often delivers a complex combination of excess

65   nutrients and contaminants (Walsh et al., 2005). Furthermore, many urban water bodies simply

66   disappear when they are hidden under concrete (Napieralski & Carvalhaes, 2016) or completely

67   dry up due to water withdrawals (Webb et al., 2014).

68   However, urbanization also can lead to the creation of novel anthropogenic water bodies,

69   such as canals, stormwater runoff basins, and ponds in urban parks. In some cases, these novel

70   habitats may become important reservoirs of biodiversity, supporting unique communities or

71   species of conservation concern (Chester & Robson, 2013; Lambert & Donihue, 2020). Aquatic

72   species must be able to colonize these novel habitats via flow connections with adjacent water

73   bodies or overland dispersal. But how quickly do species find these habitats and successfully

74   colonize them? And are the communities that develop therein unique, or are they similar to those

75   from natural habitats or older urban habitats? Novel urban waters could provide an intriguing

76   window into community assembly processes, but these systems were mostly ignored by

77   ecologists for much of the 20th century (Grimm et al., 2008). One challenge is that rigorous study

78   of these systems requires coordination between urban planners and ecologists, which is not

79   common practice (Hunter & Hunter, 2008; Lambert & Donihue, 2020).

80   Effluent-dependent streams, which rely on discharge from wastewater treatment plants
81   for their baseflow, are increasingly common in urban areas (Hamdhani et al., 2020). In fact,
82   effluent discharge in arid regions has restored flow to some urban streams that were dry for
83   decades because of groundwater overdraft and upstream diversions (Webb et al., 2014). Despite
84   decades of research regarding water quality in these effluent-dependent streams (Brooks et al.,
85   2006), only recently have we begun to study their potential biodiversity value (Bischel et al.,
86   2013; Luthy et al., 2015; Peschke et al., 2019). Wastewater treatment plants often discharge
87   effluent into riverbeds simply because there is nowhere else to put it—and it is not customary to
88   notify ecologists when discharge begins or ends (Brooks et al., 2006; Hamdhani et al., 2020).
89   In this study, we document colonization and community assembly of dragonflies and
90   damselflies (hereafter, odonates) in a new effluent-dependent reach of the Santa Cruz River in
91   Tucson, AZ (USA). We compare community structure in this new reach with that from a nearby
92   effluent-dependent reach that had been flowing for decades. This rare study opportunity arose
93   because urban planners publicly announced they would begin discharging effluent into the new
94   reach several months prior to flow initiation. We asked three primary research questions: (1) how
95   quickly do dragonflies and damselflies (odonates) colonize novel habitat?, (2) can effluent-
96   dependent streams support diverse odonate assemblages?, and (3) how do drying events in these
97   novel habitats affect odonates? The third question arose because occasional periods of
98   infrastructure or channel maintenance can lead to cessation of discharge in effluent-dependent
99   streams.
100   We focused our surveys on odonates for several reasons. First, they tend to be strong
101   dispersers and are known to colonize novel anthropogenic habitats (Corbet, 1999; Prescott &
102   Eason, 2018; Cerini et al., 2019). Second, diverse assemblages of odonates have been found in
103   urban water bodies in many cities (Willigalla & Fartmann, 2012; Goertzen & Suhling, 2015;
104   Holtmann et al., 2018). Third, odonates can be visually surveyed and easily identified to species.
105   Fourth, odonates can be used for biotic indices that assess environmental conditions and
106   ecological integrity in streams (e.g. Chovanec et al., 2015; Golfieri et al., 2016; Vorster et al.,
107   2020). Finally, they are conspicuous, colorful, and charismatic, which are useful traits for
108   environmental education and ecotourism (Lemelin, 2007; Clausnitzer et al., 2017). These
109   potentially important cultural and economic links to urban residents could inspire more
110   collaborations between planners and ecologists to study novel water bodies.
111
112

113   **Materials & Methods**
114   *Study system*
115   Historically, the Santa Cruz River had alternating sections of perennial, intermittent, and
116   ephemeral flow throughout its course, from its headwaters in southern Arizona and northern
117   Sonora (Mexico) to its confluence with the Gila River near Phoenix, Arizona (Webb et al.,
118   2014). However, diversions and groundwater pumping caused 99% of the river to become
119   ephemeral by the 1940s; groundwater levels have fallen as far as 80 meters below the riverbed in

120   Tucson (Carlson et al., 2011). Discharge of effluent (treated municipal wastewater) into the dry
121   riverbed has occurred in two reaches of the lower Santa Cruz River since at least the 1970s,
122   restoring perennial surface flow in those sections (Figure 1). Although water quality in these
123   effluent-dependent reaches was initially very poor, treatment plants were upgraded in 2013 and
124   have produced high quality tertiary-treated effluent ever since (Sonoran Institute, 2017).
125   In 2019, a third effluent-dependent reach of the river was created in downtown Tucson as
126   part of the Santa Cruz River Heritage Project (Figure 1). The purpose of this new reach is to
127   enhance recharge of the local aquifer and create a new recreational, ecological, and economic
128   feature in the city (Tucson Water, 2020). For this new reach, effluent is piped from treatment
129   plants in the north to an outfall location 10 km south of the two established reaches (Figure 1).
130   Flow began in this new reach on 24 June 2019, but occasional flow reduction or cessation events
131   occurred in the following months as operational issues arose or infrastructure upgrades were
132   needed (Supplemental Figure 1). In May 2020, effluent releases ceased in the new reach to allow
133   for sediment removal from the flood control channel, but there are plans to resume flow later in
134   the year (Tucson Water, 2020). The nearest naturally perennial stream to all three effluent-
135   dependent reaches is Sabino Canyon, a canyon-bound headwater stream 23 km to the east. The
136   nearest low gradient naturally perennial rivers are the San Pedro and Gila Rivers, >70 km to the
137   east and northeast, respectively.
138
139   *Sampling design*
140   We selected three study sites on the Santa Cruz River to survey for adult odonates: (1) a
141   reference site on one of the long-established effluent-dependent reaches, (2) a site near the
142   effluent outfall of the new reach (Starr Pass Blvd), and (3) a site 2km downstream of the outfall
143   (Cushing St) near the end of the new reach (Figure 1). The reference site was selected because it
144   supports the highest diversity of aquatic invertebrates (including larval odonates) known from
145   various biomonitoring sites along the established reaches (Sonoran Institute, 2017; Eppehimer et
146   al., 2020).
147   At each of the three survey sites, we established 400m long transects to survey for adult
148   odonates. This length of transect was chosen to incorporate multiple distinct habitat units in one
149   transect to maximize the potential for odonate species richness. In each site, there was at least
150   one riffle, one pool, one run, and one backwater (i.e. off-channel isolated pool), and usually at
151   least two of each, but we did not quantify the exact proportion of each habitat unit within sites.
152   Each of the three sites was located within flood control levees, so while there was a small
153   amount of sinuosity in the actively flowing channel at each site, meandering was limited by
154   levees (Figure 1).
155   From 1 June 2019 to 10 May 2020, we conducted monthly 90-minute adult odonate
156   surveys along each transect, always between 11:00 and 15:00 hours, under partly sunny to clear
157   skies, with minimal winds and warmer temperatures (>15ºC). Although ≥80% of odonate species
158   in a site can be detected with shorter surveys (e.g. 30 minutes), additional survey time allows
159   greater detection of rare species (Bried et al., 2012). During each survey, the same observer

160 (MTB) slowly walked along and in the water through the 400m reach while identifying adult
161 odonates by sight and occasionally using a hand-net. Voucher photos for each species observed
162 at each site were taken using a digital camera (Canon Powershot SX60 with 65x optical zoom)
163 and shared with regional odonate experts for taxonomic confirmation (Bailowitz et al., 2015).
164 Additionally, during each survey, each odonate species observed was scored into one of three
165 abundance categories: (1) *rare*: <10 individuals seen and no breeding activity observed; (2)
166 *uncommon*: 10 to 100 individuals and breeding activity observed; (3) *common*: >100 individuals
167 with breeding activity observed. There were no instances where less than 10 individuals of a
168 species were seen but breeding was observed among those few individuals. During each survey
169 across the 10 months, larval exuviae and teneral adults were also sought to confirm that a
170 successful reproduction event for a given species observed as adults at a given site.
171   Surveys at each site generally were conducted on consecutive days within a month, but
172 occasionally occurred as far as 4 days apart so that weather conditions were optimal for each
173 survey. In addition to monthly surveys at all sites, biweekly surveys were conducted at one site
174 (Starr Pass Blvd) on the Heritage reach. These additional surveys were intended to detect new or
175 rare species as soon as possible when they colonized this newly flowing reach, because biweekly
176 surveys can reveal species that monthly surveys fail to capture (Bried et al., 2007). During each
177 survey, we recorded weather conditions and measured air temperature and a suite of
178 physiochemical water quality factors (e.g. temperature, conductivity, pH, dissolved oxygen)
179 during each monthly survey.
180   Finally, to create a list of all odonate species currently known from the lower Santa Cruz
181 River in the metro Tucson region, and provide context for the results of our surveys, we
182 compiled records from regional experts (Rich Bailowitz, Doug Danforth, and Pierre Deviche,
183 pers. comm.), a regional field guide (Bailowitz et al., 2015), and online databases [Arizona
184 Dragonflies (azdragonfly.org), iNaturalist (inaturalist.org), and Odonata Central
185 (odonatacentral.org)].
186
187 *Data analyses*
188   Survey data were used to calculate species richness values for each site by month. These
189 data were plotted to examine changes in species richness over time at the reference and newly
190 flowing sites, and to see how richness values responded to occasional stream drying events. We
191 also use the Hill numbers approach (Chao et al., 2014) to extrapolate the full species richness of
192 each site if additional sampling events were to occur. Estimates of the first Hill number ($q = 0$ for
193 species richness) were made with the package iNEXT (version 2.0.19) in R Version 3.5.3 (Hsieh
194 et al., 2016). To ensure fair comparisons, we used only monthly survey data to generate richness
195 estimates, excluding the additional biweekly survey data from the Starr Pass site.
196   Differences in adult odonate assemblage composition across all sites and survey dates
197 were visualized with non-metric multidimensional scaling (NMS) in PC-ORD Version 5 (MJM
198 Software, Gleneden Beach, Oregon) using Sorensen distance as the measure of community
199 dissimilarity (McCune et al., 2002). For ordination analyses, we used survey abundance codes (0

200 = undetected, 1 = rare, 2 = uncommon, 3 = common) so that species with higher abundances
201 would have more influence on the ensuing ordination than rare species. To assess which species
202 were most influential in the observed ordination patterns, we calculated linear correlation values
203 between species abundances and ordination axes. We also calculated linear correlation
204 coefficients between measured environmental variables and ordination axes. Finally, we
205 examined temporal trends in abundance for each species in the newly flowing reach to visualize
206 colonization patterns in this novel habitat.
207
208

209 **Results**
210 Within 6 hours of flow initiation in the newly flowing sites (on 24 June 2019), 7 odonate
211 species (*Enallagma civile*, *Erythrodiplax basifusca*, *Ischnura demorsa*, *Orthemis ferruginea*,
212 *Pachydiplax longipennis*, *Sympetrum corruptum*, and *Tramea onusta*) were observed mating and
213 ovipositing (Figure 2). Additional species quickly arrived in the following weeks, and species
214 richness at the Starr Pass site reached or exceeded that of the reference site within 3 months
215 (Figure 3). Species richness values at the Cushing site, which experienced several drying events
216 during the course of the study, remained lower than Starr Pass but exhibited similar seasonal
217 trajectories (i.e. lower in winter months, higher in spring and summer months). Species richness
218 in both of the newly flowing sites plummeted when flow ceased in May 2020 (Figure 3). The
219 Hill numbers estimation of species richness found almost complete overlap in 95% confidence
220 intervals for the Starr Pass and reference sites, but values at Cushing were predicted to remain
221 lower even with numerous additional monthly sampling events (Figure 4). Across all sites and
222 dates, we observed 50 of the 53 odonate species currently known from the entire lower Santa
223 Cruz River, including 44 species at the reference site, 43 species at Starr Pass, and 28 species at
224 Cushing (Table 1). We confirmed successful recruitment via larval exuviae and/or teneral adults
225 for 35 species at the reference site (80%), 28 species at Starr Pass (65%), and 17 species at
226 Cushing (61%).
227 Assemblage composition between Star Pass and the reference site converged within 3
228 months (Figure 5; NMS results: stress = 0.14, final instability > 0.00001, cumulative R^2 = 0.84, p
229 = 0.004). Surveys from the reference site generally occupied the lowest region of NMS axis 2,
230 remained stable through summer 2019, and were characterized by high abundances of several
231 damselflies (e.g. *Argia sedula*, *Hetaerina americana*, *Argia pallens*, *Telebasis salva*) and
232 dragonflies (e.g. *Anax junius*, *Libellula saturata*) (Table 2). Assemblages at all three sites moved
233 to right along NMS axis 1 for the winter months, exhibiting lower abundances of monsoonal or
234 summer dragonflies (e.g. *Orthemis ferruginea*, *Pantala flavescens*, *Tramea lacerata*) and two
235 species of damselflies (*Ischnura demorsa*, *Enallagma civile*) (Table 2). Overall, the reference
236 site exhibited less variation in assemblage composition through time than the two newly flowing
237 sites (Figure 5). Both water and air temperatures were strongly negatively correlated with NMS
238 axis 1 (r = -0.77 and -0.73, respectively); all other measured variables were only weakly
239 correlated with ordination axes (i.e. -0.5 < *r* < 0.5).

240   Of all species known to have breeding populations in the reference site, only 6 failed to
241 become established at the new sites within 10 months (Table 1). We also found 7 species in the
242 newly flowing sites that were absent from the reference site; however, 6 of these were rare and
243 were never observed breeding. Only one species of damselfly (*Argia extranea*) became
244 established at the new sites but was never observed at the reference site. Several different
245 colonization modes were observed among the species documented in the newly flowing sites
246 (Figure 6). Some species colonized on the first day of flow initiation, quickly established robust
247 breeding populations, and remained abundant through the course of the study, while other
248 species colonized rapidly but exhibited seasonal variation in abundances thereafter. Yet other
249 species took a few months to colonize and remained at relatively low abundances, which varied
250 seasonally. Finally, some species were vagrants that only appeared once or twice and did not
251 appear to have breeding populations in any of the sites (e.g. *Libellula luctosa*).
252
253

254 **Discussion**

255   Dragonflies and damselflies colonized a new effluent-dependent reach of the Santa Cruz
256 River incredibly fast, with 7 species arriving on the first day of flow, each of which successfully
257 established breeding populations. This was especially surprising because flow began during the
258 hottest and driest part of the year, and many aquatic insects in the region only disperse aerially
259 after summer rains begin (Bogan & Boermsa, 2012). Within three months, species richness
260 values of adult odonates were equal in the new reach and the long-established reach more than
261 10 km away. Although previous studies have found that odonates can disperse tens to hundreds
262 of kilometers across arid landscapes (Suhling et al., 2017), the speed at which species arrived
263 here was still impressive. It often takes >2-3 months for odonates to find novel water bodies,
264 with lower colonization rates usually observed at more isolated waters (McCauley, 2006; Bogan
265 & Boersma, 2012; Groover, 2017).
266   Both the rapid colonization rates and the high overall species richness values observed
267 were surprising. Across all dates, we found 50 odonate species in our three effluent-dependent
268 study sites, which is >35% of the species known from the entire state of Arizona (Bailowitz et
269 al., 2015). For comparison, only 58 species were found in the entire Grand Canyon (Stevens &
270 Bailowitz, 2009), an area is many times larger than our study area and encompasses many desert
271 and montane springs, streams, and rivers. Odonates thrive in warm environments (Corbet, 1999),
272 so the warm air temperatures and mild winters of southern Arizona may be partly responsible for
273 the high odonate diversity we observed. Although nearly 100 odonate species are known from
274 Pima County, where the lower Santa Cruz River is located, the county hosts aquatic habitats in
275 areas ranging from hot deserts (<275 m asl) to cold montane forests (>2,700 m asl) (Bailowitz et
276 al., 2015). So, the fact that over half of the species known in the county were found in a single,
277 effluent-dependent urban river—an artificial ecosystem—is remarkable.
278   We could not compare our findings to those from naturally perennial rural reaches of the
279 river outside of Tucson because none remain (Webb et al., 2014). However, nearly 70% of

280 published studies report some reduction in odonate species richness in urban cores, with species
281 losses often being related to pollution issues (Villalobos-Jimemez et al., 2016). Interestingly,
282 many of these studies reported reductions in odonate richness in ponds rather than rivers. For
283 example, a study from Kentucky (USA) found no difference in odonate diversity between urban
284 and rural streams, but urban ponds were less diverse than rural ponds (Prescott & Eason, 2018).
285 The high diversity we observed in the Santa Cruz River also could be due in part to the relative
286 lack of industrial pollution (e.g. factories) and high-density development in Tucson.
287 Furthermore, the warm water temperature regimes of effluent-dependent streams (Bischel et al.,
288 2013) may be ideal for the growth and development of odonates. In fact, some odonates we
289 observed, such as the Neotropical bluet (*Enallagma novaehispaniae*), are tropical species that
290 have only colonized Arizona in the past decade (Bailowitz et al., 2015). To date, they have only
291 been found in effluent-dependent streams, whose warm waters may mimic their tropical home
292 streams (Bailowitz & Deviche, unpubl. data). Similar patterns have been observed in central
293 European cities, where southern Mediterranean odonate species have been documented
294 expanding their range northward (Willigalla & Fartmann, 2012).
295   Although we found diverse odonate assemblages in the tertiary-treated wastewater of the
296 Santa Cruz River, this does not mean that wastewater is always beneficial to odonates. Untreated
297 wastewater (i.e. raw sewage) generally reduces the abundance and diversity of odonates
298 (Henriques-de-Oliveira et al., 2007). In fact, within wastewater treatment facilities, odonate
299 species richness and abundance increase dramatically from initial wastewater lagoons to
300 subsequent treatment ponds with better water quality (Catling, 2005). Given these sensitivities to
301 organic pollution, odonates are often used as bioindicators (Júnior et al., 2015; Mendes et al.,
302 2017; Miguel et al., 2017). Some species are known to tolerate inputs of raw or poorly treated
303 sewage (e.g. *Anax junius*, *Enallagma civile*: Catling, 2005). Unfortunately, there are no historical
304 odonate data available from our reference site on the Santa Cruz River when it was receiving
305 lower quality effluent (1970s to 2013). However, studies from the upper Santa Cruz River, 60
306 km to the south of our study sites, may be informative. Boyle & Fraleigh (2003) found only six
307 odonate genera in the upper Santa Cruz River when it was fed by low quality effluent in the
308 1990s. In contrast, we found 27 genera in the lower Santa Cruz. These findings suggest that
309 wastewater treatment plant upgrades are at least partly responsible for the high odonate diversity
310 we observed.
311   One risk of living in effluent-dependent streams is that drying events can occur when
312 infrastructure fails (e.g. pipes break) or discharge is paused to allow for channel maintenance
313 (Tucson Water, 2020). In naturally flowing streams, increased frequency or duration of drying
314 events usually causes reductions in the diversity of aquatic invertebrates (Datry et al., 2014;
315 Stubbington et al., 2017). For odonates, drying events eliminate larvae of most species, and these
316 losses will have cascading impacts on adult populations (McPeek, 2008). In our study, we
317 observed much higher richness of adult odonates in the site that dried infrequently versus the one
318 that dried multiple times (Figure 3). However, short periods of flow cessation (e.g. hours to a
319 couple days) did not seem to have a dramatic effect, as odonate larvae likely found refuge in

320 damp algal mats or remnant pools (Stubbington et al., 2017). To maximize odonate diversity in
321 effluent-dependent streams, managers should minimize the duration and frequency of shutoff
322 events that result in stream drying, and avoid shutting off flow during the hottest, driest times of
323 the year, when in-stream refuges would quickly disappear.
324   Although recurring drying events are likely the primary cause of reduced species richness
325 observed at the Cushing site, that site's species richness trajectory was lower than that of the
326 nearby Starr Pass even before drying began (Figure 3). One potentially important factor that we
327 did not measure is the structural complexity of riparian vegetation. Neither site had well-
328 developed mesophilic riparian vegetation; however, the Starr Pass site included the effluent
329 outfall, where discharge flowed for ~60 meters across a vegetated terrace (Figure 2) before
330 dropping into the active river channel. This area may have provided an enhanced number of
331 perches or structural complexity that were 'attractive' to odonates (e.g. Samways & Steytler,
332 1996). After several months of flow, however, the complexity of riparian vegetation seemed to
333 increase at both sites as wetland plants colonized the river (e.g. *Typha* sp.: Figure 1). Future
334 studies of new effluent-dependent stream reaches should quantify riparian vegetation complexity
335 before and after flow begins.
336   One major limitation of our study is that there are no historical data available from when
337 our study reaches were naturally perennial in the early 1900s. We do not know what the diversity
338 or composition of odonates was in the natural Santa Cruz River. However, studies from other
339 regions suggest that the lower Santa Cruz River, as diverse as it is today, may still lack species
340 which were present historically. For example, the odonate fauna of California today is more
341 homogeneous than it was 100 years ago, with sharp losses of habitat specialist species in
342 urbanized areas (Ball-Damerow et al., 2014). Additionally, we know that vegetation along the
343 Santa Cruz River has changed dramatically in the last century, with the elimination of floodplain
344 forests and the extirpation of many native plant species (Webb et al., 2014). Odonate diversity
345 generally increases with the diversity and complexity of riparian vegetation in both urban and
346 rural habitats (Samways & Steytler, 1996; Goertzen & Suhling, 2013; Dutra & De Marco, 2015).
347 Thus, historic vegetation losses along the Santa Cruz River may have led to the extirpation of
348 some odonate species that were historically present.
349   Finally, it is likely that odonate recolonization of the Santa Cruz River is still happening.
350 The river was dry for many decades in all reaches, even in the long-established effluent-
351 dependent reaches, water quality has only been high since 2013. So, the river has only been
352 'palatable' to many odonate colonizers for a few years. Further, the nearest naturally perennial
353 stream is a small headwater stream over 20 km away, and the nearest perennial rivers of similar
354 size to the Santa Cruz are over 70 km away. Rare and stochastic colonization events from these
355 distant source streams and rivers may take time and likely are still occurring. For example, the
356 dragonfly *Stylurus plagiatus* is known from natural rivers in Arizona (Bailowitz et al., 2015), but
357 it was not known from the effluent-dependent Santa Cruz River until we found larvae and adults
358 in two reaches in 2019 (Bogan, unpubl. data). Even over the relatively short duration of the
359 current study, we observed that colonization rate and success varied greatly among odonate

360   species (Figure 6). Repeat surveys and long-term studies along the Santa Cruz River will be
361   invaluable for documenting colonization processes in this novel urban ecosystem.
362
363

364   Conclusions

365   Odonates were surprisingly diverse in the effluent-dependent Santa Cruz River,
366   supporting nearly 40% of all species known in the state of Arizona. Additionally, numerous
367   odonate species rapidly colonized a newly-established reach of the river. In the absence of
368   prolonged drying events, assemblage composition in the new sites was indistinguishable from
369   the reference site within three months. These results suggest that consistent discharge of high-
370   quality effluent into dry streambeds can be an important tool for promoting urban biodiversity,
371   especially in arid and semi-arid regions (Bischel et al., 2013; Luthy et al., 2015). However, it
372   remains to be seen how quickly and effectively less vagile taxa (e.g. mayflies, caddisflies) will
373   colonize novel reaches, and this topic deserves further study. Furthermore, our study ended
374   because flow ceased in the newly-established reach to allow for sediment removal and flood risk
375   mitigation (Tucson Water, 2020). This dramatic ending highlights the fact that urban streams
376   will always be highly managed systems. But with collaboration between ecologists and urban
377   planners, these management activities can be modified to maximize aquatic biodiversity while
378   still achieving public safety goals (Hunter & Hunter, 2008). Collaborations between ecologists
379   and planners also would enhance ecotourism opportunities and better connect urban residents
380   with their local ecosystems (Lemelin, 2007; Clausnitzer et al., 2017). The 20th century was a
381   difficult time for urban streams and the species that resided in them, but there is hope for better
382   ecological outcomes by the end of the 21st century.
383
384

385   Acknowledgements

386   The study reaches of the Santa Cruz River are part of the traditional homeland of the Tohono
387   O'odham, and the river runs through portions of both the Tohono O'odham and Pascua Yaqui
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395
396

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Figure 1

Map with photos of study sites along established and new effluent-dependent reaches of the Santa Cruz River.

Map of ephemeral and effluent-dependent perennial reaches of the lower Santa Cruz River in and near Tucson, Arizona, USA. Two separate reaches in the northern part of the region have been flowing since the 1970s, while the Heritage Project established a new effluent-dependent reach in the southern part of the region in June 2019. Photos illustrate the three study sites: (A.) a reference site on a long-established portion of the river, and two sites on the new reach at (B.) Cushing Street and (C.) Starr Pass Boulevard.

Perennial effluent
Ephemeral runoff
* Survey location

N

4km

Flow began 1970s

Flow began 2019

* A.

* B.
* C.

A.

B.

C.

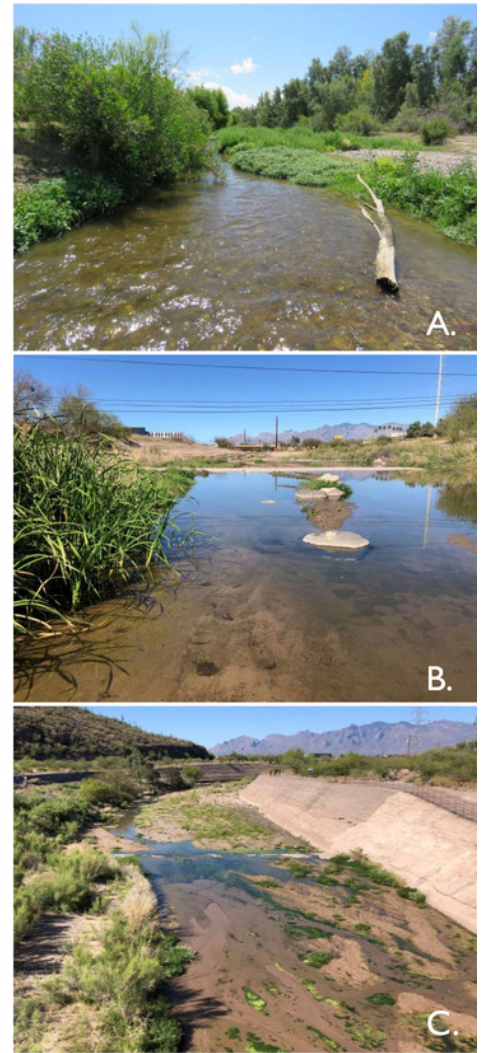
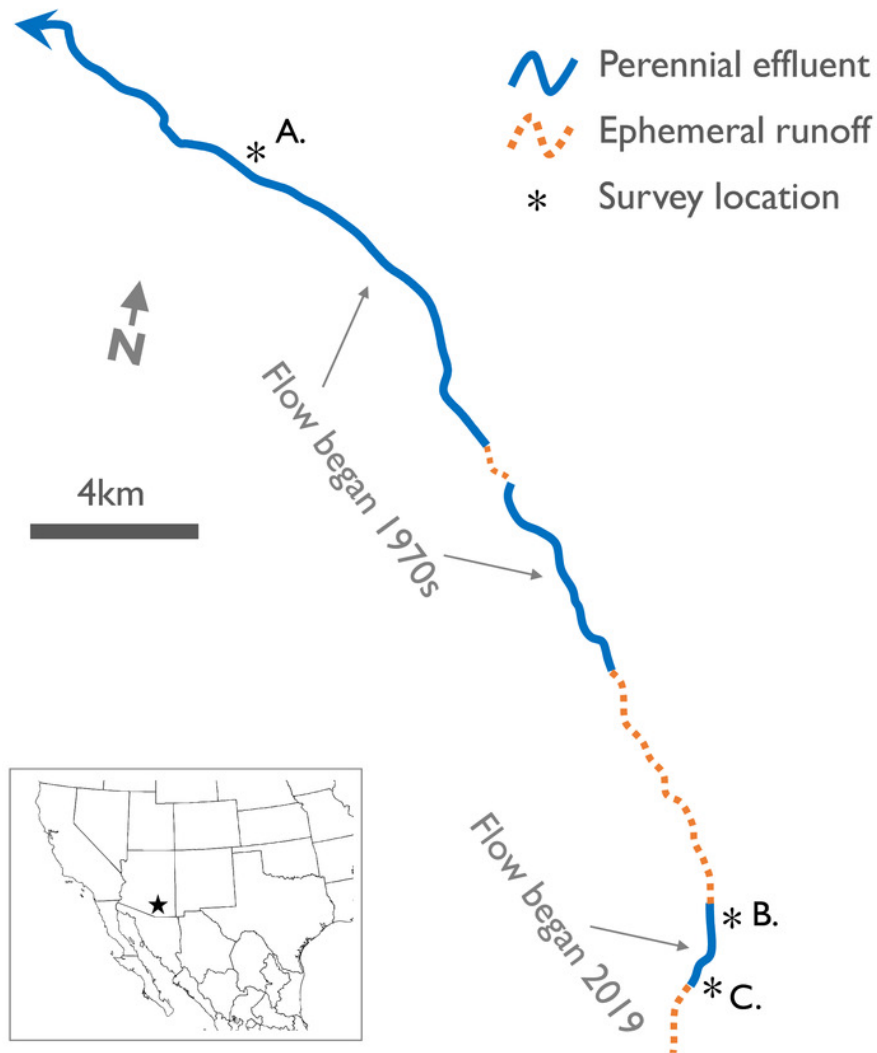



Figure 2

First day of flow initiation and early odonate colonists in the Santa Cruz River

Photos from the first day that treated effluent was released into the previously-dry channel of the Santa Cruz River as part of the Heritage Project in Tucson, AZ [A]. Odonate colonists arriving within 6 hours of flow initiation included Red Saddlebags (*Tramea onusta*) and Roseate Skimmers (*Orthemis ferruginea*) [B], Blue Dashers (*Pachydiplax longipennis*) [C], and Familial Bluets (*Enallagma civile*) [D].

Figure 3

Odonate species richness across the 10-month study period at three sites along the effluent-dependent Santa Cruz River

Odonate species richness values observed during monthly surveys at two sites (Starr Pass Blvd and Cushing St) sites in the newly flowing reach of the Santa Cruz River, and at a reference reach downstream that has been flowing with effluent since the 1970s. Small grey arrows indicate times when a site dried up due to reduced effluent discharge into the new reach.

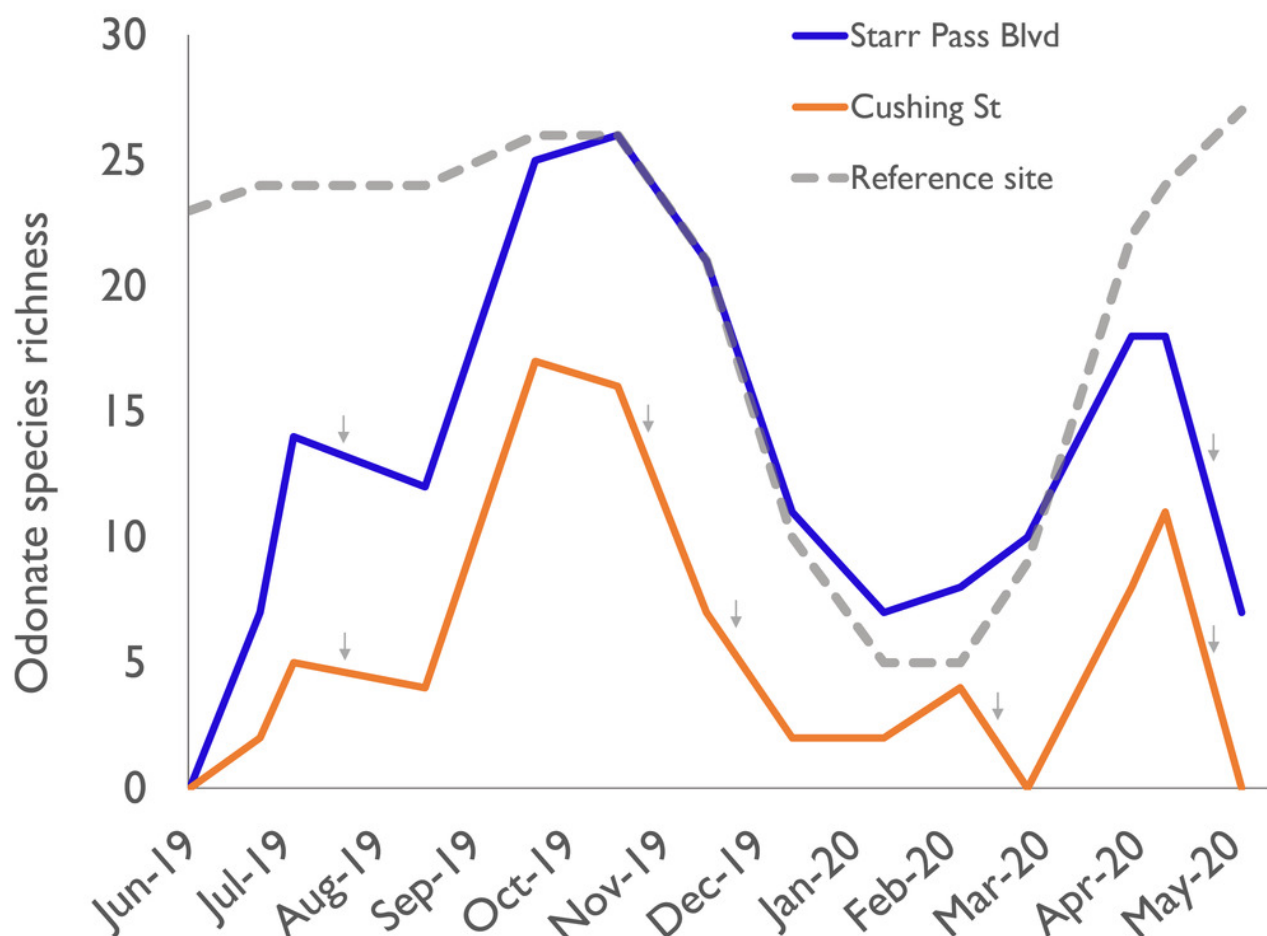



Figure 4

Interpolated and extrapolated values for cumulative odonate species richness at three sites along the effluent-dependent Santa Cruz River

Cumulative odonate species richness by site after each monthly sampling event (solid lines: interpolated) and projected values (dashed lines: extrapolated) if additional sampling months were to occur, as predicted using Hill numbers for species richness (q=0). Shaded areas represent a 95% confidence interval.

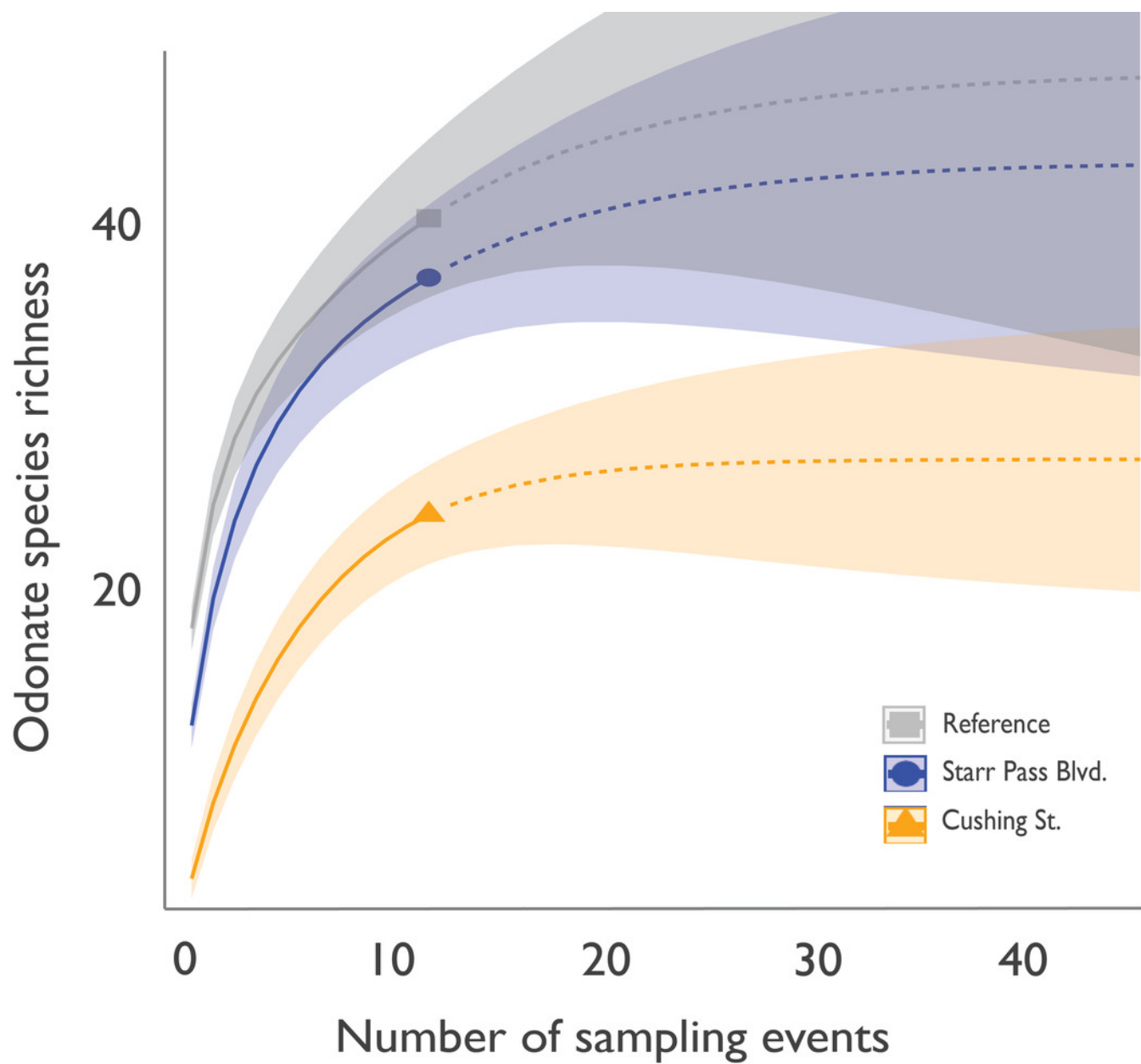



Figure 5

Ordination plot of changes in odonate assemblages over time at three study sites along the effluent-dependent Santa Cruz River

NMS ordination plot visualizing odonate assemblage composition from all surveys at the three study sites along the Santa Cruz River from June 2019 to April 2020. Vectors link subsequent surveys at each site and illustrate trajectories of compositional changes through time.

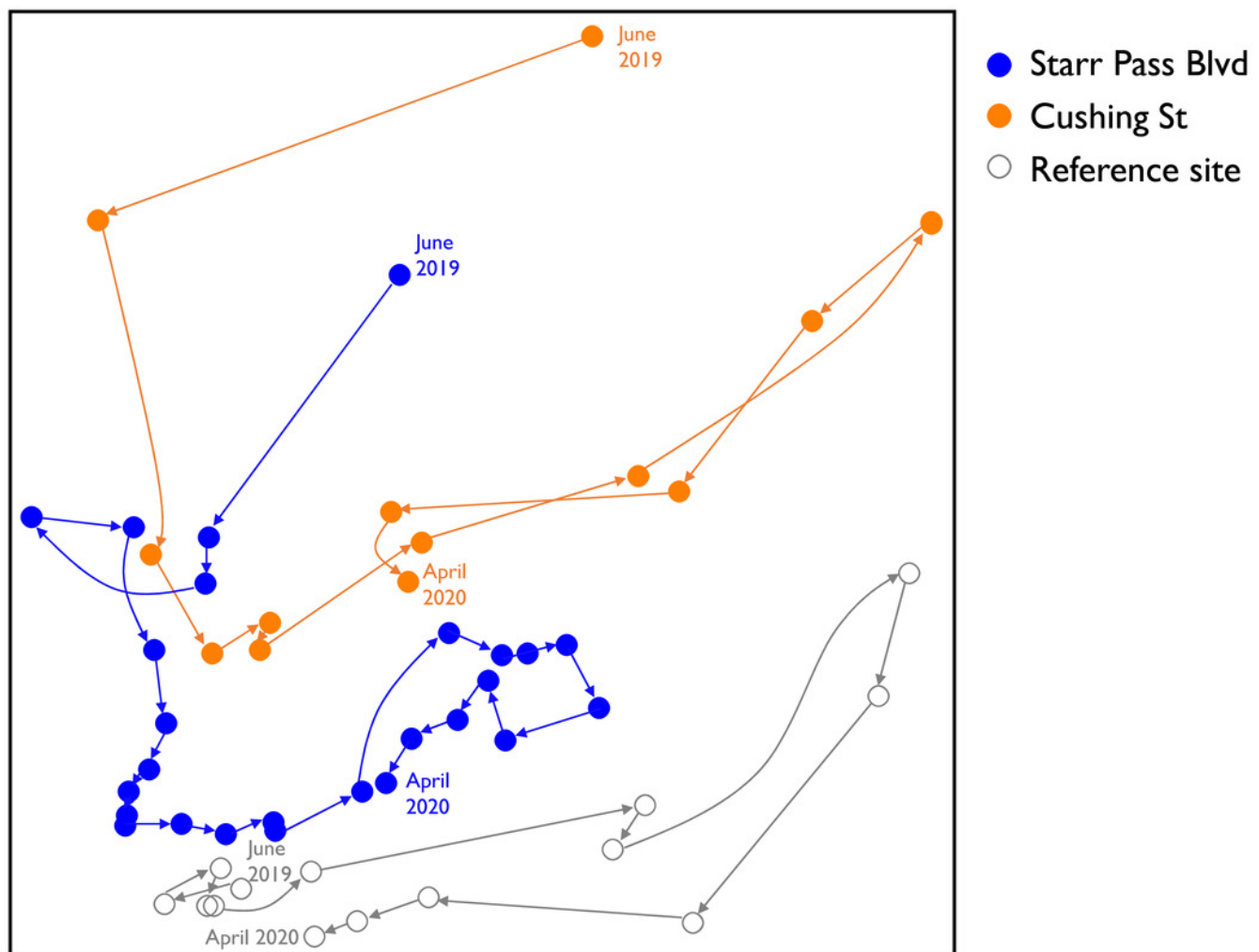
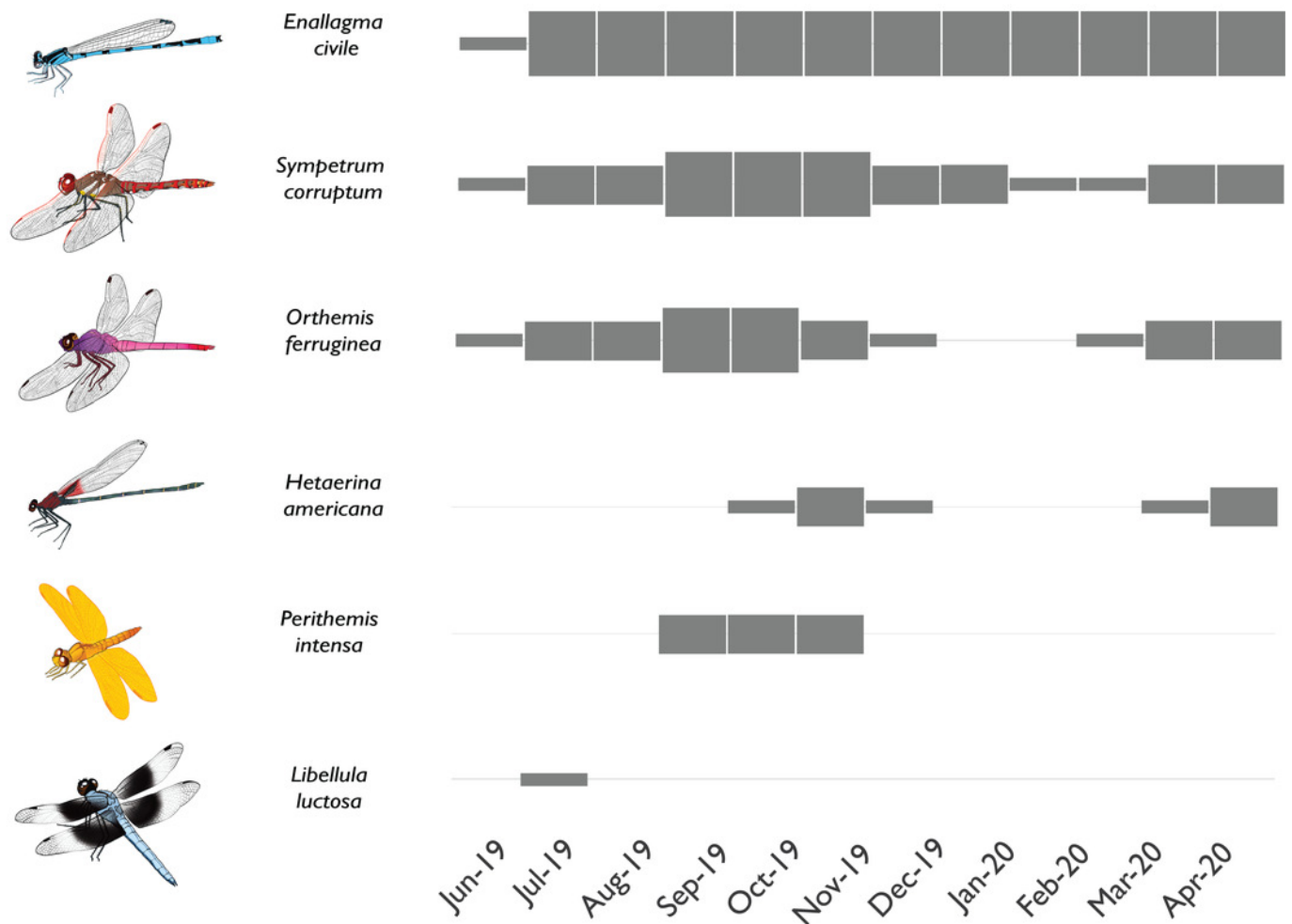



Figure 6

Phenology of selected odonate colonists in a newly-flowing reach of the effluent-dependent Santa Cruz River

Phenology plot illustrating the presence and abundance of different odonate species through time in the newly flowing Heritage reach of the Santa Cruz River (thin grey box = rare; medium gray box = uncommon but breeding; thick grey box = common and breeding). Some species rapidly colonized the new reach quickly and were abundant through the study (e.g. *Enallagma civile*) or were at least abundant during warmer weather (e.g. *Sympetrum corruptum*, *Orthemis ferruginea*). Other species took longer to colonize and had limited seasons of adult flight activity (e.g. *Hetaerina americana*, *Perithemis intensa*). Other species were vagrants that appeared once or twice but failed to establish populations (e.g. *Libellula luctosa*).

Odonate species encountered at three sites along the effluent-dependent Santa Cruz River

Each species was scored into one of three abundance categories for each site: (1) rare: <10 individuals seen; (2) uncommon: 10 to 100 individuals; (3) common: >100 individuals. We observee evidence of reproduction success at a given site (e.g. teneral adults) for species classified as common or uncommon, but not for those classified as rare. Species marked with an asterisk were not found during the surveys for this study, but have been documented from adjacent reaches of the Santa Cruz River in existing databases (e.g. iNaturalist, Odonata Central).

Suborder	Family	Species	Reference	Starr Pass Blvd	Cushing St
Anisoptera	Aeshnidae	*Anax junius*	Common	Common	Common
		Anax walsinghami	Rare	Rare	
		Rhionaeschna multicolor	Common	Rare	Rare
	Gomphidae	*Erpetogomphus compositus*	Common	Rare	
		Erpetogomphus lampropeltis		Rare	
		Progomphus borealis	Common	Common	Rare
		Stylurus plagiatus*			
	Libellulidae	*Brachymesia furcada**			
		Brechmorhoga mendax	Uncommon	Uncommon	
		Dythemis nigrescens	Uncommon	Rare	
		Erythemis collocata	Common	Common	Uncommon
		Erythemis vesiculosa	Rare		
		Erythrodiplax basifusca	Common	Common	Uncommon
		Libellula forensis	Rare		
		Libellula luctuosa	Rare		Rare
		Libellula pulchella	Rare	Rare	Rare
		Libellula saturata	Common	Common	Uncommon
		Macrothemis inacuta	Uncommon	Uncommon	
		Orthemis ferruginea	Common	Common	Common
		Pachydiplax longipennis	Common	Common	Rare
		Paltothemis lineatipes		Rare	
		Pantala flavescens	Common	Common	Uncommon
		Pantala hymenaea	Uncommon	Uncommon	Uncommon
		Perithemis intensa	Common	Common	Rare
		Plathemis lydia*			
		Pseudoleon superbus	Uncommon	Uncommon	Rare
		Sympetrum corruptum	Common	Common	Common
		Sympetrum illotum		Rare	
		Tramea lacerata	Common	Common	Uncommon
		Tramea onusta	Uncommon	Common	Uncommon
Zygoptera	Calopterygidae	*Hetaerina americana*	Common	Uncommon	
	Coenagrionidae	*Argia extranea*		Common	
		Argia immunda	Uncommon	Rare	
		Argia moesta	Common	Rare	Rare
		Argia nahuana	Uncommon	Common	Rare
		Argia pallens	Common	Common	Uncommon
		Argia sedula	Common	Common	Uncommon
		Argia tezpi	Rare	Rare	
		Argia translata	Uncommon		

	Enallagma basidens	Common		
	Enallagma civile	Common	Common	Common
	Enallagma eiseni	Rare		
	Enallagma novaehispanae	Common	Rare	
	Enallagma praevarum	Common	Common	Rare
	Enallagma semicirculare	Rare		
	Hesperagrion heterodoxum		Rare	
	Ischnura cervula	Uncommon	Uncommon	
	Ischnura demorsa	Common	Common	Common
	Ischnura hastata	Common	Common	Uncommon
	Ischnura ramburii	Common	Common	Uncommon
	Telebasis salva	Common	Common	Common
Lestidae	*Archilestes californicus*	Rare	Rare	
	Lestes alacer		Rare	Rare

Correlations between odonate species abundances and NMS ordination axis values

Pearson's correlation coefficients between abundances of individual odonate species and NMS axis 1 and 2. Species only showed strongly negative correlation values (<-0.5) with either or both axes; no strongly positive correlation values (>0.5) were observed.

Species	Axis 1 r	Species	Axis 2 r
Orthemis ferruginea	-0.79	*Argia sedula*	-0.78
Pantala flavescens	-0.69	*Hetaerina americana*	-0.67
Ischnura demorsa	-0.68	*Argia pallens*	-0.67
Tramea lacerata	-0.61	*Anax junius*	-0.66
Libellula saturata	-0.60	*Telebasis salva*	-0.64
Erythrodiplax basifusca	-0.57	*Libellula saturata*	-0.61
Erythemis collocata	-0.56	*Enallagma novaehispanae*	-0.61
Tramea onusta	-0.51	*Sympetrum corruptum*	-0.60
Enallagma civile	-0.51	*Perithemis intensa*	-0.58
Anax junius	-0.50	*Ischnura ramburii*	-0.58
		Argia moesta	-0.53