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Does sexual dimorphism predispose dioecious riparian trees to extreme sex ratio imbalances under climate change?

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Abstract:	Environmental changes have resulted in significant declines in native riparian forests that are comprised largely of dioecious tree taxa, including boxelder and iconic cottonwood / willow gallery forests. Dioecious species may be especially vulnerable to the effects of climate change given that they often exhibit skewed sex ratios that are reinforced by physiological and morphological specialization of each sex to specific microhabitats. A comprehensive data synthesis suggests that male individuals of boxelder and cottonwood taxa have a higher representation on dry microhabitats than females and are less physiologically sensitive to increased aridity than co-occurring females. Consequently, extreme male-biased sex ratios are possible under future climate conditions that could reduce population fitness below a sustainable threshold. Riparian willows, on the other hand, generally do not express obvious sexual dimorphism in habitat preference or physiological sensitivity to aridity. Thus, it is unclear whether climate change will impact population structure of willows in ways that parallel other dioecious riparian tree taxa. Future riparian tree restoration programs should aim to maintain future sex ratio balance that maximizes population fitness under projected hydro-climatological conditions. Recent advances in genomics will likely provide the critical tools for early sex determination in pre-reproductive trees across riparian tree species such that sex ratio balance could be targeted during initial stages of restoration, along with adaptations for drought tolerance and other key traits that are essential for survival under future conditions.

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Dr. Russell Monson
Editor and Chief (Plant Physiological and Ecosystem Ecology)

Dear Dr. Monson,
Please find submitted a copy of our manuscript “Does sexual dimorphism predispose dioecious riparian trees to extreme sex ratio imbalances under climate change?" for publication in *Oecologia*. The manuscript is intended for the **Ehleringer Special Issue** and we have made every effort to conform to the style of the journal.

The paper asks the question: Are dioecious riparian tree species (including cottonwoods, willows and boxelder) especially vulnerable to the effects of climate change given that they often exhibit skewed sex ratios, reinforced by physiological and morphological specialization of each sex to different microhabitats. Although, there have been many papers published on sexual dimorphism in relation to environment, we believe this paper strikes new ground for a number of reasons. For one, to our knowledge, we report the most comprehensive synthesis to date on sexual dimorphism of key ecophysiological trait characteristics in response to aridity-induced stress in these important foundation tree species. Second, the paper merges the reported trait characteristics with sex ratio evolution theory to evaluate how the sexes may or may not differentially respond to the predicted effects of climate change. And finally, we evaluate the potential cascading consequences skewed sex ratios may have on ecosystem community structure and stability of highly valued riparian ecosystems.

If you have any questions regarding the submission of this manuscript feel free to contact me at any time. My co-authors and I look forward to your response to our efforts.

Sincerely

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Does sexual dimorphism predispose dioecious riparian trees to extreme sex ratio imbalances under climate change?

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Running headline: Sexual dimorphism in dioecious tree species

Abstract

Environmental changes have resulted in significant declines in native riparian forests that are comprised largely of dioecious tree taxa, including boxelder and iconic cottonwood / willow gallery forests. Dioecious species may be especially vulnerable to the effects of climate change given that they often exhibit skewed sex ratios that are reinforced by physiological and morphological specialization of each sex to specific microhabitats. A comprehensive data synthesis suggests that male individuals of boxelder and cottonwood taxa have a higher representation on dry microhabitats than females and are less physiologically sensitive to increased aridity than co-occurring females. Consequently, extreme male-biased sex ratios are possible under future climate conditions that could reduce population fitness below a sustainable threshold. Riparian willows, on the other hand, generally do not express obvious sexual dimorphism in habitat preference or physiological sensitivity to aridity. Thus, it is unclear whether climate change will impact population structure of willows in ways that parallel other dioecious riparian tree taxa. Future riparian tree restoration programs should aim to maintain future sex ratio balance that maximizes population fitness under projected hydro-climatological conditions. Recent advances in genomics will likely provide the critical tools for early sex determination in pre-reproductive trees across riparian tree species such that sex ratio balance could be targeted during initial stages of restoration, along with adaptations for drought tolerance and other key traits that are essential for survival under future conditions.

Keywords: riparian cottonwoods, riparian willows, boxelder, leaf gas exchange, sex ratio bias

Introduction.

Native riparian tree species in the western United States are among the most charismatic, widely distributed and important foundation species throughout their range. These iconic species, including *Populus* spp. (cottonwoods), *Salix* spp. (willows) and *Acer negundo* Sarg (boxelder) are highly valued for providing habitat for rare and threatened taxa, recreation and aesthetics, among many other services. However, native riparian forests are among the most threatened of all forest types in North America (Stromberg 1993). Over the last century, riparian gallery forests in the arid and semiarid regions of North America (primarily comprised of cottonwoods and willows) have been in decline due to a combination of intensive land development and grazing, alterations to fluvial hydrology and non-native species invasions (Stromberg et al. 2007; Hultine et al. 2010; Merritt and Poff 2010; Nippert et al. 2010; Stella et al. 2010). These ongoing impacts to native riparian vegetation are being amplified by the effects of climate change that are bringing warmer temperatures, higher evaporative demand, earlier snow melt, and subsequently reduced stream discharge in a region where net primary productivity and biodiversity are already limited by seasonal aridity (Leung et al. 2004; Stewart et al. 2004; Barnett et al. 2008).

Despite a considerable phylogenetic separation, riparian cottonwoods and willows share many ecological, morphological and physiological traits with boxelder. Among these shared traits is a dioecious reproductive strategy that is relatively rare among plant species. Dioecy occurs in only 6% of all angiosperm species but is approximately distributed across half of all angiosperm families (Renner and Ricklefs 1995; Heilbuth 2000). Dioecy is commonly associated with the evolution of sexual dimorphism in secondary sex characteristics (i.e., differences between the sexes in characteristics that do not involve sexual organs). Boxelder, in particular, has served as a model system for understanding the potential causes and consequences of sexual dimorphism in secondary sex characteristics in trees. Previous studies have identified sexual dimorphism in habitat preference, physiology and growth (Dawson and Ehleringer 1993; Ward et al. 2002; Dawson et al. 2004; Hultine et al. 2008). Results from these studies have yielded strong evidence that male and female individuals have evolved specific functional traits that predispose each sex to specialize in habitats varying in resource availability and competition (Hultine et al. 2016, reviewed in detail in the following section). Conversely, sexual dimorphism in secondary traits is not as well established in riparian cottonwoods or willows as in boxelder, but some evidence has emerged showing disparate secondary trait characteristics between the sexes.

This review explores whether dominant riparian woody species in the western United States and Canada share similar dimorphic traits in habitat preference, physiology and sensitivity to stress. We evaluate whether the effects of climate change and resource limitations related to human caused alterations to the water cycle differentially impact male and female individuals in similar (or non-similar) ways across species. We begin by reviewing known patterns of sexual dimorphism in model boxelder that shares similar dimorphic patterns with other dioecious species, including those occurring outside of riparian zones (namely with males occurring in higher frequencies in more stressful habitats). We focus on the influence of photosynthetic gas exchange and growth patterns on the overall population sex ratios of woody riparian species. We then explore potential impacts of climate change on sex-specific patterns of gas exchange and growth and evaluate the extent to which population sex ratios may be altered under future climate conditions. Finally, we review the potential impacts of skewed sex ratios on population fitness and the capacity of these tree species to provide the foundation for riparian community structure and ecosystem function. We present two inter-related hypotheses related to sexual dimorphism in riparian cottonwood / willow taxa as follows: 1) as with boxelder, male individuals express a higher physiological stress tolerance to water limitations and aridity than co-occurring females, and 2) forecasted increases in aridity (i.e., increased vapor pressure deficit, reduced stream discharge and subsequent water availability) over the next century will differentially impact male and female individuals, such that some populations may develop highly biased male sex ratios.

Sexual dimorphism in boxelder

Perhaps no plant organism presents a better example of sexual dimorphism in habitat preference, physiology and growth than boxelder, which occurs in the intermountain west of the United States. Boxelder displays strong female-biased sex ratios in habitats with high water availability, such as along perennial streams, whereas sex ratios tend to be inverted in continuously drier margins of boxelder's habitat with increasing male bias (Dawson and Ehleringer 1993; Ward et al., 2002). How these sex ratio patterns develop is not well understood. However, there is no known sex switching in boxelder and it does appear that male-biased sex ratios in dryer habitats may evolve from greater incidence of drought induced mortality in female trees than in males (Dawson and Ehleringer 1993). Therefore, male-biased sex ratios in dry sites can be attributed at least partially to post-germination physiological processes such as intersexual differences in sensitivity to soil water deficits.

Patterns of spatial segregation of the sexes in boxelder tend to mirror physiological differences between sexes such that females express traits that maximize resource uptake in high-resource environments at the expense of lower resource-use efficiency in stressful environments (Dawson and Ehleringer 1993; Dawson and Geber 1999; Dawson et al. 2004;

Hultine et al. 2007; 2008). For example, female boxelder trees in high water locations display higher rates of leaf gas exchange, higher intercellular CO_2 concentrations (c_i), higher leaf nitrogen concentrations, and higher rates of above ground growth than males (Dawson and Ehleringer 1993; Ward et al. 2002; Dawson et al. 2004; Hultine et al. 2008). However, where (and when) water is less available, the patterns of gas exchange and growth converge between genders (Ward et al. 2002; Dawson et al. 2004), or becomes male biased (Dawson et al. 2004). Likewise, female boxelder trees are apparently more sensitive to the effects of warm temperature anomalies, even under well-watered conditions (Hultine et al., 20013, 2016). The higher heat-induced stress in females relative to males suggests that the effects of climate change may yield higher rates of mortality in females, resulting in extreme male-biased sex ratios even if hydrological conditions remain constant (Hultine et al. 2013; 2016).

Sex ratio patterns in riparian cottonwoods and willows

The plant family Salicaceae is ubiquitous in riparian ecosystems of western North America, but contains only two genera: *Populus* (i.e. cottonwoods, poplars, aspens) and *Salix* (i.e. willows) (Landis et al. 2003). There are 36 recognized species in the genus *Populus*, and perhaps as many as 500 species in the genus *Salix*, with diversity hot spots in the north temperate and subarctic regions of the world. Individual plants in both genera are almost always dioecious with only rare exceptions where plants are monoecious (Rowland et al. 2002). As with many dioecious species, sex ratio biases often occur in populations of both *Populus* and *Salix* species. Dioecious plants that display skewed sex ratios tend to have male individuals that outnumber females in a given population (Field et al. 2012; Sinclair et al. 2012), and species in the genus *Populus* generally follow this pattern, at least in populations where sex ratio biases are present (Letts et al. 2008;

Xu et al. 2008; Petzold et al. 2013; Lei et al. 2017). However, sex ratios in the genus *Salix* are more often skewed towards females than males, and these female biased sex ratios are consistent across a broad range of habitats and geographic locations (Alliende and Harper 1989; Ueno et al. 2007; Myers-Smith and Hik 2012; Che-Castaldo et al. 2015; Lei et al. 2017). The factors that drive these reverse sex ratio patterns in *Salix* are potentially wide ranging and likely include some combination of genetic and environmental factors

Riparian cottonwood and willow species in arid and semi-arid regions make up only a small fraction of the total number of species in the Salicaceae family. However, cottonwood / willow gallery forests are still the most common, and arguably ecologically most relevant, forest type in riparian zones of the western United States and Canada. Sex ratio patterns are not as pronounced in riparian cottonwoods and willows as they are in boxelder populations that dominate semi-arid riparian areas of the western US, but some patterns have emerged. Skewed sex ratio biases have been reported for some riparian cottonwood species, hybrids and populations (Braatne et al. 1996; 2007; Rowland and Johnson 2001), but not others (Kaul and Kaul 1984; Stanton and Villar 1996; Gom and Rood 1999a; b). As with boxelder, where sex ratios are more highly skewed, there tends to be male bias in areas where water resources are less favorable, such as greater distances from stream microhabitats in Utah (Dawson and Ehleringer 1993; Ward et al. 2002), locations where irrigation withdrawals have depleted groundwater availability along the Yakima River in central Washington (Braatne et al. 2007) and in the driest riparian environments studied along the Rio Grande River in New Mexico (Rowland and Johnson 2001). Conversely, to our knowledge there are no obvious examples of female biases sex ratio in riparian cottonwoods, although female individuals of clonal cottonwood species, such as *P. angustifolia*, *P. balsamifera* and *P. deltoides* have been shown to produce a higher number of clonal trunks than co-occurring males, particularly in low elevation, streamside habitats (Gom and Rood 1999a; b).

Information on sex ratio biases in riparian willows is fairly limited compared to riparian cottonwoods. Strong sex ratio biases have been reported for “non’ riparian species of willows in North America such as *S. arctica* (Dawson and Bliss 1989), and *S. glauca* (Dudley 2006), and for riparian willows in Sweden (Hughes et al. 2010) and Japan (Ueno et al. 2007), with female plants occurring at higher frequencies than males in high resource locations (less stressful), and at lower frequencies in low-resource locations (more stressful). Conversely, *S. amygdaloides* had equal numbers of male and female individuals in wetland areas in Nebraska (Kaul and Kaul 1984), while a 1.7:1.0 male biased sex ratio was reported for *S. exigua* plants occurring along the Assinboine River in Manitoba, Canada (Ottenbreit and Staniforth 1992). Unfortunately, to our knowledge there are no sex ratio data for riparian willows occurring in the arid regions of the southwestern US. Thus, it is currently an open question as to what extent this biologically important taxa expresses spatial segregation of the sexes across local aridity gradients.

Sex ratio biases, if present in riparian cottonwoods and willows are often difficult to detect due to various biotic constraints. One problem in sex ratio studies is that determining the sex of cottonwood and willow individuals is often challenging since neither sex typically retains reproductive structures for more than a few weeks per year. Compounding this challenge is that flower and seed phenology can vary dramatically over short distances since mature trees release seeds to match periods of high stream flows and high residual soil moisture. This phenological pattern, in turn, maximizes the odds for successful germination in a given fluvial system (Braatne et al. 1996; Stella et al. 2006), but makes biogeographical studies of reproductive phenology and sex ratios difficult without sophisticated phenocam systems. A potentially greater challenge is determining the sex of individuals that become non-reproductive under stress. For example, mature cottonwood trees exposed to water deficits along the middle Rio Grande River in New Mexico often failed to produce reproductive structures (Rowland and Johnson 2001), making it impossible to determine the sex of these individuals and evaluate population sex ratios under conditions of great interest. Another challenge with determining population sex ratios revolves around the clonal habit of most cottonwood and willow species. For example, non-native willows occurring along high-elevation streams in Colorado were almost 100% female due to a complete lack of sexual reproduction (Shafroth et al. 1994). Likewise, clonal reproduction was attributed to a near 2:1 female-biased sex ratio of individual ramets of three riparian cottonwood species in Alberta, Canada, although a 1:1 sex ratio was observed among individual genets (i.e. clones) (Gom and Rood 1999a). Therefore, a key component of sex ratio studies requires the identification of genets (i.e. clones) via molecular approaches when possible (Vandepitte et al. 2009; Dering et al. 2016).

It is also possible that sex ratios and spatial segregation of the sexes rarely emerge in riparian cottonwood and willow populations due to a limited habitat niche, or because of Fisherian sex ratio balance mechanisms that arise when the mean fitness of the rare sex exceeds that of the common sex (Fisher 1930; Bull and Charnov 1988; Wade et al. 2003). Unlike box elders, riparian cottonwoods, and especially willows rarely occur in upper terraces of riparian areas and are instead confined to the immediate stream margins (Snyder and Williams 2000). These obligate phreatophytes, therefore, are typically found within narrow resource gradients, reducing opportunities for spatial segregation of the sexes and potentially limiting population sex ratio biases along stream reaches (Hultine et al. 2007). Likewise, non-uniform sex ratios – where they do arise - may eventually be balanced by Fisherian forces (Bull and Charnov 1988; Wade et al. 2003).

Sexual dimorphism in *Salicaceae*

One way to evaluate potential sex ratio patterns and to predict whether extreme sex ratio biases are likely under future climate conditions, one must identify the potential tradeoffs between secondary sex characteristics related to physiology and growth. To examine whether physiological tradeoffs exist between such traits, we reviewed 27 published studies addressing intersexual differences in instantaneous leaf-level gas exchange and growth among *Populus* and *Salix* species (Appendix Table 1). Two clear patterns emerged with respect to leaf gas exchange. The first was that under well-watered, ambient temperature conditions (labeled Control in Figure 1), neither gender expressed an advantage over the other in leaf stomatal conductance [$g_{\mathrm{male}}:g_{\mathrm{female}} = 1.07$, $P = 0.43$, n = 18, (paired *t*-test), Figure 1a] or carbon assimilation [$A_{\mathrm{male}}:A_{\mathrm{female}} = 1.03$, $P = 0.87$, n = 19, paired *t*-test Figure 1b). Alternatively, when a drought and / or temperature warming treatment was added to the experiment, males significantly outperformed females in leaf stomatal conductance [$g_{\mathrm{male}}:g_{\mathrm{female}} = 2.51$, $P = 0.0074$, n = 12, (paired *t*-test), Figure 1a] and carbon assimilation [$A_{\mathrm{male}}:A_{\mathrm{female}} = 2.31$, $P = 0.0017$, n = 11, paired *t*-test Figure 1b). Intersexual differences in growth mirrored intersexual patterns in leaf gas exchange (Figure 1c). Under control conditions, growth—evaluated from either radial increment, height growth or increases in dry weight mass—was equal between sexes [$P = 0.99$, n = 16, (paired *t*-test) Figure 1c], but on average was 59% higher in males under drought / warming conditions [$P = 0.0068$, n = 7 (paired *t*-test) Figure 1c].

Perhaps a more consequential analysis comes from separating *Populus* from *Salix* taxa when analyzing intersexual differences in gas exchange (Figure 2). Data for *Populus*, independent of *Salix*, again show that neither gender expressed an advantage over the other in leaf stomatal conductance [g_{male}:g_{female} = 1.12, $P = 0.25$, n = 14, (paired *t*-test), Figure 2a] or carbon assimilation [A_{male}:A_{female} = 1.07, $P = 0.11$, n = 14, (paired *t*-test) Figure 2c] under ambient conditions. Conversely, when subjected to drought / high temperature conditions, males significantly outperformed females in leaf stomatal conductance [g_{male}:g_{female} = 3.05, $P = 0.0390$, n = 6, (paired *t*-test), Figure 2a] and carbon assimilation [A_{male}:A_{female} = 2.24, $P = 0.0150$, n = 7, (paired *t*-test) Figure 2c]. Alternatively, gas exchange in *Salix* does not follow the same obvious sexual dimorphic pattern as *Populus*. There were no intersexual differences in stomatal conductance under ambient [$P = 0.28$, n = 4, (paired *t*-test), Figure 2b], or drought / temperature warming conditions [$P = 0.27$, n = 5, (paired *t*-test) Figure 2b] and no differences were detected in carbon assimilation under ambient [$P = 0.51$, n = 5, (paired *t*-test) Figure 2d], or drought / temperature warming conditions [$P = 0.35$, n = 5, (paired *t*-test) Figure 2d]. The disparate patterns in sexual dimorphism between *Populus* and *Salix* seem to reflect previously observed patterns in sex ratio biases that seem to favor males in *Populus* and females in *Salix*. However, the limited number of gas exchange studies in *Salix* makes it difficult to draw strong conclusions regarding sexual dimorphism in this genus. Another limitation with this data synthesis is that none of these studies were conducted on riparian tree species that occur in western North America, although numerous studies were conducted on similar *Populus* species in Asia. Therefore, these studies should provide an important analog for predicting sexual dimorphism in habitat preference, productivity, and climate sensitivity of cottonwood gallery forests in the arid western US, and western North America as a whole.

Taken together, these previous studies suggest that female *Populus* trees are more sensitive to resource limitation and stress than males. Likewise, other stress mechanisms besides drought and high temperature, including high soil salinity and high UV radiation, may have a more profound impact on females than males. For example, salinity has a greater negative impact on growth, gas exchange and relatively competitiveness in females of several riparian *Populus* species in China compared to males (Chen et al. 2010; Chen et al. 2010; Li et al. 2016). Males are also more tolerant of the effects of high UV-B radiation than females in *P. cathayana* trees in China (Xu et al. 2008; Zhang et al. 2017). On the other hand, females have been reported to be more tolerant of high UV-B radiation than males in *S. myrsinifolia* trees occurring in Finland (Randriamanana et al. 2014), providing further evidence that sexual dimorphic patterns in *Salix* often do not parallel those of *Populus*.

Evidence for sexual dimorphism in riparian cottonwoods and willows

The synthesized gas exchange data in Figures 1 and 2 indicate that unlike the patterns seen in boxelder, female individuals in the genus *Populus* generally do not express a higher resource uptake capacity that would convey an advantage over males in optimal conditions or habitats. However, the data are congruent with the results seen when boxelder genotypes were transplanted to a warmer environment in that females expressed a much larger decline in gas exchange and growth relative to males under heat stress (Hultine et al. 2013). These results therefore invite the question, why are females less tolerant of stress given that, in general, they have no apparent advantage over males when conditions are optimal? One explanation is that our literature review of leaf-level gas exchange is limited in scale because the surveyed studies did not address whole-canopy gas exchange, or potential differences in total photosynthetic area or total leaf area ratio (photosynthetic surface area per unit plant biomass) between male and female plants. Alternatively, it may be that females only express higher rates of resource uptake when sink strength is maximized during periods of flowering and fruit set (Hultine et al 2008). If so, many studies – particularly those in greenhouse settings - may miss periods when sink strength in females outweighs that of males.

One approach to capture seasonal patterns in resource acquisition, including possible shifts in sink strength among the sexes, is to continuously monitor whole-plant water use using stem sap flux techniques. For example, a previous sap flux study on mature Fremont cottonwood trees (*P. fremontii* Wats.) indicates that females maintain higher water use rates than males. In this study, conducted over a three-week period from mid-June to early July of 2005, it was shown that stem sap flux density (J_s) was 25% higher in females than in co-occurring males growing at a location with shallow groundwater along the Jordan River near Salt Lake City, UT (n = 8 trees per sex, Figure 3a). Sap flux was also higher in streamside female boxelder trees than co-occurring males in Red Butte Canyon, east of Salt Lake City (n = 6 trees per sex, Figure 3b). It is worth noting that J_s in boxelder converged significantly in late June (starting on about Day 173) between male and female boxelder trees, a period that follows the completion of seed set in this population. Perhaps the high cost for reproduction in female box elder trees elevates the sink strength and resource uptake in females relative to males in microsites with high resource availability (Hultine et al. 2008). Conversely, Fremont cottonwood trees maintained a consistently higher J_s along the Jordan River during periods following flower production and seed set, indicating that females may have a consistent advantage over males in high resource locations.

Sap flux patterns reflect long-term trends in growth among boxelder and cottonwood species in western North America (see Fig. 3). For example, radial growth rates in ten year-old boxelder trees planted in a common garden in Salt Lake City, UT were 28% higher in females than in males during wet years (Ward et al. 2002). Similarly, growth rates along the Oldman River in Lethbridge, Alberta, Canada were 21% higher in mature female narrowleaf cottonwood (*P. angustifolia* James) trees than in co-occurring males during years with high river discharge (Rood et al. 2013). A major difference, however, between species is that in box elder, inter-sexual differences in growth coincided with females having a 0.52‰ to 0.67‰ lower $\delta^{13}C$ abundance in wood cellulose during wet years, indicating that female individuals maintained a higher internal to ambient CO_2 concentration (c_i:c_a) over the growing season. On the other hand, whole-wood $\delta^{13}C$ in narrowleaf cottonwood during high discharge years was similar between the sexes (Rood et al. 2013), and leaf gas exchange collected repeatedly at the same cottonwood stand in 2006 (a moderate river discharge year) revealed no inter-sex differences in g, A or c_i:c_a (Letts et al. 2008). It is worth noting that radial growth in the same narrowleaf cottonwood stand was 38% higher in females than in males during years with low river discharge (Rood et al. 2013), while during dry years, radial growth was equal between male and female box elder trees in the Salt Lake common garden (Ward et al. 2002). These data suggest that regardless of leaf gas exchange or integrated c_i:c_a patterns, higher radial growth rates in female narrowleaf cottonwood trees is a sustained trait, that ultimately may not reflect population sex ratio. Conversely, sexual dimorphism in radial growth appears to be much more plastic in box elder.

Climate change impacts on dioecious riparian tree species

Causal relationships between sexual dimorphism in physiological climate sensitivity and mortality - a likely mechanism for skewed sex ratios - have yet to be comprehensively explored in dioecious riparian tree species. Therefore, it is necessary to establish a fundamental basis for why differential rates of resource uptake between sexes may result in acute resource limitations and subsequently, higher rates of mortality in one sex over the other. It appears that males in the genus *Populus* consistently maintain higher rates of g and A under sub-optimal environmental conditions than co-occurring females (Fig. 1, 2). Likewise, male box elder trees also maintain higher rates of g and A than co-occurring females during periods of excessive high temperature and VPD conditions (Hultine et al. 2013). Not surprisingly there is a clear link between chronic reductions in stomatal conductance and woody-plant mortality (Martinez –Vilalta et al. 2002; Plaut et al. 2012; Andregg et al. 2014; Sevanto et al. 2014). These and other studies have primarily focused on the physiological mechanisms that ultimately result in whole-plant hydraulic failure and / or carbon starvation (McDowell et al. 2008; Sperry and Love 2016). A primary driver of whole-plant hydraulic failure is drought-induced xylem cavitation that results in lower g and increases the threat of cell turgor loss (Brodribb and Holbrook 2006). This would set off a feedback loop that increases the reliance on non-structural carbohydrate storage (NSC), not only to prevent carbon starvation during extended periods of low g and A, but also for osmotic regulation to maintain turgor and leaf function (Zwieniecki and Holbrook 2009); Vilagrosa et al. 2010), and / or refill embolized xylem (Bucci et al. 2003; Salleo et al. 2009). However, to our knowledge, there are no studies that compare NSC storage in dioecious riparian tree species from western North America, and the limited data for xylem function in box elder shows no sexual dimorphism in xylem cavitation vulnerability (Hultine et al. 2008). Future studies that evaluate sex-specific patterns in xylem function and labile carbon storage will greatly improve our understanding of the mechanisms that underpin sex ratio biases and spatial segregation of the sexes that arise in dioecious plant populations.

The relationship between physiological stress and sex ratio bias will depend largely on a combination of factors including the magnitude and rate of climate change, life history strategies, local adaptation and generation turnover times among others. A major tenet of sex ratio theory is that non-uniform sex ratios will eventually be balanced by Fisherian forces because the mean fitness of the rare sex exceeds that of the common sex (Fisher 1930; Bull and Charnov 1988; Wade et al. 2003). In theory, Fisherian sex ratio balance could counter the impact that increased aridity will have on dioecious plant populations, even those that express strong sexual dimorphism in physiological traits related to stress. Fisherian forces are most likely to counter the effects of climate change in species with rapid generation turnover rates, such as herbaceous annuals and short-lived perennials that also occur in locations where the effects of climate change occur relatively slowly. However, for many dioecious plant populations, the rate of change in sex ratio caused by increasing aridity may have the potential to outpace the rebalancing effects of Fisherian sex ratio selection, with negative impacts on successful mating. Woody plants such as boxelder, for example, may have sex ratios that are highly susceptible to rapid shifts in climate due to their relatively long generation turnover times that restrict the rate of adaptation to rapid changes to environmental conditions. If climate change brings warmer and dryer conditions to the western U.S. as expected, box elder populations may experience strong male-biased sex ratios, depending on whether Fisherian balancing mechanisms can outpace the effects of climate change on aridity and water availability from stream systems (Figure 4a).

With riparian cottonwoods, it is unclear whether or not Fisherian balancing mechanisms would play a significant role in managing sex ratio biases for two reasons. The first is that, unlike box elder, cottonwoods do not consistently express strong sex ratio biases, although male-biased sex ratios often emerge in the most stressful end of a population's environmental niche (reviewed above). The second reason is that under stress, cottonwoods often become "non-reproductive" (Rowland and Johnson 2001), although it is currently unclear whether one sex is likely to become non-reproductive at a higher frequency than the other sex. Given these patterns, it may be that increased aridity from climate change leads to a larger percentage of the population becoming non-reproductive (Figure 4b), which could have an extreme deleterious impact on population fitness, even if population sex ratios remain fairly static. Ultimately climate change may have severe consequences on the fitness of box elder and riparian cottonwoods in western North America as a result of gender and reproductive effects, even if the mechanisms that drive reduced fitness differ (Figure 4). Unfortunately, the limited data on sexual dimorphism in riparian willows makes it difficult to make predictions of future population sex ratios and fitness in response to climate change.

Future directions and conclusions

As discussed throughout this review, there are many knowledge gaps regarding sex ratio patterns and sexual dimorphism in secondary traits among dioecious riparian tree species in western North America, and especially for populations occurring in the arid southwestern U.S. In addition to these knowledge gaps, two questions are critical to address in future studies: 1) do inter-sexual differences in traits related to stress, resource use efficiency and productivity emerge at the pre-productive stage and 2) to what extent will extreme sex ratios impact the capacity of dioecious tree populations to serve as foundation species in riparian communities where they account for extensive ecosystem services?

Determining whether sexual dimorphism in secondary sex traits are present at the pre-productive stage is a difficult task, largely because these long-lived riparian tree species, such as box elder, cottonwoods and most willow species do not produce reproductive structures until several years after germination. However, recent advances in genomics and other molecular technologies are providing new opportunities to evaluate the sex of dioecious plants during early stages of development (Tuscan et al. 2006; Yin et al. 2008). *Populus* genomic resources, in particular, have grown rapidly, culminating in the whole-genome sequence database for black cottonwood (*P. trichocarpa*, Torr. & Gray) (Tuscan et al. 2006) that has more recently been extended to other species in the Salicaceae family (Hanley et al. 2006; Yin et al. 2008). Three subsequent mapping studies have revealed that there is a single locus that controls sex determination in *Populus* (Gaudet et al. 2007; Markussen et al. 2007; Yin et al. 2008), although it is worth noting that a single locus might encompass multiple genes underlying sex determination (Yin et al. 2008). The identification of sex-determination to a single identifiable locus may open a wide range of opportunities to explore mechanisms that underlie sex ratio biases at multiple life history stages. For example, future studies can evaluate whether sexual dimorphism in stress tolerance and resource acquisition emerge in seedlings or after they reach sexual maturity. In turn, sex identification of individual genotypes could improve the chances of successful restoration projects that aim to restore native cottonwood / willow forests in riparian areas impacted by land use, species invasion and climate change. Restoration projects would have the necessary tools to target sex ratio balance or spatial segregation of the sexes such that population fitness is most likely maximized under future environmental conditions, especially in locations where Fisherian balance cannot be achieved quickly.

Riparian restoration projects not only aim to reestablish populations of native tree species, but also preserve ecosystem function and community structure of riparian areas that are biodiversity hotspots in arid regions of the western U.S. Phenotypic variation between male and female genotypes has significant and predictable consequences to ecosystem functions such as soil carbon fluxes and nutrient transformation rates, and to community composition of associated plants, invertebrates, and micro-organisms (Gehring and Whitham 1992; Varga and Kytöviita 2010; Petry et al. 2013). Functional traits such as foliar nutrient content, carbon to nitrogen ratios, and defensive strategies vary between the sexes of riparian box elder trees (Jing and Coley 1990; Dawson and Ehleringer 1993; Dawson et al. 2004; Hultine et al. 2013), and these traits are well known to drive ecosystem function and community structure (Lavoral and Garnier 2002; Hart et al. 2005). Therefore, altered trait expression in box elder by environmental selection during climate change, may not only result in shifting sex ratios, but also have potential cascading impacts on ecosystem function and community structure of highly valued riparian ecosystems. However, information on the foundational capacity of each sex of riparian cottonwoods and willows is currently lacking, and should be explored further in future studies.

Our data synthesis of physiological traits in *Populus* species (Figure 2) suggests that riparian cottonwoods likely share similar sexually dimorphic traits with box elder such that males have a greater stress tolerance than females (i.e. Hypothesis 1). These patterns will likely amplify male biased sex ratios and alter population structure in both box elder and cottonwoods under future climate conditions (i.e. Hypothesis 2). On the other hand, there is no obvious evidence for sexual dimorphism in physiological traits or sex ratio bias in riparian willow populations in part given due to a generally lack of information for willow taxa. Ecologists and plant biologists will need to resolve many unknown factors to better predict the extent to which climate change may impact the population structure of dioecious riparian tree species. Specifically, more work is needed to successfully integrate analysis of sexual dimorphism in key traits related to climate sensitivity within sex ratio theory. We advocate for approaches that emphasize long-term trends and/or broad spatial scales, for example tree-ring analysis of growth and stable isotope variability in woody tissues (Ward et al. 2002; Rood et al. 2013), and monitoring sex-specific shifts in reproductive phenology using existing landscape-scale phenocam networks (Brown et al. 2016). Likewise, researchers should take advantage of recent technologies that can acquire vast amounts of genomics data in order to link sex-related traits to specific molecular markers (Yin et al. 2008). In turn, this information could help researchers determine when sexual dimorphism emerges during the life history of plants, including if patterns emerge before plants reach reproductive maturity. Finally, the use of reciprocal transplants and common garden experiments established across broad climate gradients would provide the necessary infrastructure to quantitatively evaluate divergent selection (Kawecki and Ebert 2004) that may drive differential patterns of local adaptation between sexes.

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Figure captions

Figure 1 - The ratio of male to female leaf stomatal conductance (g), net carbon assimilation (A), and measurements of productivity synthesized from previous studies (Appendix Table 1) of sexual dimorphism in *Populus* and *Salix* species. Experiments took place under ambient temperatures and well-watered conditions (Control) and experiments where plants were subjected to either temperature warming of drought conditions (Drought / Warming). (a) The comparison of leaf g in male and female *Populus* and *Salix* plants under control conditions ($g_{\text{male}}:g_{\text{female}} = 1.07$, $P = 0.43$, n = 18) and under Drought / Warming conditions ($g_{\text{male}}:g_{\text{female}} = 2.51$, $P = 0.0074$, n = 12). (b) The comparison of A in male and female plants under control conditions ($A_{\text{male}}:A_{\text{female}} = 1.03$, $P = 0.87$, n = 19) and under Drought / Warming conditions ($A_{\text{male}}:A_{\text{female}} = 2.31$, $P = 0.0017$, n = 11). (c) The comparison of productivity using measurements of either biomass production, height growth or radial growth of male and female plants under control (M:F = 1.00, $P = 0.99$, n = 16), and under drought / warming conditions (M:F = 1.59, $P = 0.0068$, n = 7).

Figure 2 - The ratio of male to female leaf stomatal conductance (g) and net carbon assimilation (A) synthesized from previous studies (Appendix Table 1) of sexual dimorphism in *Populus* and *Salix* species. Experiments took place under ambient temperatures and well-watered conditions (Control) and experiments where plants were subjected to either temperature warming of drought conditions (Drought / Warming). (a) The comparison of leaf g in male and female *Populus* plants

under control conditions (g_{male}:g_{female} = 1.12, P = 0.25, n = 14) and under Drought / Warming conditions (g_{male}:g_{female} = 3.05, P = 0.0390, n = 6). (b) The comparison of leaf g in male and female *Salix* plants under control conditions (g_{male}:g_{female} = 0.88, P = 0.28, n = 4) and under Drought / Warming conditions (g_{male}:g_{female} = 1.65, P = 0.27, n = 5). (c) The comparison of A in male and female *Populus* plants under control conditions (A_{male}:A_{female} = 1.07, P = 0.11, n = 14) and under Drought / Warming conditions (A_{male}:A_{female} = 2.24, P = 0.0150, n = 7). (d) The comparison of A in male and female *Salix* plants under control conditions (A_{male}:A_{female} = 0.93, P = 0.51, n = 5) and under Drought / Warming conditions (A_{male}:A_{female} = 2.18, P = 0.35, n = 5).

Figure 3 – Difference in sap flux density (J_s), calculated in grams of water per cm of sapwood area per day, between co-occurring male and female individuals relative to the mean of male and female trees combined (i.e. horizontal lines). a. J_s in mature male and female Fremont cottonwood (*Populus fremontii*) trees occurring next to the Jordan River, near Salt Lake City, UT, measured from June 21 (Day 172) to July 11 (Day 192), 2005. b. J_s in mature male and female box elder (*Acer negundo*) trees occurring within 1 m of a perennial stream channel in Red Butte Canyon near Salt Lake City, UT, measured from June 10 (Day 161) to June 30 (Day 180), 2005. Figure 3 is based on sap flux data originally reported by Hultine et al (2007; 2008). Error bars represent ± 1 standard error of the mean.

Figure 4 - Expected male to female ratios under current and predicted future climate conditions. a. Population sex ratios in box elder (*Acer negundo*) in relation to distance from the immediate stream channel. Under current climate conditions, sex ratios vary from being female-dominated near the stream channel to male-dominated further from the channel (black solid line), but the

population overall maintains a 1:1 ratio (horizontal line). With climate change – predicted to bring more extreme growing season temperatures and lower stream discharge - populations are expected to shift in sex ratios such that they become significantly male-dominated (red solid line), depending on the rate of climate change and the potential for Fisherian processes to balance sex ratios. b. Population sex ratios in riparian cottonwoods (*Populus* spp.) in relation to distance from the immediate stream channel. In contrast to box elder, cottonwood populations are not expected to express female biased sex ratios in high resource environments, or strong male-biased sex ratios in low-resource locations. However, the proportion of non-reproductive individuals in the population should increase with distance from the stream channel (dashed black line). With predicted climate change, the number of non-reproductive individuals (red dashed line) should increase to include a higher proportion of the population than under current conditions.

707 Figure 1

708

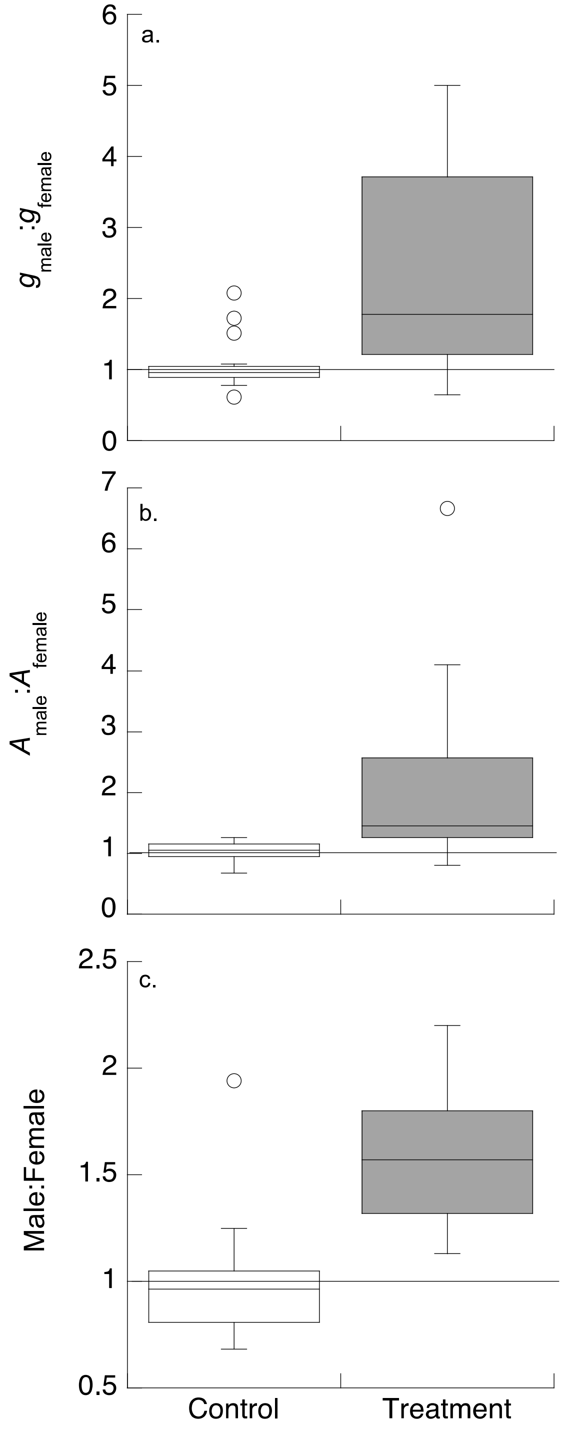
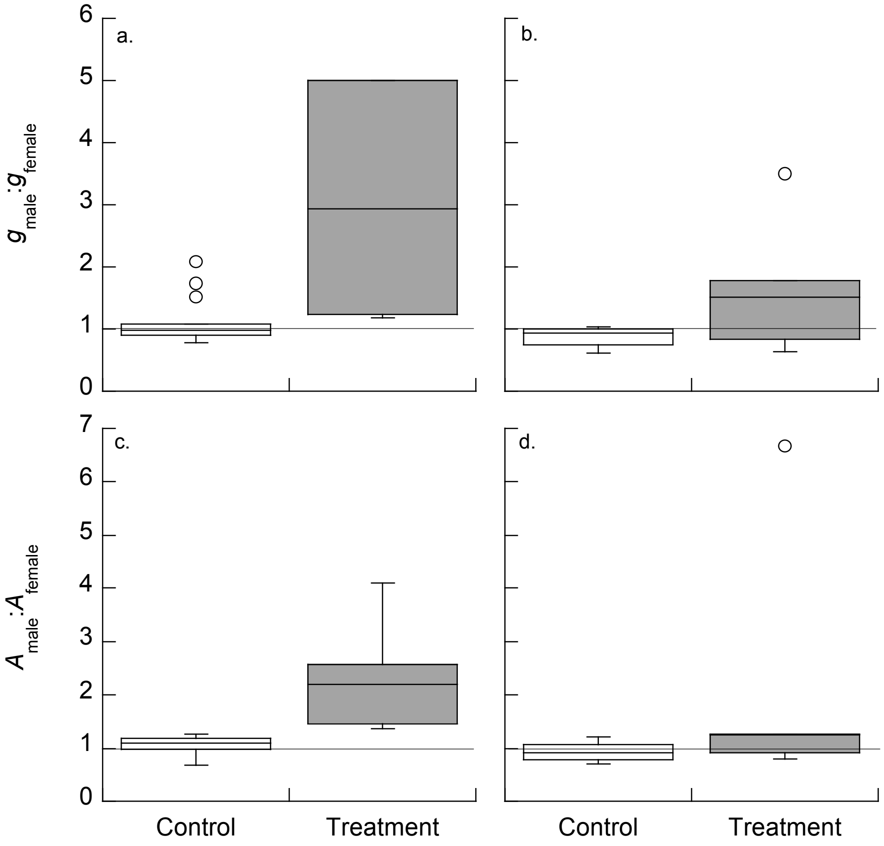


Figure 2


a.
b.
c.
d.
$g_{male}:g_{female}$
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0
1
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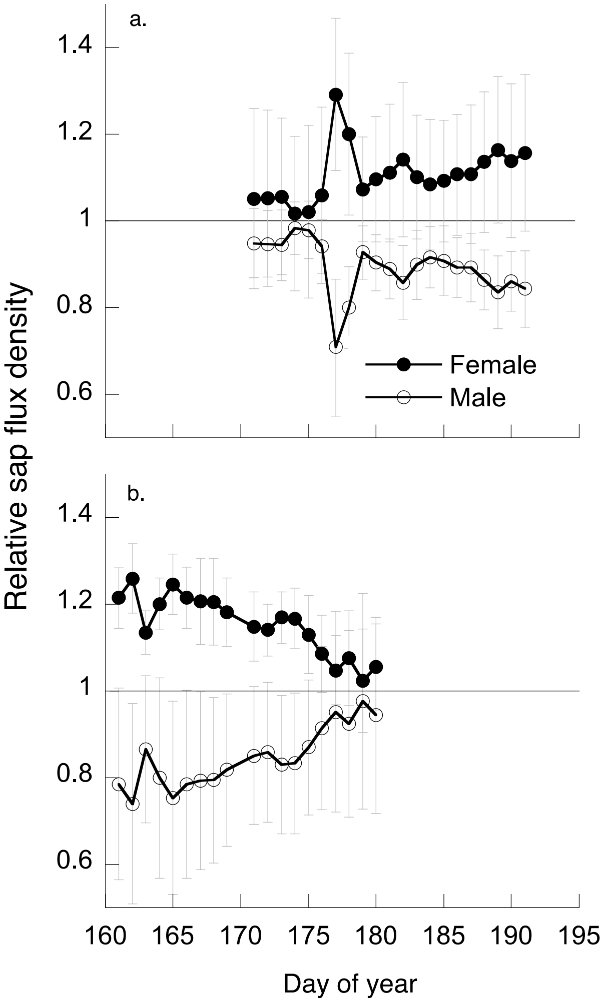
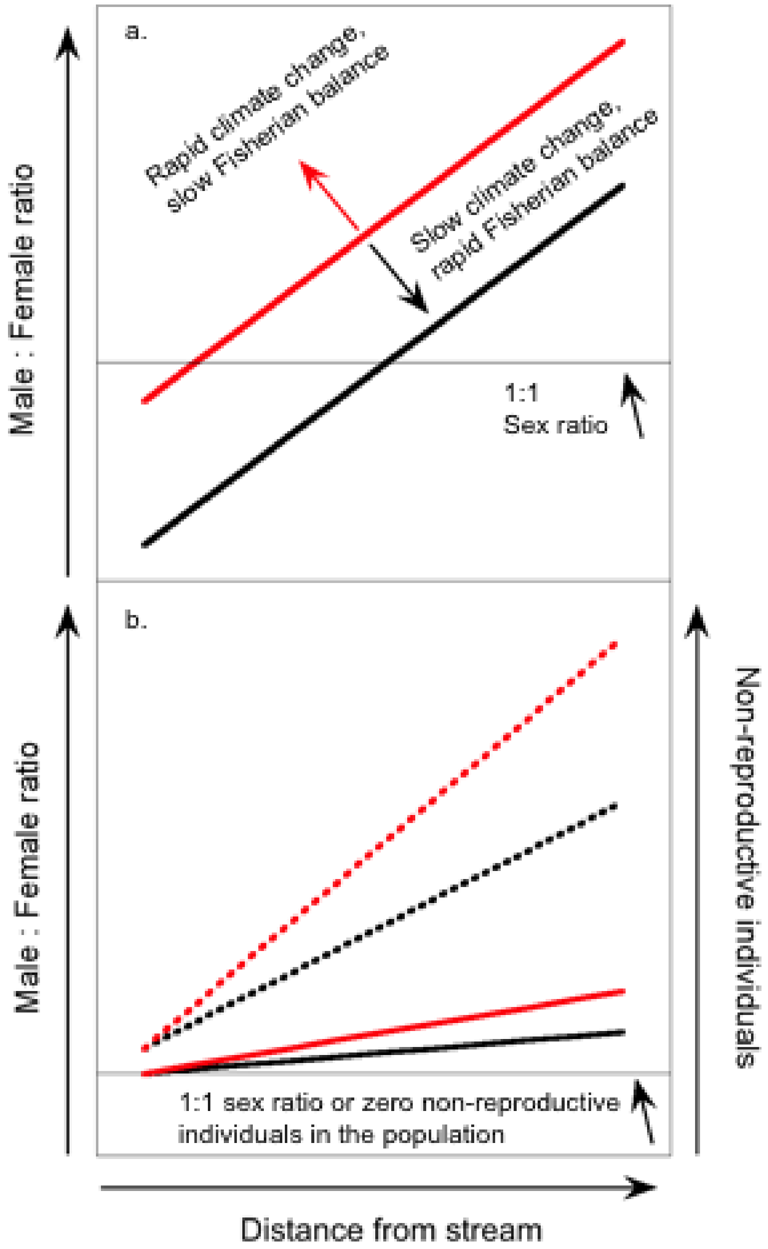
Control
Treatment
Control
Treatment

Figure 3


a.
b.
Relative sap flux density
1.4
1.2
1
0.8
0.6
Female
Male
160
165
170
175
180
185
190
195
Day of year

714 Figure 4

715



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