

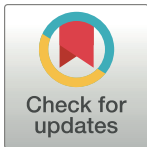
RESEARCH ARTICLE

Assisted migration experiments along a distance/elevation gradient show limits to supporting home site communities

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Abstract

We addressed the hypothesis that intraspecific genetic variation in plant traits from different sites along a distance/elevation gradient would influence the communities they support when grown at a new site. Answers to this hypothesis are important when considering the community consequences of assisted migration under climate change; i.e., if you build it will they come?. We surveyed arthropod communities occurring on the foundation riparian tree species *Populus angustifolia* along a distance/elevation gradient and in a common garden where trees from along the gradient were planted 20–22 years earlier. Three major patterns were found: 1) In the wild, arthropod community composition changed significantly. Trees at the lower elevation site supported up to 58% greater arthropod abundance and 26% greater species richness than more distant, high elevation trees. 2) Trees grown in a common garden sourced from the same locations along the gradient, supported arthropod communities more similar to their corresponding wild trees, but the similarity declined with transfer distance and elevation. 3) Of five functional traits examined, leaf area, a trait under genetic control that decreases at higher elevations, is correlated with differences in arthropod species richness and abundance. Our results suggest that genetic differences in functional traits are stronger drivers of arthropod community composition than phenotypic plasticity of plant traits due to environmental factors. We also show that variation in leaf area is maintained and has similar effects at the community level while controlling for environment. These results demonstrate how genetically based traits vary across natural gradients and have community-level effects that are maintained, in part, when they are used in assisted migration. Furthermore, optimal transfer distances for plants suffering from climate change may not be the same as optimal transfer distances for their dependent communities.

Introduction

With the impacts of climate change now affecting many ecologically important foundation plant species, assisted migration may be required to maintain populations of vulnerable species

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that cannot naturally migrate quickly enough to keep pace with climate change [1–6]. Two types of assisted migration are generally recognized, species rescue assisted migration to avoid extinction among species threatened by climate change and forestry assisted migration to identify populations and genotypes that would achieve higher survival and growth with climate change than local stock and is focused on commercially important, widespread species [7]. The assisted migration strategy to mitigate the impacts of climate change has also begun a meaningful debate about how it may affect target and associated species [8]. We refer to this third type as community assisted migration that is focused on the dependent communities of plant species, which we address in the present study. With assisted migration there has been much discussion about the effects of introducing genetically unrelated individuals into native populations and the potential for genetic pollution [8]. However, transfer distances need not be great and may be conducted within the same population [9]. Especially important for the purposes of our study, there are few studies that have examined the possible genetic effects of assisted migration on the associated communities of plant species and the potential loss of biodiversity that might result from assisted migration (but see [10], and modeling by: [11]). As assisted migration to mitigate the impacts of climate change has become adopted as policy in British Columbia, Canada [3, 12–14], this approach is likely to become more widespread where the impacts of global change are most threatening. There is a great need for studies that test how assisted migration, especially of long-lived foundation species such as trees, will affect their associated communities and the resulting changes in the biodiversity of their respective ecosystems. Importantly, optimal distances for plant transfers based on plant performance (e.g., survival and growth) in response to climate change [15], may not be the optimal transfer distances for their associated community members (e.g., biodiversity or maintaining home site communities) such as insects and it is important for climate change mitigation to be considered within a community context [16, 17].

Although most studies have focused on the assumption that climate change will result in upward shifts in plant distributions, several studies have now documented downward shifts with climate change that are thought to be due to altered precipitation regimes [18–22]. Thus, examination of both up and downward shifts in plant distributions are important to understand in the context of their associated communities. Examination of how plant species and their associated communities may change along a distance/elevation gradient is a first step in being able to predict the responses of plants and their associated communities to a changing climate. While many studies have shown that plant functional traits vary along an elevation gradient [23], and that intraspecific variation may account for a significant portion of this variation [24–26], few have linked those changes to differences in the communities they support and their trophic level interactions (but see [27]). Because intraspecific variation in plant traits along abiotic gradients has been shown to have community and ecosystem consequences [28–36], it is important to also examine how variation in traits along gradients may be affected by climate change [31, 37]. If plant trait variation along a gradient shifts due to a changing environment there is the potential for large effects on dependent communities.

While many studies have examined how intraspecific variation in plant traits affects communities using either observational studies in the wild or common garden experiments (e.g., [38–40]), very few have simultaneously compared naturally occurring trait variation along a gradient and in a common garden to determine if similar patterns emerge. Using distance/elevation gradients has the potential to greatly inform plant and arthropod community responses to climate changes. This concept has previously been referred to as space for time substitution [41].

Here, we examine arthropod communities on the foundation tree species *P. angustifolia* along a distance/elevation gradient and in a 20yr common garden experiment to differentiate

between hypotheses that affect the role of assisted migration to preserve associated species that might otherwise go locally extinct due to a changing environment [42]. By using a common garden to control for environment combined with populations of trees transferred different distances (i.e., 18, 48, and 90 km along an elevation gradient of 100, 320, and 530 m, respectively, from the common garden site) we were able to address three hypotheses related to elevation diversity gradients and climate change: 1) Populations of the foundation tree species *P. angustifolia* along an elevation gradient in the wild will support different arthropod communities; 2) When planted in a common garden replicated tree genotypes from along the elevation gradient will support levels of arthropod abundance and species richness more similar to their home site; and 3) Trees moved farther (i.e., both distance and elevation) from their home site will experience more change in the composition of their arthropod communities. To differentiate among these hypotheses, we quantified the communities in the wild across the gradient. We then quantified the communities that colonized individual tree genotypes in a common garden in which genotypes from across the gradient were planted in the same common garden at the lower elevation edge of the species' distribution. By planting higher elevation genotypes at the low edge of the species' distribution we achieved an assisted migration experiment, and simulated a climate change event in which the planting site averaged 0.5°C, 1.0°C, and 1.5°C warmer than the low, mid and high elevation sites (NOAA), respectively in this river system. This temperature increase reflects past and ongoing changes that are projected to be much greater. For example, in the American southwest, from 1886–2016 temperature has increased by 0.9°C and projected changes through the rest of this century are for temperatures to increase by as much as 4.8°C, which will be accompanied by chronic future precipitation deficits [43]. Currently, the American southwest is suffering from an ongoing megadrought that began in 2000 that is considered to be the 2nd worst in 1200 years [44].

The outcome of this experiment is especially important to the assisted migration debate as one of the goals of assisted migration is to not only preserve the plant species that might be lost with climate change, but also the communities they support [17]. Here we hypothesize that the communities plants support will be more similar to their home site rather than transfer site until transfer distance/elevation becomes too great (i.e., there exists a maximum community transfer distance). This would suggest that assisted migration when done correctly will also benefit the associated communities from plants' home sites; i.e., if you build it they will come. If assisted plants support only the communities from their new environment, then one of the major goals of assisted migration will be negated. We also examine potential mechanisms that could affect this hypothesis; i.e., we show that average leaf area, a trait known to be under genetic control [45], is significantly correlated with arthropod abundance and richness along the gradient and is likely responsible for some of the variation in arthropod community differences.

Methods

Study sites and common garden

Our study was conducted along the Weber River in and near Ogden Utah and at the Ogden Nature Center. The distance and elevations of these sites in the wild from the common garden were approximately: Low = 18 km up river and 100 m higher than the common garden, Medium = 48 km and 320 m, and High = 98 km and 530 m. These three sites were chosen due to their being the sources for the tree genotypes that were initially planted in the common garden. The low elevation site occurs just above the hybrid zone where both Fremont cottonwood (*P. fremontii*), narrowleaf cottonwood (*P. angustifolia*) and their hybrids naturally co-occur to form stands of complex backcross hybrids. Introgression is unidirectional in which F₁ hybrids

backcross with *P. angustifolia*, but not *P. fremontii* [46, 47]. The common garden was located at the Ogden Nature Center in the city of Ogden (966 W 12th St, Ogden, UT 84404) and was at an elevation of approximately 1300 m above sea level.

The common garden was established 20–22 yrs ago with replicated clones of different *P. angustifolia* genotypes. This cottonwood is a dominant of riparian habitats and is widely distributed throughout the Rocky Mountains of the U.S. and southern Canada [48]. All trees planted in the common garden had been randomly collected from an interbreeding population [47] along the Weber River, northern Utah, U.S. and planted in a random haphazard design. Ten tree genotypes that originated from each of the elevation sites were haphazardly selected, yielding a total of 30 trees to pair with trees from the wild sites. Trees averaged 10–15 m tall at the time of our arthropod surveys.

Arthropod surveys

Arthropod surveys were conducted using the methods of [49] where leaf area was standardized using timed, observational censusing conducted for 20 minutes per tree. Any arthropods not recognized were collected and later identified to the highest taxonomic level possible. To adjust for changes in leaf flush phenology across this elevation gradient, surveys were performed in early June (1st–7th) at the low elevation site, mid-June (11th–18th) at the mid elevation site and late June (25th–30th) for the high elevation site. This adjustment in the time of arthropod censusing attempted to equalize the time the arthropod community had to develop after leaf flush and was timed to maximize the yearly richness and abundance of the arthropod community [50]. Surveys in the common garden (similar elevation to low site) were also done in early June at a time when arthropod communities have been shown to be experiencing peak abundances [49].

Measurements of functional traits

Using previously collected data for individual tree genotypes in the common garden we examined five different tree traits likely to be under genetic control (nitrogen content, % dry weight condensed tannins and salicortin (plant defensive compounds; [51–53]), growth rate constant, and average leaf area). We used standard chemistry analyses for the phytochemical traits (see [50]). Diameter at breast height (DBH) ([54]) was used to examine growth rates, and standardized measurements of ten leaves from each of five trees was used to determine average leaf area. In a post-hoc analysis of leaf area to account for potential genotypic differences among trees in the wild, we examined the average leaf area of ten leaves among ten different tree genotypes at each elevation. Five sun leaves from the north and south sides of each tree were selected in the mature portion of the tree canopy.

Statistical analyses

To test for differences in the richness and abundance of arthropod communities along the elevation gradient and in the common garden, we used General Linear Models (GLM) followed by a Tukey's HSD test to determine differences among groups. We conducted separate tests for the arthropod abundance and species richness among trees along our elevation gradient and the trees within the common garden. To examine the effect of elevation/distance and origin across all trees, we used a General Linear Mixed Model (GLMM) with a grouping variable to combine the effects of site elevation and tree genotype origin where genotype was a random effect nested within all trees and site was a fixed effect used as our predictor variable (Nested ANOVA). Abundance data was relativized by species maximum to prevent common species such as aphids from driving community patterns.

Standard linear regression was used to test for correlations of arthropod species richness and abundance with functional tree traits in the common garden trees. We tested the plant traits of plant productivity (Growth Rate Constant), defensive chemistry (salicortin and condensed tannins), leaf nitrogen content, and average leaf area for correlations with the arthropod community factors of species richness and abundance. We again used GLM followed by a Tukey's HSD to determine differences. All statistical tests were performed using SAS statistical software [55].

Non-Metric Multidimensional Scaling (NMDS) analysis was performed using PcOrd version 5 [56]. To compare differences in arthropod community composition among wild and common garden trees we used analysis of similarity (ANOSIM) performed in the statistical software program Primer [57]. All analysis of similarity tests used Bray-Curtis dissimilarity matrices and square root transformations. ANOSIM (analysis of similarity) results were interpreted by "Global-R" which is a score between zero and one where a score of 1.0 would be completely different communities and a score of 0.0 would be identical communities.

Results

Hypothesis 1: In the wild, populations of P. angustifolia along an elevation/distance gradient support different arthropod communities

In support of our first hypothesis, we found that wild trees at our low elevation/distance site supported significantly higher (25%) average species richness of an arthropod community consisting of 61 total species ($F_{(2,27)} = 9.61$, $P = 0.0007$) than trees at medium and high sites. Similarly, low elevation/distance trees also supported significantly higher (32%) average arthropod abundance ($F_{(2,27)} = 4.34$, $P = 0.02$) than trees at medium and high sites (Fig 1A). Richness and abundance did not significantly differ between mid and high elevation sites.

Hypothesis 2 –In a common garden, tree genotypes derived from along the elevation/distance gradient will support levels of species richness and abundance similar to their home sites.

We found evidence that strongly supports this hypothesis. First, in the common garden using ANOVA tests to compare communities on trees from low, medium, and high origin, we found that trees from low elevation origin supported significantly higher (up to 26%) arthropod richness ($F_{(2,27)} = 6.09$, $P < 0.007$) than trees from medium and high origins. Second, trees in the common garden from low origin also supported significantly higher (up to 58%) arthropod abundance ($F_{(2,27)} = 20.21$, $P < 0.0001$) (Fig 1A) than medium and high origin trees. These findings were similar to our findings in the wild but with all trees in one location (i.e., a standardized environment) and suggest that patterns of richness and abundance are likely due to differences in genetically controlled plant traits that in this case have been maintained twenty plus years after trees were clonally replicated and moved from their home site to the common garden.

Although patterns reported above utilized all the species encountered, we sought to examine the potential for rare species or species restricted to one site to drive overall differences in our observed patterns. Therefore, we performed the same analyses using only the 13 common (i.e., ubiquitous) species found at all sites. Similar to our analyses of the whole community, when we examined the abundance of the 13 ubiquitous species we again found support for our hypotheses that trees at the lower elevation wild site and trees in the common garden of low elevation origin continued to support higher arthropod abundance than trees from higher elevation origins (Wild- $F_{(2,27)} = 9.78$, $P < 0.001$, Garden- $F_{(2,27)} = 31.40$, $P < 0.0001$) (Table 1) (Fig 1B). However, when we independently examined the 13 ubiquitous species community we

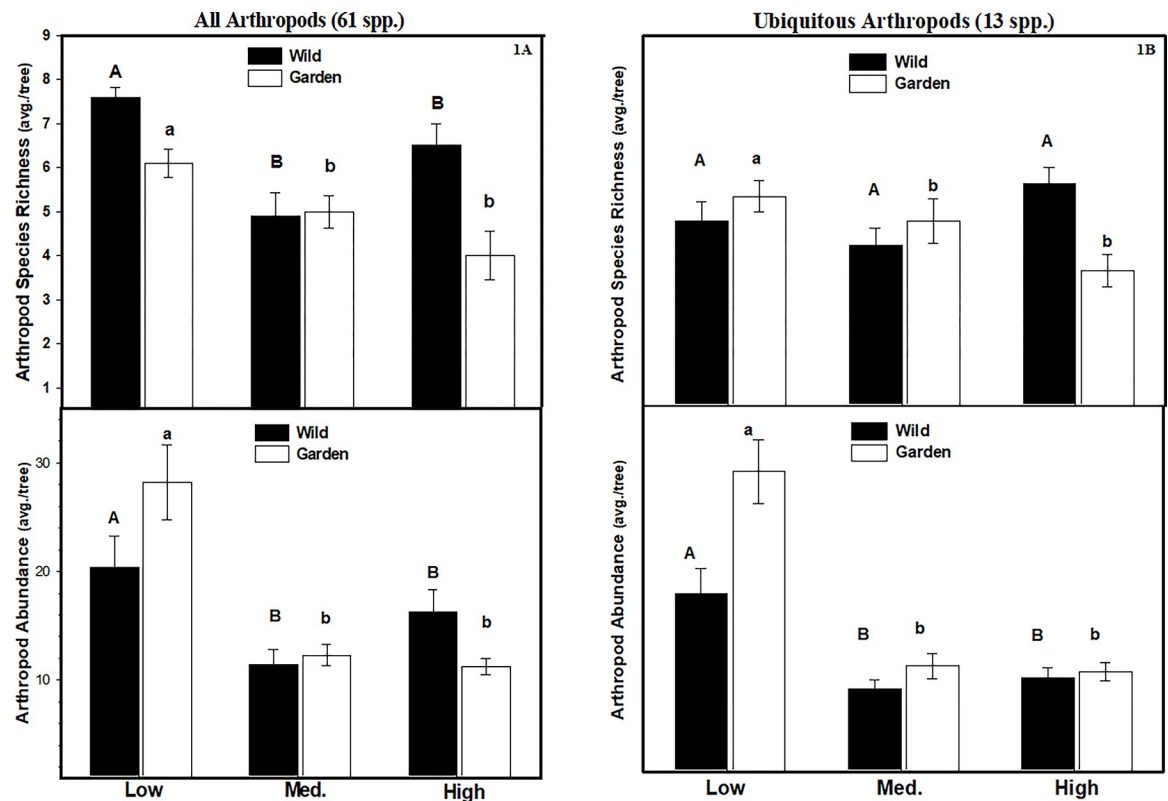


Fig 1. A. ANOVA results of differences in arthropod species richness and abundance for a community composed of 61 species. Trees at low elevation sites supported significantly greater arthropod species richness than trees at medium and high elevation sites in both the wild and in a 20 yr old common garden (Wild: $F_{(2,27)} = 9.61$, $P = 0.0007$) (Garden: $F_{(2,27)} = 6.09$, $P < 0.007$). Trees at low elevation/distance sites also supported significantly greater arthropod abundance than trees at medium and high elevation sites in both the wild and common garden (Wild: $F_{(2,27)} = 4.34$, $P = 0.02$) (Garden: $F_{(2,27)} = 20.21$, $P < 0.0001$). Uppercase letters indicate significant differences among trees in their respective locations (Wild vs. Common Garden) (example: Arthropod Species Richness at the low elevation site in the wild (A) was significantly different from species richness at the medium and high sites in the wild (a)). **B.** ANOVA results of differences in arthropod species richness and abundance for 13 ubiquitous species. Trees at the lower elevation site and trees in the common garden of low elevation/distance origin supported higher arthropod abundance than trees from higher elevation origins (Wild- $F_{(2,27)} = 9.78$, $P < 0.001$, Garden- $F_{(2,27)} = 31.40$, $P < 0.0001$). However, when we examined the 13 ubiquitous species community we found only a marginal difference in species richness among trees in the wild (Wild- $F_{(2,27)} = 2.97$, $P < 0.06$) while trees from low elevation/distance origin in the common garden supported significantly higher species richness than medium and high trees (Garden- $F_{(2,27)} = 4.24$, $P < 0.02$). Uppercase letters indicate significant differences among trees in their respective locations (Wild vs. Common Garden) (example: Arthropod Abundance at the low elevation site in the common garden (B) was significantly different from abundance at the medium and high sites in the common garden (b)).

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Table 1. Results of nested ANOVA analysis. A grouping variable was used to combine the effects of site elevation and tree genotype origin where genotype was a random effect nested within all trees and site was a fixed effect used as our predictor variable. Trees from low elevation and low origin supported significantly higher arthropod species richness and abundance when compared to medium and high elevation trees.

Nested ANOVA Results			
Effect test			
Trees [Elevation/Origin]	df	F	P
Arthropod Richness	2	5.76	0.01
Arthropod Abundance	2	8.37	0.001

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found no significant differences in species richness among trees in the wild (Wild- $F_{(2,27)} = 2.97$, $P < 0.06$) while trees from low elevation origin in the common garden supported on average significantly higher species richness than medium and high trees (Garden- $F_{(2,27)} = 4.24$, $P < 0.02$) (Fig 1B). This marginal result ($P < 0.06$) may have been due to the considerably smaller pool of species examined (i.e., less possible variation in richness). These results demonstrate that arthropod community differences found on trees at sites along an elevation gradient in the wild are conserved in a common garden made up of trees from those different sites after being moved to a lower and warmer elevation.

Hypothesis 3—Trees moved farther from their home site will experience more change in the composition of their arthropod communities.

Three lines of evidence support of our third hypothesis. First, we found that changes in elevation/distance affected the similarity of the communities trees supported. By using non-metric multidimensional scaling (NMDS) and analysis of similarity (ANOSIM) we found that as trees were moved farther from their home site the communities they supported became less similar to the home site. While all communities found at wild sites were significantly different from the communities found on corresponding trees of elevation/origin in the common garden ($P < 0.05$), the arthropod communities from the low elevation site in the wild were more similar in composition to the arthropod communities found on low elevation tree genotypes in the common garden (i.e., their NMDS points were closer to each other in ordination space) (Anosim- $R = 0.319$, (where R ranges from 0.0–1.0)) (Fig 2). Additionally, the tests showed that arthropod communities found on trees from the medium elevation site in the wild and medium elevation sourced trees in the garden had less similar communities (Anosim- $R = 0.681$) than between the low sites. Finally, the communities found at the high elevation sites in the wild and high elevation sourced trees in the common garden had the least similar communities (Anosim- $R = 0.804$) (Fig 2). In other words, the farther trees were moved, the greater the differences between their communities in the garden relative to their home sites.

Second, when we performed the same tests on the 13 species ubiquitous community, we found the same pattern in which low elevation communities in the wild were most similar to their corresponding genotypes in the garden, high elevation communities were least similar to those planted in the common garden and the middle elevation site was intermediate (Low, $R = 0.235$, Medium, $R = 0.483$, High, $R = 0.872$). These results demonstrate that as trees were moved farther from their home sites their communities become more different. Thus, with transfers > 50 km and elevation > 320 m, the environment may become a stronger factor shaping arthropod communities than differences in genetically controlled plant traits (Fig 2).

Third, using Shannon's Diversity Index we found that trees moved farther from their home site experienced significant changes in the diversity of their arthropod communities. The high elevation/distance trees moved to the common garden had significantly less community diversity (Shannon's Diversity H : Elevation gradient in the wild = 2.04, Garden = 1.50)(t -test: $F = 108.53$, $p < 0.0001$) (Fig 3) while the diversity of communities on low and medium site trees in the wild were not significantly different from their corresponding tree genotypes in the garden.

These results demonstrate that when trees are moved along a distance/elevation gradient the composition of the communities they support changes, and as transfer distance increases communities become less similar and less diverse.

Variation in tree traits as potential mechanisms

Of six functional tree traits known to be under genetic control [45], we found that average leaf area was correlated with differences in arthropod communities both in the garden and along

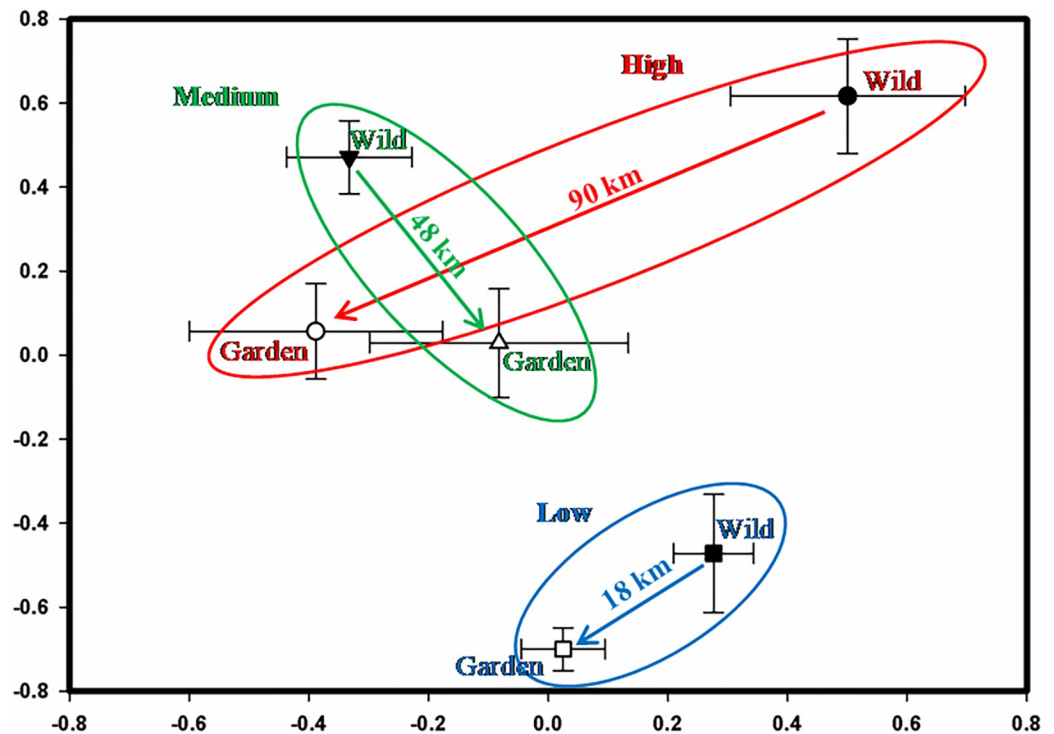


Fig 2. Non-Metric Multidimensional Scaling (NMDS) figure comparing arthropod communities on trees along an elevation gradient and in a common garden. Communities that are more similar appear closer together while communities that are more dissimilar appear farther apart. Centroids represent community genotype means while error bars represent 95% confidence limits. All wild communities were significantly different from their common garden communities ($P < 0.05$). Arthropod communities found on trees from the low elevation site were more similar to the communities found on trees from low elevation origin that were grown in a 20 yr. common garden (Anosim- $R = 0.319$) (R values range from 0.0–1.0. R values closer to 1.0 represent more dissimilar communities and R values closer to 0.0 represent more similar communities. Additionally, the communities found on trees from the medium elevation site and garden were more dissimilar than between low elevation trees (Anosim- $R = 0.681$). While communities found on trees of high elevational in the wild and of high origin but grown in a lower, warmer common garden were the most dissimilar (Anosim- $R = 0.804$).

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the elevation/distance gradient. Using previously collected data from replicated tree genotypes in the common garden (see [methods](#)) we examined the plant traits (productivity, nitrogen content, defensive chemistry (condensed tannins, salicortin) and average leaf area). We found that only one, average leaf area, was correlated with differences in arthropod communities found in the garden on tree genotypes originating from the elevation/distance gradient.

Three lines of evidence support the importance of leaf area. First, in the common garden when we examined tree genotypes originating from along the gradient but transferred to the common garden, we found that arthropod species richness among trees in the common garden increased with increasing leaf area ($P = 0.04$, $R^2 = 0.14$) ([Fig 4](#)). Second, we also found that arthropod abundance significantly increased with increasing leaf area ($P = 0.03$, $R^2 = 0.15$) ([Fig 4](#)). The fact that arthropod species richness and abundance show a positive relationship with leaf area suggests that leaf area may be responsible for some of the differences found in communities on trees from different elevations/distances. Third, in the wild, a post hoc analysis of leaf area among the three sites of origin showed that leaf area at the lower site was significantly greater than both the medium and high elevation sites ($F = 125.53$, $P < 0.0001$) ([Fig 5](#)), but there were no differences between the medium and high sites. This result is similar to and supports the above findings of differences in arthropod richness and abundance found on

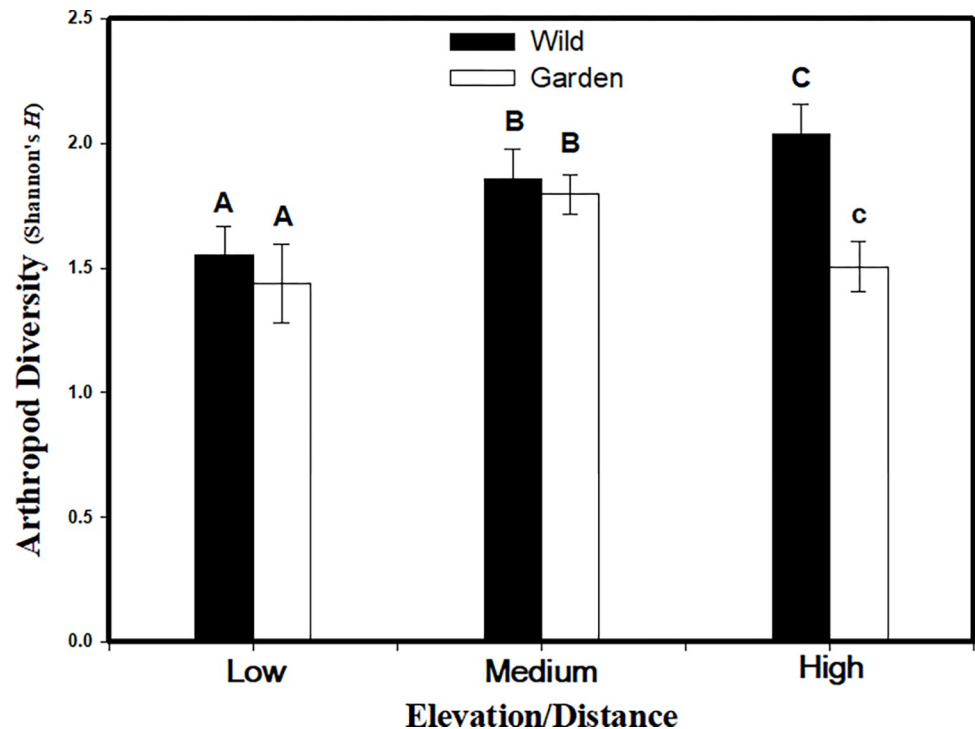


Fig 3. Bar graph showing Shannon's diversity index of arthropod communities. (Shannon's Diversity H' : Elevation gradient in the wild = 2.04, Garden = 1.50)(t -test: $F = 108.53$, $p < 0.0001$). High elevation trees in the wild (C) had significantly less diverse arthropod communities than high elevation trees in the common garden (c). Diversity of arthropod communities on low and medium site trees in the wild (A, B) were not significantly different from their corresponding tree genotypes in the garden (A, B).

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trees at the low site in the wild and low origin trees in the garden, but no significant differences between the medium and high sites in the wild.

Discussion

Genetic differences of trees affect communities along an elevation/distance gradient

In support of our first hypothesis, our findings demonstrate that arthropod community differences on a foundation tree species in the wild exist along a distance/elevation gradient. Because these differences in communities could be due to genetic differences among trees, environmental effects on arthropod communities, or both, a common garden study was used to differentiate among these effects. Our second hypothesis that tree genetics along the gradient played an important role in defining arthropod communities was largely supported in common garden studies, but there were important systematic differences related to our third hypothesis. Our third hypothesis accurately predicted that trees moved farther in both distance and elevation to the common garden site would experience greater changes in the composition of their arthropod communities to become more of a blend of new and home site communities. Thus, in agreement with many other studies showing a strong genetic component to arthropod community assembly based upon intraspecific genetic variation within a plant population (e.g., [38–40]), these findings also support a genetic component to arthropod community assembly that is defined, in part, by intraspecific genetic variation in plants along an elevation gradient of only a few hundred meters and distance of <100km.

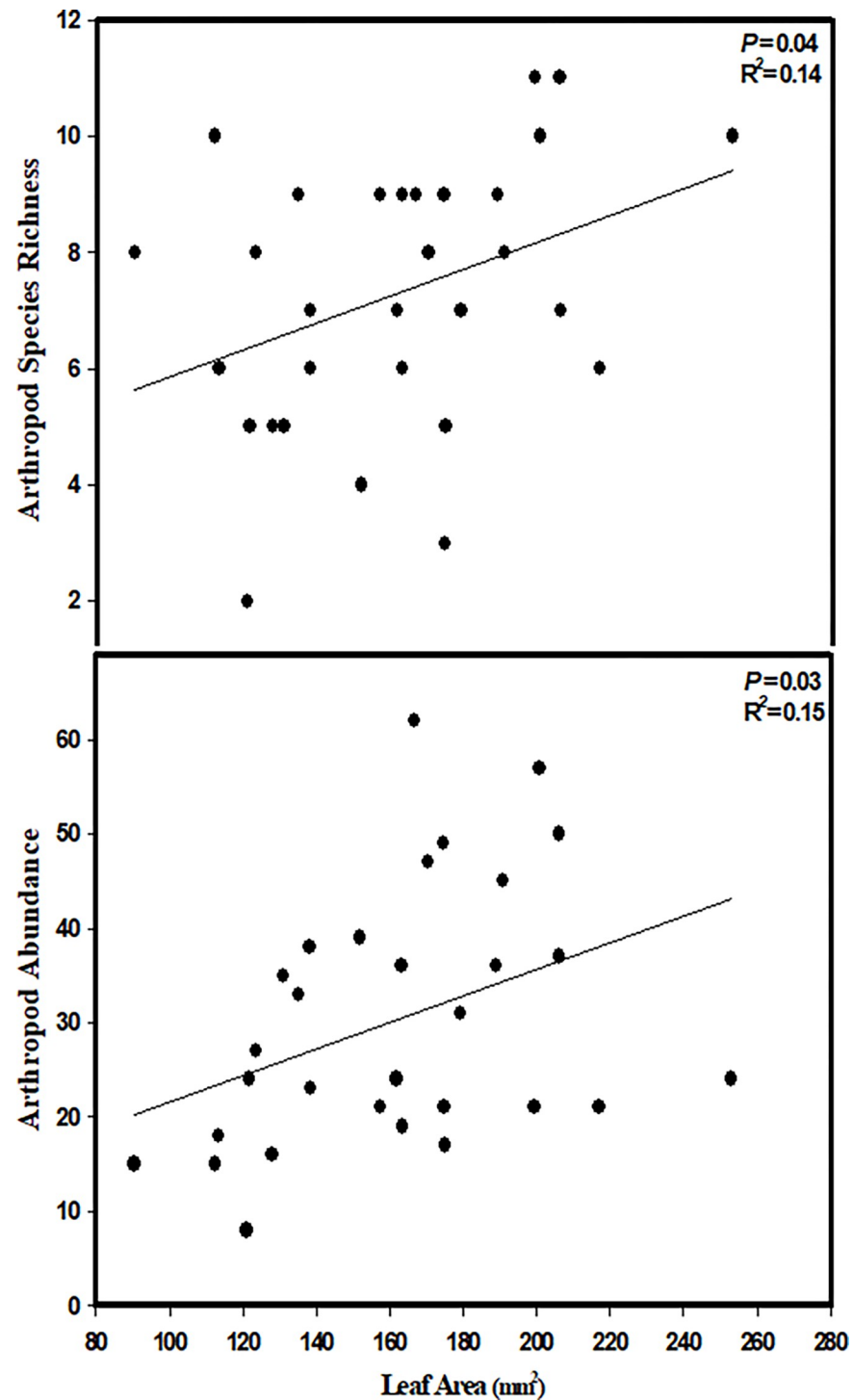


Fig 4. A. Plot of linear regression of the effects of leaf area on arthropod species richness within a common garden. Leaf area varies with elevation and is positively correlated with arthropod species richness ($P = 0.04$, $R^2 = 0.14$). B. Plot of linear regression of the effects of leaf area on arthropod abundance within a common garden. Leaf area, a genetically controlled trait, varies with elevation and is positively correlated with differences in arthropod abundance ($P = 0.03$, $R^2 = 0.15$).

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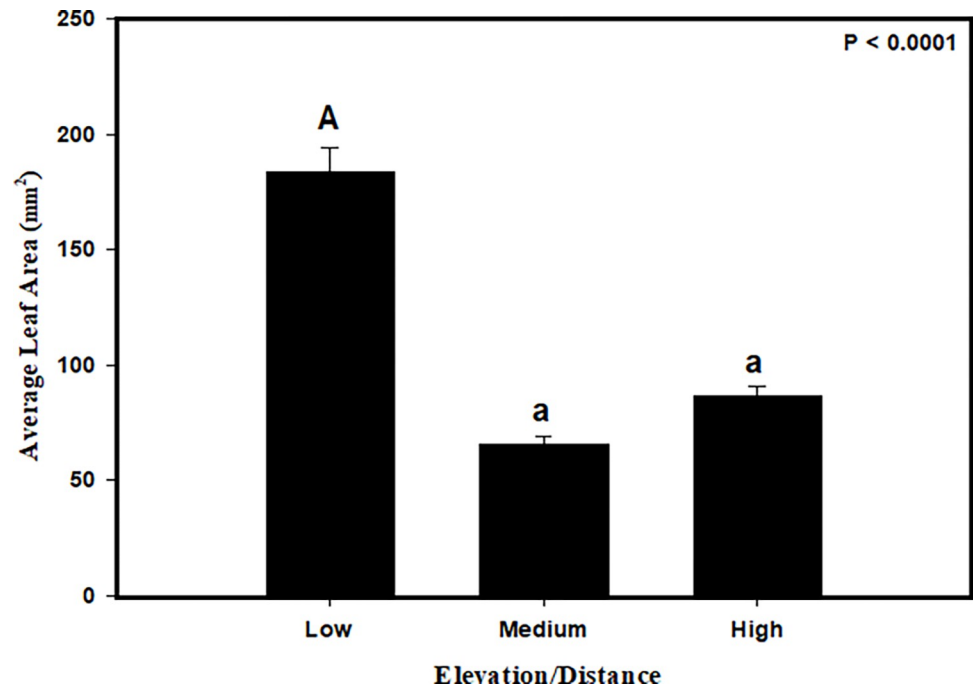


Fig 5. Bar graph of differences in leaf area among the different elevation sites where arthropod surveys were conducted in the wild. Leaf area was significantly greater at the low elevation site where arthropod abundance and species richness were also greater ($F = 125.53$, $P < 0.0001$).

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We suggest that the most likely explanation for these results is that natural selection on plant functional traits and local adaptation has occurred due to environmental differences along the gradient, and that those differences in turn affect arthropod community structure. Studies of several plant species using common gardens and plants collected from different elevations has provided evidence for genetically-based ecotypic variation in leaf size, morphology, chemistry, phenology and ecophysiology of plants [58–62]. Factors such as changes in partial pressures of CO_2 , differences in temperature and UV exposure, length of growing season, and soil quality can affect the phenology, morphology, physiology, and chemistry of plants, which in turn have consequences for their dependent insect communities [63]. Such differences have been quantified along a latitudinal gradient with *P. angustifolia* [64], and along an elevation gradient with *P. fremontii* [6, 15, 29, 62]. Importantly, F_{ST} and Q_{ST} studies by Evans et al. [64] over a gradient of 1700 km and 15.9° latitude showed that climate has selected for differentiation in phenology and growth traits across the gradient, which has led to local plant adaptation with predictable impacts on the arthropod community. Furthermore, observational studies in the wild have documented how galling insects, which are common in our studies, generally decline with increases in elevation [65] and especially in xeric habitats [66], but few studies have experimentally differentiated the genetic and environmental components of these findings (but see [67]).

Potential mechanisms for community assembly and stability

Our study shows that genetics-based population differences in leaf area exist and are consistent with expectations along an elevation gradient (smaller leaves at higher sites and bigger leaves at lower sites) and that these differences remain when transplanted to a low elevation common garden. Genetic-based differences in leaf size have long been recognized in this system as

being related to leaf economic traits associated with plant stress (e.g., [45]) and to the gall forming aphid *Pemphigus betae* that survives and reproduces far better on large versus small leaves both within and among trees [68–70]. Larson et al. [71] and Compson et al. [72] showed that aphid performance was strongly related to sink-source relationships and the aphid's ability to create artificial sinks on susceptible trees that had larger leaves relative to resistant trees. These trees also differed greatly in their phytohormone profiles [53] and several candidate genes for aphid resistance have now been identified [73]. In turn, these leaf size, sink-source and phytochemical differences define the interactions of trees and aphids, which in turn affects a diverse community of organisms of up to 139 species [49, 74, 75].

While we've demonstrated a genetics-based correlation of leaf area with differences in arthropod abundance and richness, there are likely suites of plant traits that vary among individual tree genotypes to also affect community composition and stability. For example, Blasini et al. [62] showed that an adaptive syndrome of physiological traits including leaf size, phenology, xylem vessel size, and stomatal density defined high and low elevation adapted ecotypes of *P. fremontii*. Such adaptive plant trait syndromes across diverse environmental gradients are likely to have extended phenotypes on associated community members, especially ones that interact in direct and indirect ways with the specific plant traits involved in an adaptive syndrome. Such cascading effects have been demonstrated by Lamit et al. [76] in which the plant genotypes that affected one community (e.g., arthropods) also simultaneously affected other disparate communities of leaf pathogens, lichens, twig endophytes, soil decomposing bacteria and fungi, and ectomycorrhizal fungal mutualists.

Community responses with assisted migration

While the majority of assisted migration efforts involve moving plants up in elevation to cooler sites (e.g., [3]), there are a surprising number of studies showing that some plants are also migrating downward [19–22]. For example, using 40 years of occurrence records for 293 plant species across Western North America, Harsch and HilleRisLambers [22] showed that many plants were just as likely to move down in elevation as up even with overall warming across the study area. Additionally, Crimmons et al. [20] examining 61 plant species showed that changes in climatic water balance can drive downward migration in species distributions. For the plants that do show significant downward shifts in their distributions with climate change, a common garden positioned at a lower elevation than the source populations in the wild (as in the present study) represents a valid assisted migration experiment. Furthermore, using downward shifts as a surrogate for climate change in which plants are grown in a hotter environment with a longer growing season suggests likely outcomes as higher elevations become increasingly warmer.

Our findings go beyond other studies in showing that community diversity and assembly in a common garden is affected not only by the underlying genetics of the plant, but also by the distances and elevations between their home sites of origin when they are transferred to a common garden or restoration site. Similarly, a study by Vandegehuchte et al. [10] showed that the introduction of non-local genotypes of a resident grass species (*Ammophila arenaria*) negatively affected local invertebrate communities, and that invertebrate diversity decreased with increasing geographical distance. However, we know of very few if any comparable studies examining an “associated community transfer distance” (see also: [77]). Our findings suggest that assisted migration of plants will affect arthropod community structure in predictable ways, which could have large ecological implications, and should therefore be explored further. Because the patterns are the same as presented in the next subsection, to avoid duplication, our discussion of these findings is presented below.

Genetic variation in arthropods could also affect assisted migration

In our downward assisted migration experiment (i.e., climate change simulation), our results show the importance of tree genetics along elevation and distance gradients in affecting arthropod community structure. Although not examined in the present study, we must also consider the hypothesis that arthropods also are genetically differentiated across distance and elevation gradients and these genetic differences could affect the outcomes of assisted migration. While most high elevation arthropod species are also present at the low elevation garden, genetic differentiation in the arthropods over an elevation gradient may result in a mis-match with the genetics of their host trees in the wild or in restoration sites. E.g., Evans et al. [78] found gall-forming mites were adapted to individual tree genotypes and performed much better on their natal trees. Similarly, Moran and Whitham [79] experimentally documented genetic based differences in the life cycle of the aphid *Pemphigus betae* at low and higher elevations that were shown to affect their performance when experimentally transferred across sites.

Another source of genetic variation that could affect assisted migration is genetic based differences in interaction networks [80]. Because lower elevation sites support a richer community with greater abundances, the community interaction networks are likely very different and these interactions can affect how communities assemble on different tree genotypes (see also [27] showing that tri-trophic interactions predictably change with elevation). Furthermore, Keith et al. [75] experimentally found that trees genetically susceptible to *P. betae* supported a much richer community with different interaction networks than trees that were resistant demonstrating how interactions can promote community diversity. Lastly, restoration biologists need to consider how the migration abilities of arthropods locally adapted to their high elevation host trees may be important such that some have migrated over the 20 year period since the establishment of our common garden, while others have not. It is difficult to parse out these effects without further studies, but for *both* individual arthropod species and their host trees, we are likely dealing with genetic effects, environmental effects and their interactions [17].

Management applications

Overall, these results suggest that tree populations found at higher elevations when challenged with future climatic conditions and/or greater transfer distances to a lower elevation climate, are less apt to support diverse communities. These differences are likely due, in part, to plant and arthropod trait differences that have locally evolved to different environmental conditions. However, low and intermediate elevation plant populations transferred to a lower garden, were more similar in their arthropod communities in the wild and in the garden (Fig 2). It appears that intermediate transfer distances or a step-wise or more gradual approach to assisted migration may be necessary to conserve biodiversity and support of associated communities from home sites. In other words, these findings argue that if you build it close enough they will come, but even then the communities will not precisely match their home communities, they will likely be somewhat intermediate between the restoration site and the wild source sites (Fig 2).

The development of optimal transfer functions for both plants and their associated communities could result in greater project success. In previous studies, a change of 500 m in elevation is likely to result in an average temperature change of between 2.25 and 3.25°C [81]. With such changes, where should the source populations of trees be derived for successful assisted migration? A study by O'Neill et al. [14] used 8 climate variables to determine an optimal transfer function for lodgepole pine (*Pinus contorta*), and similarly Grady et al. [15] used Mean Annual Maximum Temperature (MAMT) to determine an optimal transfer function for assisted

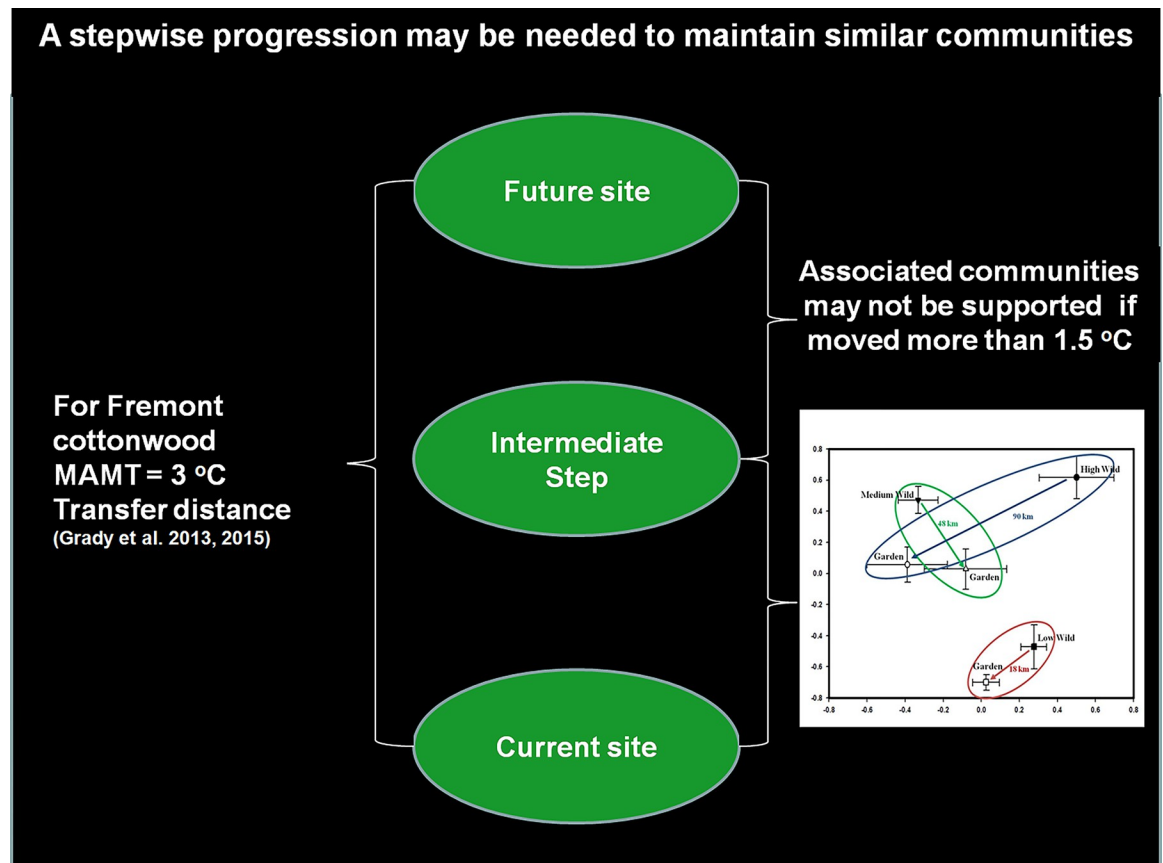


Fig 6. Conceptual diagram of stepwise progression procedure for assisted migration of host plants while maintaining their home site arthropod communities. If home site arthropod communities are to be kept intact then a stepwise progression is likely needed. To maintain site of origin arthropod communities we suggest assisted migration efforts for narrowleaf cottonwood trees should not exceed distances greater than 50km and a change in elevation greater than 250m in elevation relative to their original location [Table 1](#).

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migration of *P. fremontii*. In examining plant survival O'Neill et al. [3], found that assisted migration distances of 200m in elevation were acceptable in several species of conifers, while Grady et al. [15] found that a temperature increase of less than 3°C would be best suited for assisted migration of Fremont cottonwood.

While the above studies show how optimal transfer functions for individual tree species with climate change has been quantified, much less is known about optimal transfer functions for their associated communities. Ikeda et al. [11] first proposed that optimal transfer functions for associated communities (both arthropods and fungal mutualists) could be quantified based on genetics based differences in productivity of their host plants. Our results suggest that a distance of greater than 50km and a temperature increase of more than 1.5°C is enough to alter community composition. Based on our 20 year-long common garden study, we suggest that to maintain their site of origin arthropod communities with the assisted migration efforts for narrowleaf cottonwood, trees should not be transferred distances greater than 50 km and a change in elevation greater than 250 m in elevation relative to their original location ([Fig 6](#)). Thus, these transfer distances define the elevation/distance limits if the goal is to attract and support the communities of the source sites.

Optimal transfer distances for other goals could also be quantified such as community diversity, stability and network structure (e.g., [49, 75, 80]). These transfer distances are

comparable with studies of optimal transfer distances for host trees discussed above and could be adapted for other plant traits that are likely to affect arthropod communities. We emphasize that optimal transfer distances for the plant may not be optimal transfer distances for the associated community and more studies are needed to identify these potentially different optima.

Differences in plant traits along elevation/distance gradients have repeatedly been shown; our findings show that for *P. angustifolia*, assisted migration efforts will also affect their associated arthropod communities. If the goal of restoration is to support local communities, local or nearby stocks would be best. However, if the goal of restoration is to support communities of the source population stocks, this can be also achieved by using more distant sourced stocks. However, which stocks to use could become a moot point with climate change where local plants become maladapted to a new environment and more distant stocks are required that will survive in the new environment. With common garden studies of *P. fremontii*, Grady et al. [15] found that restoration with local stock and intermediates up to 3°C transfer distance seems likely to ensure plant survival for both current and future conditions with no loss in plant survival and growth. However, if climate changes exceed 3°C, Grady et al. [15] found greater transfer distances resulted in poorer performance at the restoration site. Thus, while these plants would perform best in the future, they were inferior for current conditions, which would require a phased or step-wise approach if projected climate change is greater than 3°C. Although Evans et al. [64] found a similar pattern with *P. angustifolia*, they did not specify a specific temperature threshold where a stepwise approach would be required. Regardless of the desired goals, our findings demonstrate that genetic differences among source plant populations are significant in which their extended community phenotypes can be utilized to achieve specific community conservation goals [16, 82] as well as climate change mitigation that ensures the survival of the foundation plant species (e.g., [15, 29] and its associated communities in a changing environment.

Supporting information

S1 Table. All arthropods sampled in study.
(DOCX)

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Author Contributions

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