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Biodiversity in assisted migration trials

– A study comparing the arthropod diversity between different populations of cottonwood (*Populus Fremontii*) translocated to new areas

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Biodiversity in assisted migration trials – A study comparing the arthropod diversity between different populations of cottonwood (*Populus Fremontii*) translocated to new areas

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Abstract

This study aims at investigating how diversity and community structure of arthropods are affected by assisted migration of foundation species. This is proposed to counter biodiversity loss in the tracks of climate change. By focusing on foundation species, a larger quantity of biodiversity could be protected. I investigated arthropod diversity and community structure linked to nine Fremont cottonwood (*Populus fremontii*) populations types from different areas planted in three common gardens at different elevations. In accordance with the mid-elevation hypothesis that states that diversity peaks at mid-elevations, the diversity and most abundances of arthropod peaked in a mid-elevation garden at 1000 m.a.s.l. However, abundances of the functional group of predators peaked at low elevations contradicting the mid-elevation diversity pattern. Earlier studies have found that genetics and local adaptation exists between arthropods and host plants. Therefore, it was hypothesized that arthropod diversity would differ between cottonwood populations with different origin. The results were non-significant but there were signs of some cottonwood populations holding a higher diversity of arthropods. The result was inconclusive although there were signs of some populations supporting higher diversities than the rest. There was an interaction effect between common gardens and cottonwood population where the most abundant population types contained higher abundances of arthropods in mid-elevation garden. The analysis were performed with a GLM (Generalized linear model) and a Tukey HSD (honest significant difference) and the variables tested was SWD Index (Shannon-Winer diversity index), Evenness and abundances. The results from this study implement that the success of assisted migration and interaction with diversity linked to foundation species need to be further investigated. The findings in this study could be the result of a variety of underlying processes, from species interactions and genetic adaptation in the foundation species and arthropod communities. Both genetics in the plants as well as the arthropod abundances linked to these trees are baselines for the rest of the biodiversity. Both biotic and abiotic factors are important for the success of assisted migration of foundation species as a counter measure to biodiversity loss.

Keywords: Assisted migration, biodiversity conservation, arthropods, climate change

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1 Introduction

The ongoing climate change will strongly impact ecosystem, cause maladaptation in stationary species like trees, and impact biodiversity (IPCC, 2014). Species ranges change in the tracks of changing climate regimes (Parmesan and Yohe, 2003) resulting in changed species interactions and trophic cascades (Hegland et al., 2009). Maladaptation in foundation species, i.e. important structural species and drivers of ecosystem processes, could lead to especially severe trophic cascades and large-scale reduction of biodiversity. However, assisted migration, i.e. the intentional translocation of genotypes or phenotypes to a new area, normally within the species natural distribution (Frascaria-Lacoste and Fernandez-Manjarres, 2012) has been proposed as a countermeasure to this development (Kreyling et al., 2011). The typical use of assisted migration is in conservation of endangered species but Kreyling et al. (2011) argues that a broader biodiversity conservation could be implemented by focusing on foundation species.

Nevertheless, the complexity of ecosystems consisting of a range of species all responsive to environmental variation makes it hard to evaluate the effects of assisted migration practices on biodiversity (Grady et al., 2015, Seager et al., 2007, Perry et al., 2012, Harrison et al., 2015, Vitt et al., 2010, Hewitt et al., 2011, McLachlan et al., 2007, Kreyling et al., 2011, Harper et al., 2011). Both abiotic and biotic factors lead to local adaptation in both host plants and associated organisms such as herbivores and thus local species interactions (Evans et al., 2012). For example, Bernhardsson et al. (2013) found that the local plant-genotypes of *Populus tremula* was subject to less herbivory by arthropods than plants from more distant locations. The explanation was thought to be the selection towards certain genes in the tree giving rise to different defensive compounds targeting the local herbivorous arthropods. Abiotic factors can also influence local adaptation of host species. This was found by Grady et al. (2015) who discovered that different genotypes of the foundation tree species of Fremont cottonwood (*Populus fremontii*) were locally adapted which resulted in decreased productivity, growth and survival the longer the transfer distance.

If plant genetics influence productivity this will likely translate to impact whole communities depending on these plants. It has been shown that primary productivity could affect diversity by influencing species interactions, for example interaction between herbivorous arthropods and host plants. Foraging pressure varies depending on the amount of nitrogen, water and defensive compounds in the plant tissues, variation which in part is genetically determined (Louda and Collinge, 1992, Underwood and Rausher, 2000, Jactel et al., 2012, Ferrier et al., 2012, Bangert et al., 2005, Grady et al., 2011). The interaction between arthropods and host plants is also important in assisted migration practices aiming to maintaining ecosystem level biodiversity in a changing climate. For example, some studies have found that different host genotypes support different arthropods communities and that arthropods could impact higher trophic levels in the ecosystem for example bird fauna (Louda and Collinge, 1992, Bangert et al., 2005, Grady et al., 2011, Evans et al., 2012, Harper et al., 2011). In studies of climate change, elevation is often used as a representation for warming. Many of those studies have been showing links to rainfall and temperature which promotes productivity in the ecosystems. Biodiversity tends to follow a hump shaped pattern along those gradients with highest biodiversity at middle elevations, and it is theorized that this is caused by overlapping species ranges and habitats (Sanders et al., 2003, Lite et al., 2005).

This study aims to investigate how different populations of Fremont cottonwood trees - a foundation tree species in riparian ecosystem of the arid southwestern USA (Grady et al., 2015)- affect associated arthropod diversity along an environmental gradient representing different climates. To accomplish this, I studied the arthropod communities associated with nine different cottonwood populations planted in three common gardens at different altitudes. The different populations originate from different regions throughout the gradient and thus represent populations adapted to different climatic conditions- from warm to cold and from arid to moist. Based on earlier studies showing that both host genetics and environment influence communities associated with foundation trees I hypothesize that 1) plant population and garden would influence diversity and abundance of associated arthropod communities and that 2) the garden influence would be due to higher biodiversity in the mid-elevation garden. Furthermore, I hypothesize 3) that arthropod community composition associated with certain plant populations will differ between gardens i.e. plant population and garden would interact to influence arthropod communities.

2 Method

2.1 Study set up

The study is performed in three Cottonwood (*Populus fremontii*) common gardens planted at three different elevations in Arizona and Utah; Yuma at 50 m.a.s.l., Agua Fria located at 1000 m.a.s.l., and Canyonlands located at 1600 m.a.s.l. The sites are significantly different in the aspect of temperature and precipitation. Yuma is warm and dry with a mean precipitation of 0.3 mm per year and an annual mean temperature of 24.5 °C. Agua Fria has the moistest climate with an annual mean precipitation of 1.3 mm and temperature of 16.9 °C. Canyonlands is the coldest of the gardens with an annual temperature of 11.9 °C and precipitation of 1.0 mm. Canyonlands is also the only garden that has snowfall in the winter and experiences minus degrees during some part of the year (w-nws.webmaster@noaa.gov). In each garden 16 cottonwood populations from different areas are planted with 4 replicates in a 4-block design (Picture 1). Each population is represented by 64 trees planted in 8 x 8 (18x18m) plot with roughly 2 meters between each tree. For this study I used 9 populations representing to represent a range of environmental adaptations that can be seen in table 1.

In each plot, 8 random trees close to the middle of the plot were inventoried for arthropods. The arthropod inventory was done by recording all arthropods on the trees during 120 seconds for each tree. The inventory were performed during May 2016 and the survey took place before lunch during each of the inventory days. Based on morphological features the arthropods were classified into different functional groups (for diversity assessment); herbivores consisting of the taxa; sawflies (*Symphyla sp*), aphids (*Aphidoidea sp*) and grasshoppers (*Caelifera sp*), predators consisting of the taxa; spiders (*Aranea sp*), ladybird beetles (*Coccinellidae sp*) and finally ants (*Formicidae sp*) represented as its own functional group. In some

cases, taxa itself were examined as to explain differences in the result for the functional groups and further investigate the differences in the arthropod community structure.

2.2 Analysis

A GLM (Generalized Linear Model) was used to test for the effect of garden, cottonwood population and their interaction on arthropod community variables. To identify wherein the differences lays a Tukey HSD (honest significant difference) test were performed. The response variables considered were SWD Index (Shannon-Wiener Diversity Index) (Equation 1), Evenness (Equation 2) and abundance of the arthropods. The abundance was tested separately for the total abundance of arthropods as well as for separate functional groups and sometimes the taxa within those to evaluate differences in arthropod diversity patterns. All data was checked for normality and equal variances using Shapiro-Wilks W and Welch's Test and when data did not fulfil assumptions (H0= Normality respectively Equality) the data was log transformed before analyses. Based on the Shapiro-Wilks W and Welch t-test all abundance data was log transformed to meet the assumptions of normality and equal variance. The analysis was done on plot level (individuals/ plot) and were performed in the statistical software JMP.

Equation 1)

$$H = - \sum_{i=1}^S P_i \ln P_i$$

H= Shannon Diversity Index, P_i = proportion of individuals of the number of species (i), S = the total number of species in the community (Begon, 2006).

Equation 2)

$$J = (\sum_{i=1}^S P_i \ln P_i) / \ln(s)$$

Were J is the Evenness and $\ln(s)$ the natural logarithm of species richness (Begon, 2006).

3 Results

The outcome from the GLM shows, that common garden had a significant effect on the SWD Index and the all the log transformed abundances (Table 2). Common garden had the greatest explanatory values for the parameters SWD Index and predator abundance. The cottonwood population effect was significant for total abundances as well as for the abundance of herbivores. However, the effect of population was in both cases influenced by garden as shown by significant garden by population interactions.

3.1 Effect by common garden

The Tukey HSD reveals that the single effect of garden, as detected by the GLM, on the SWD Index was explained by a significantly higher diversity in the mid-elevation garden, Agua Fria (mean and SE=0.75 ±0.08) in comparison to the low elevation garden, Yuma (0.34 ±0.06) and the high elevation garden, Canyonland (0.48 ±0.10), (Fig 1). Furthermore, the predator abundance was significantly higher in Yuma (4.14 ±0.61) compared to Agua Fria (1.58 ±0.28) and Canyonland (0.53 ±0.14), mainly due to the high abundance of spiders found in Yuma.

There were more significant findings by the GLM, however not as single effects (table 2). This was found for abundance of herbivores. The Tukey HSD found herbivores to be significantly more abundant in Agua Fria (5.86±1.75) compared to Yuma (0.25±0.09) and Canyonlands (1.53±0.94), Fig1. This was likely influenced by the high amount of *Symphtha* findings in Agua Fria (3.57 ±0.47) compared to Canyonlands (2.38 ±0.50) and Yuma (1.50 ±0.50). The high abundance of herbivores likely influenced the total arthropod abundance that was significantly higher in Agua Fria (9.94 ±2.31) compared to the other gardens. Canyonlands had higher abundance of arthropods (5.89 ±1.260) than Yuma (4.75 ±0.64). Further the GLM revealed that garden also influenced the abundance of ants, however no significant

results could be derived by the Tukey HSD. Canyonland had the highest mean abundance, 2.69 ± 0.79 , compared to Agua Fria (1.53 ± 0.44), and in Yuma no ants was found.

Overall these findings give support the second part of hypothesis 1) that garden would influence diversity and abundance of associated arthropod communities. That the SWD Index and total arthropod abundance(log) is highest in the mid-elevation garden also gives proof for the second hypothesis 2) that the garden influence would be due to higher biodiversity in the mid-elevation garden.

3.2 Effect by Fremont cottonwood population

No single effect could be found by the GLM (table 2), but there were still effects by cottonwood population on arthropod diversity. Cottonwood population significantly affected both total abundance and the abundance of herbivores associated with the trees. However, the subsequent Tukey HSD test could not distinguish between different populations. As can be seen in figure 2 the total abundances of arthropods, the functional group of herbivores and predators show large among population variation, but also large within population variation as shown by high standard error (SE) thus giving rise to the inconclusive results of the Tukey HSD.

Although the inconclusive results of the Tukey HSD there were some large variation in arthropod abundances among different populations. However arthropod abundance was not evenly distributed between the cottonwood population types. Of the total abundance of arthropods most of it were found in the three populations MRN-RAT, SCT-MEX and LBW-BIL. These populations were all, except for SCT-MEX, from mid elevation sites with relatively warm climate and high precipitation. The SCT-MEX population originates from a dry area at low elevation (table 1). In each of these 3 populations 7-14% more arthropods was found as compared to the other 6 populations. Aphids were almost conclusively found in these populations and almost with no findings in the others.

3.3 The interaction effect by garden and population

The interaction effect by common garden and population gave significant effects, (GLM, Table 2). The significant results found were for all abundances except for the functional group of predators. The Tukey HSD however, was inconclusive although there was still large variation between populations and in this case within population, depending on which garden the population was planted in.

The abundance of arthropods over the gardens was mostly concentrated to the population types of SCT-MEX, LBW-BIL and MRN-RAT in the mid-elevation garden, Agua Fria. The abundances in these populations in this garden was up to 9% higher than otherwise, fig3 and fig4. This pattern was mostly the same for the abundance of herbivores. The populations held low abundances of herbivores in Yuma and highest in Agua Fria. Predator abundances however were mostly distributed to the garden of Yuma within all the populations. The abundances of predators were more evenly distributed among populations although MRN-RAT in Yuma had a high predator abundance 13%/population/ garden. The highest ant abundance/population/garden were mostly found in Canyonlands although there was no clear pattern of a preference for any population type.

4 Discussion

The aim of this study was to investigate the practice of assisted migration of foundation species as a mean to preserve biodiversity under climate change. Arthropod diversity associated with different populations of Fremont cottonwood was examined in different common gardens representing different climates. In line with the first hypothesis common gardens had a significant effect on arthropod diversity (SWD Index) although the cottonwood population only had significant effects through the interactions with garden. Predator abundance is one important functional group that were significantly affected as well. Further arthropod diversity and abundances was also highest in the mid-elevation garden, Agua Fria, which gives support to the second hypothesis that the garden influence would be due to higher biodiversity in the mid-elevation garden were species ranges may overlap. However, these patterns were not consistent for all functional groups, i.e. whereas the abundance of herbivores coincided with the mid-elevation theory, predator abundance decreased with elevation and ant abundance was highest in the high elevation garden, Canyonlands, while missing completely in the low-elevation garden, Yuma. The Fremont cottonwood population influenced associated arthropods only through interactions with garden, i.e. the potential of the different populations to support arthropods differed among gardens, thus supporting the third hypothesis.

At mid-elevation sites temperature and humidity promotes higher ecosystem productivity allowing overlap in habitats and species ranges which in turn promotes higher biodiversity (Lite et al., 2005). The arthropod diversity and most abundances peak in the mid elevation garden, Agua Fria, however this were not always the case for the different functional groups. Ants tended to become more abundant at higher elevations and were missing completely in Yuma. Similar findings of ant diversity have been found by for example, Sanders et al. (2003) who found that species richness and diversities of ants increased with elevation, not peaking in the mid-elevation. However, a similar study by Orabi et al. (2011) investigating several gradients found that abundance also could peak in the mid-elevations as well as at high ele-

variations. They found that communities between high and middle elevations was distinct from low elevations and that the ant communities was tightly linked to different plant-species, suggesting that diversity pattern can't be explained by elevation alone. Furthermore, in my results the predator abundance decreased with rising elevation not peaking in mid-elevation, influenced by high abundances of spiders in Yuma. Some spiders can produce toxins that enables the specimen to function neurologically normal even during heat and water stress (Rall et al., 2010). In combination with ambush as hunting strategy these spiders waste less energy and are thus less susceptible for negative metabolic impact caused by heat stress that in arthropods can lead to starvation (Rall et al., 2010). Usually the rate of metabolism in arthropod is doubled with every 10 °C degree. Consequently, leading to increased foraging and changed species interactions in the food web matrix under warmer climates. This could affect the host plants which responses in turn is affected by underlying genetics (Rall et al., 2010, Clarke and Fraser, 2004, Perry et al., 2012).

Different genotypes of a tree species have different adaptations to environment and climate which affects the success of assisted migration as found by Grady et al. (2015). The genetic adaptation accounts for species interactions as well. In a study by Ferrier et al. (2012) who studied patterns of arthropod diversity between different genotypes of Fremont cottonwood, the species composition differed between genotypes. Because each genotype of the cottonwood tree supported a certain part of the arthropod fauna populations with higher several genotypes held a higher species diversity of arthropods. Similar findings have been found by scientists like Lau et al. (2016) like and Wimp et al. (2005) who studied other species of cottonwood. This host plant-arthropod interactions might be the explanation for the patterns that cottonwood population in my study did not differ significantly from each other although there were signs of some population types being more favored. Some of the populations might have a larger genetic variation thus supporting a larger variety of arthropod species. It has even been found that plant hybrids among host plants and different cross types of those can lead to higher diversity of arthropods (Wimp and Whitham, 2001). When comparing the three types of cottonwood that had the highest abundance and diversity of arthropods all, but one came from relatively arid areas. In interaction with cottonwood garden they supported the highest abundance as well as diversity of arthropods in Agua Fria, especially herbivores. The studies mentioned above never tested if the different genotypes of cottonwood supported higher species richness in new environments. But as my results suggest this might be the case.

Arthropod diversity and plant survival are both influenced by productivity (Grady et al., 2011, Evans et al., 2012). When the climate in southwestern USA gets warmer, heat stress in the plants is likely to occur. When heat stress strikes cottonwood that are not adopted in such extreme environments the plant productivity is

severely decreased (Amlin and Rood, 2003) and this leads to cascading effect that affects both trees and dependent arthropods. Example of such trophic cascades are that prey-predator interactions, among arthropods as well as between arthropods and plants, change litter decomposition, which is an important component in the nitrogen-carbon cycling in ecosystems. The biodiversity effect on ecosystem functioning under climate change has been shown to be important as in a review of 46 diversity experiments (Isbell et al. ,2015). In this review it was discovered that in the 46 diversity experiments less diverse ecosystem had a drop of up to 50 % in productivity during a warming experiment. It also turned out that these population were less resilient in response to changes and disturbances. This illustrates the importance of understanding the biodiversity response of assisted migration at the translocation site and the effects different genotypes have on the biodiversity.

I show that there is an interaction effect between the common gardens and the different populations of Fremont cottonwood affecting the arthropod diversity and community structure. Further investigation is important as biodiversity can influence ecosystem processes. Future studies should be longer and include measures of the compounds of cottonwood plants, species specific studies on arthropod and plant-herbivore-predator interactions. Earlier studies have already found that high genetic variability in host plant host more diversity of arthropods. This implicates that assisted migration of a variative of genotypes of the host species as well as different host species is important to preserve if the goal is to preserve biodiversity. By studying the biodiversity response to different genotypes, the survival of host plants as well as their effect on food webs at the translocation site could be measured. To include genetics in further experiments is also important to understand ecosystem processes. As shown by Schweitzer et al. (2005) the presence of gal-forming aphids on leaves indirectly decreased the decomposition rate of the leaf litter. In turn different genotypes of the host plant effected the presence of aphids. Longer studies can focus on seasonal and daily variations in arthropod fauna and quality and survival of different cottonwood population types. In this study we only examined the morning fauna during spring. But as shown in a study by Vonshak et al. (2009) arthropod taxa could shift greatly between day and night in desert landscapes. Thus, in this study parts of the diversity of arthropods could have been overseen. Also, repeated sampling could prove to give more information about the diversity.

5 Conclusion

The arthropod diversity and community structure shifted between common gardens. The differences in arthropod diversity between different populations of Fremont cottonwood was only significant in interaction with the common gardens. The diversity tended to peak at mid-elevation and there were signs that at least three cottonwood populations were supporting higher diversities of arthropods than the rest, independent of common gardens. However, that pattern where even stronger in the mid-elevation garden leading to the interaction with garden being significant. If assisted migration should work as a mean of preserving a wider biodiversity this interaction between population types (different genotypes) and the environment needs to be further evaluated. Understanding that different genotypes will support different diversities in new environments is crucial for conservation under new climates where local ecosystems face reduced biodiversity. Further studies should be done on the topic which could lead to more successful assisted migration in terms of biodiversity conservation and ecosystem functioning.

6 Tables and figures

6.1 Tables

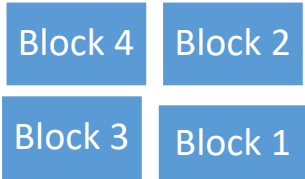
Table 1. The climate factors; (elevation (m.a.s.l.), average temperature (°C)/year and average precipitation (mm)/year) in the origin area of 9 different Fremont Cottonwood Populations. Temperature and precipitation is the annual average for the years 1985-2015(w-nws.webmaster@noaa.gov).

Freemont Cottonwood Population	Elevation (m.a.s.l.)	Average Temperature °C	Average Precipitation (mm/year)
SCT-MEX	100	24.5	0.3
CCR-COL	100	23.4	0.3
LBW-BIL	200	22.5	0.3
CCU-CAV	600	21.6	0.7
MRN-RAT	1300	8.1	1.8
BCE-BUL	1000	10.0	1.8
JLA-JAK	1500	13.2	0.5
KKH-OPI	1900	13.8	0.5
CLF-LCR	1300	14.1	0.5

Table 2. The result from a GLM (Generalized Linear Model) on the effect of garden and population on arthropod communities associated with Fremont cottonwood (*Populus fremontii*) trees from nine different populations planted in three different common gardens (Yuma at 50 m.a.sl., Agua Fria at 1000 m.a.sl. and Canyonlands at 1600 m.a.sl.). Response variables are; Shannon Wiener Diversity Index (SWD Index) and Evenness, and arthropod abundance for different groups; herbivores, predators and ants (Formicidae). Stars indicates that the results are significant between some of the parameters in the model.

Variabales	Source	DF	L-R ChiSquare	Prob>ChiSq
<i>Shannon-Wiener Diversity Index</i>	Garden	2	6.1492109	0.0462*
	Population	8	3.086971	0.9288
	Garden x Population	16	8.9537745	0.9153
	Block	1	1.7012308	0.1921
<i>Evenness</i>	Garden	2	1.082495	0.582
	Population	8	1.0296483	0.9981
	Garden x Population	16	1.6824425	1.0
	Block	1	0.2494295	0.6175
<i>Total abundance (log)</i>	Garden	2	37.355765	<.0001*
	Population	8	94.086771	<.0001*
	Garden x Population	16	98.518524	<.0001*
	Block	1	41.101076	<.0001*
<i>Herbivore abundance (log)</i>	Garden	2	135.52055	<.0001*
	Population	8	29.223029	0.0003*
	Garden x Population	16	101.54746	<.0001*
	Block	1	29.748161	<.0001*
<i>Predator abundance (log)</i>	Garden	2	80.819194	<.0001*
	Population	8	11.273143	0.1867
	Garden x Population	16	24.900636	0.0716
	Block	1	3.5342941	0.0601
<i>Ant abundance (log)</i>	Garden	2	110.83667	<.0001*
	Population	8	0.0001198	1
	Garden x Population	16	45.784318	0.0001*
	Block	1	7.6436118	0.0057

6.2 Figures and pictures



Picture 1. The Common Garden in Canyonlands and the block design of the garden. In each block a square of each of 16 population of cottonwood (*Populus fremontii*) are planted. In each square 8*8 trees are planted.

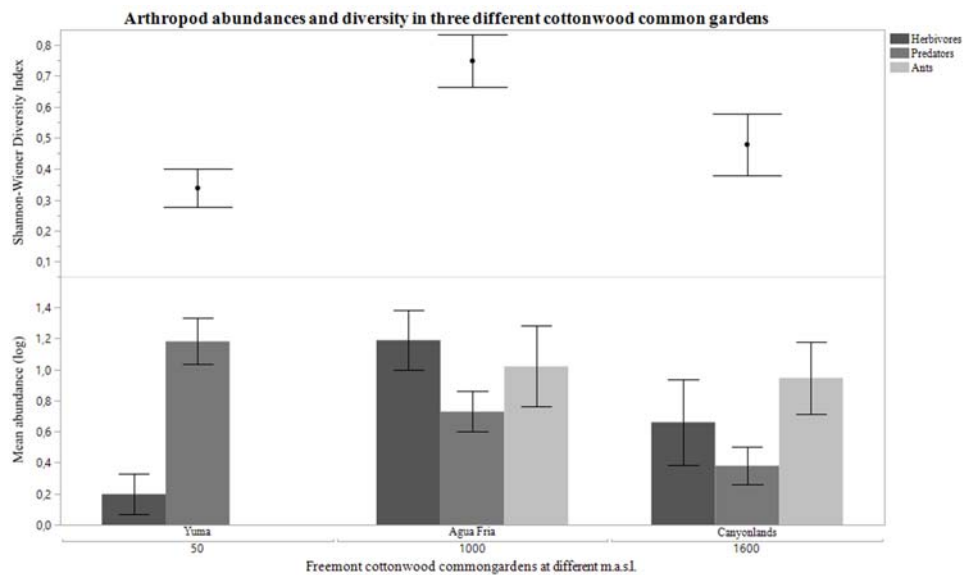


Figure 1. The average and SE (standard error) of SWD Index and log transformed abundances (individual/plot) of three functional groups of arthropods (herbivores, predators, ants (Formicidae) in three Fremont cottonwood (*Populus fremontii*) common gardens, Yuma at 50 m.a.s.l., Agua Fria at 1000 m.a.s.l. and Canyonlands at 1600 m.a.s.l. Significant differences are indicated by nonoverlapping SE and different letter (Tukey HSD $P < 0.05$).

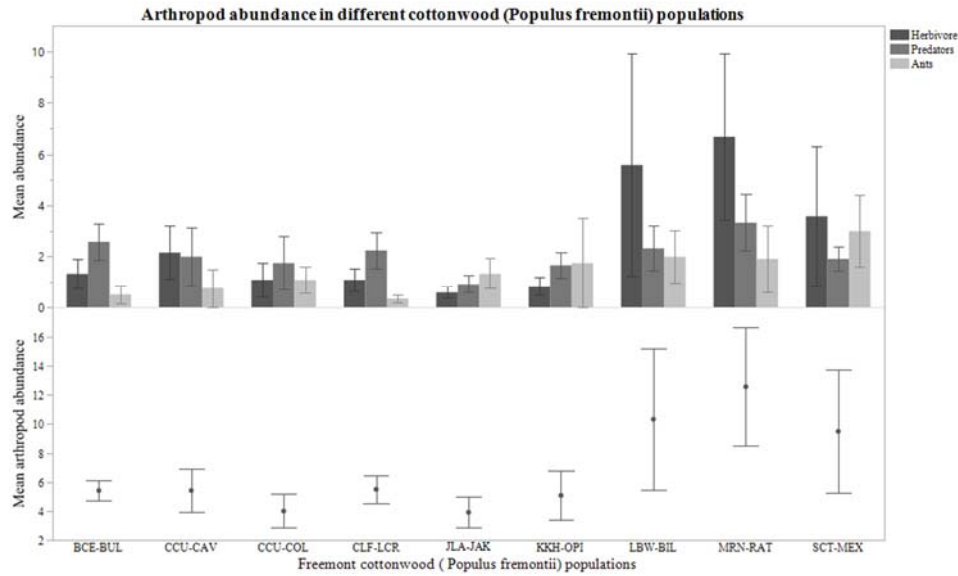


Figure 2. The average (individuals/plot) and SE (standard error) of the total abundance as well as the abundance of three different functional groups of arthropods; herbivores, predators and ants (Formicidae) in nine Fremont cottonwood (*Populus fremontii*) populations. As indicated by SE the differences were not significant as shown by a Tukey HSD ($P < 0.05$) even if GLM ($P > 0.05$).

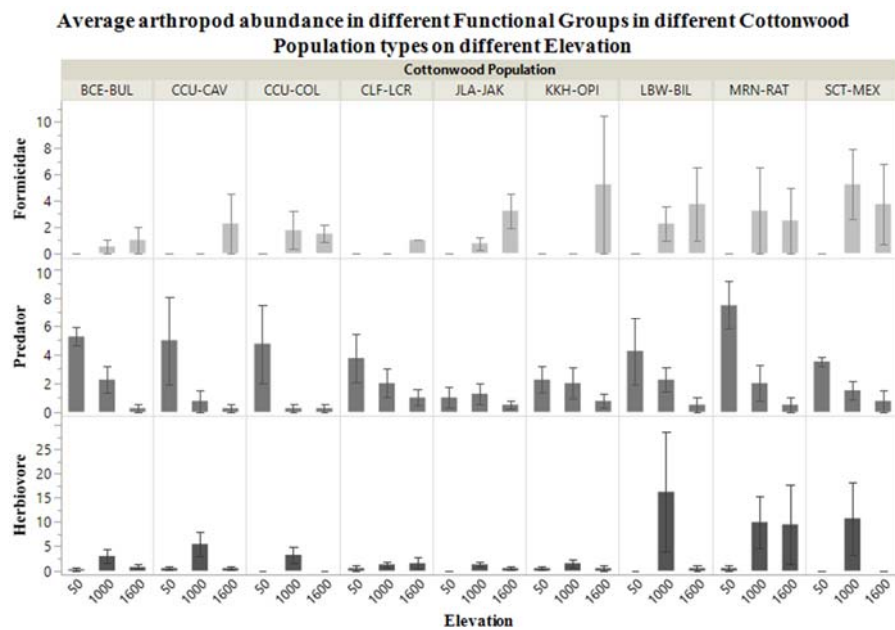


Figure 3. The average (individual/plot) abundance \pm SE (standard error) of arthropods in different functional groups: herbivores, predators, and ants (Formicidae) in different Fremont cottonwood populations (*Populus fremontii*) in three different common gardens (Yuma at 50 m.a.s.l, Agua Fria at 1000 m.a.s.l and Canyonlands at 1600 m.a.s.l).

Arthropod Abundance, Evenness and Shannon Diversity Index in different Cottonwood Population types on different Elevation

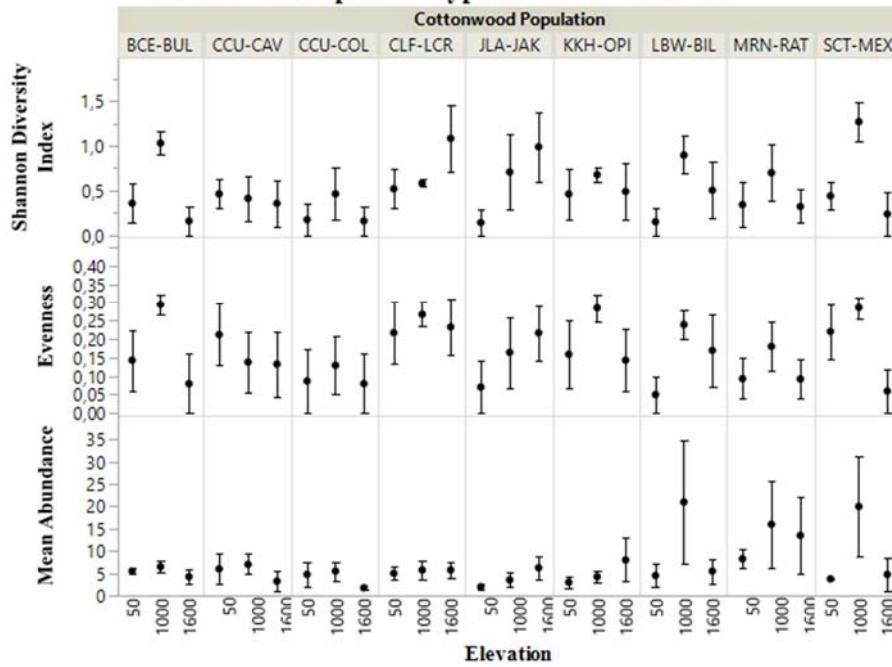


Figure 4. The average abundance (individual/plot), Evenness and SWD Index of arthropods found on Fremont cottonwood (*Populus fremontii*) trees from 9 different populations growing in three different common gardens at different elevation (Yuma at 50 m.a.s.l, Agua Fria at 1000 m.a.sl. and Canyonlands at 1600 m.a.s.l). As indicated by a GLM there were significant effects but in comparison with at Tukey HSD the SE were overlapping thus not significantly different from each other.

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