

# The relative influences of host plant genotype and yearly abiotic variability in determining herbivore abundance

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**Abstract** Both plant genotype and yearly abiotic variation affect herbivore population sizes, but long-term data have rarely been used to contrast the relative contributions of each. Using a hierarchical Bayesian model, we directly compare effects of these two factors on the population size of a common herbivore, *Aceria parapopuli*, on *Populus angustifolia* × *fremontii* F<sub>1</sub> hybrid trees growing in a common garden across 8 years. Several patterns emerged. First, the Bayesian posterior estimates of tree genotype effects on mite gall number ranged from 0.0043 to 229 on a linear scale. Second, year effect sizes across 8 years of study ranged from 0.133 to 1.895. Third, in comparing the magnitudes of genotypic versus yearly variation, we found that genotypic variation was over 130 times greater than variation among years. Fourth, precipitation in the previous year negatively affected gall abundances, but was minimal compared to tree genotype effects. These findings demonstrate the relative importance of tree genotypic variation

in determining herbivore population size. However, given the demonstrated sensitivity of cottonwoods to drought, the loss of individual tree genotypes from an altered climate would have catastrophic impacts on mites that are dependent upon these genotypes for their survival.

**Keywords** *Populus* · *Aceria parapopuli* · Hierarchical model · Genotypic effects · Annual variation

## Introduction

Host plant genotype can strongly influence herbivore population sizes and dynamics (Underwood and Rausher 2000; McIntyre and Whitham 2003; Helms and Hunter 2005; Whitham et al. 2006). Accounting for such variation among genotypes is crucial, because studies that do not may inaccurately estimate herbivore population growth or size (Helms and Hunter 2005), and because plant genotypic variation can structure communities of herbivores, predators, and parasites, and multitrophic interactions (Crawford et al. 2007; Whitham et al. 2006). Furthermore, recognizing how host genotype affects population sizes of dependent organisms has important conservation and evolutionary implications (McIntyre and Whitham 2003; Whitham et al. 2006; Evans et al. 2008).

Abiotic variation can strongly affect herbivore populations both directly and indirectly (Andrewartha and Birch 1954; Kingsolver 1989; Bale et al. 2002; Price 2003). Temperature (Ritchie 2000; Bale et al. 2002; Lombardero et al. 2003; Yarnes and Boecklen 2005), soil nutrient levels (Ritchie 2000), drought (English-Loeb 1990; Trotter et al. 2008), and humidity (Yarnes and Boecklen 2005) have powerful effects on arthropods. For example, in a 22-year

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study, precipitation accounted for 52–69% of the variation in the abundance of willow sawfly galls (Price and Hunter 2005). Through direct effects on herbivores' physiological processes and indirect effects through host plants and symbionts, abiotic factors can have pervasive effects on population sizes.

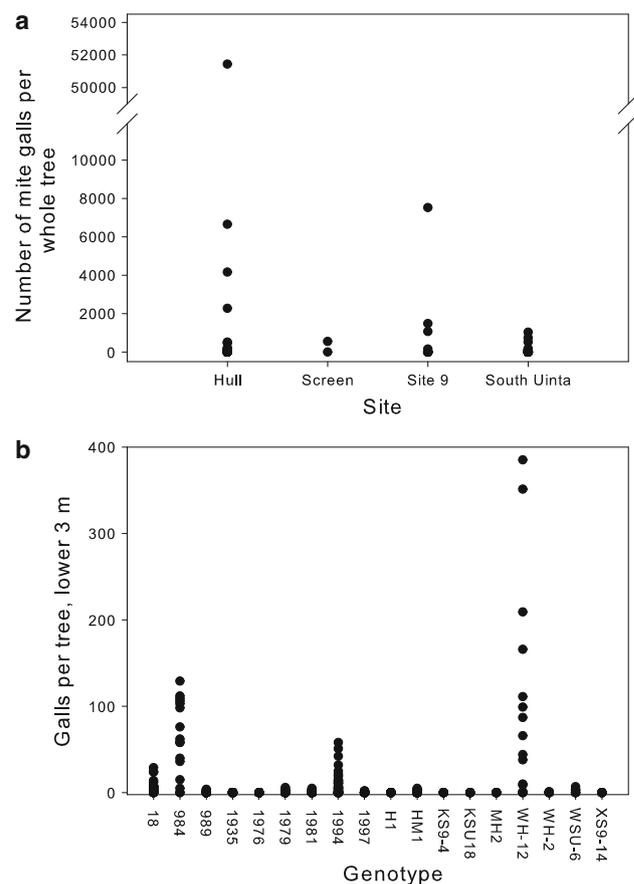
Despite the clear and strong effects of both abiotic factors and plant genotype on dependent herbivores, few studies have integrated both to determine their relative influence, especially in the context of long-term datasets. Of those that have tested both plant genotype and abiotic factors, they appear to have produced contrasting results. In extensive studies of willow sawflies, Price (2003) and Price and Hunter (2005) found significant effects of willow clones on sawfly populations, but in the field, weather swamped out clonal effects. Alternatively, Ylioja et al. (1999), studying the agromyzid fly *Phytobia betula*, found overwhelming effects of host variation (*Betula* spp.), including individual tree effects, and little evidence of abiotic (e.g., climate) influences. While suggestive of genetic effects, replicated *Betula* genotypes were not used, thus individual tree effects cannot be attributed to genetic variation alone. Studying the free-feeding aphid *Uroleucon nigrotuberculatus* on *Solidago altissima*, Maddox and Cappuccino (1986) found effects of both plant genotype and watering conditions. Louda and Collinge (1992) found both chewing and mining herbivores were affected by both plant genotype and abiotic stress, but not sap-feeders. The relative magnitudes of environmental and plant genotypic effects in general remain uncertain.

We explore the relative influences of host genotype and yearly abiotic variability on a bud-galling mite, *Aceria parapopuli*, which lives on cottonwood (*Populus* spp.). Cottonwood susceptibility to these mites is genetically based (Kalischuk et al. 1997; Whitham et al. 1999). Using observations in common garden and mite transfer experiments, McIntyre and Whitham (2003) found that successful gall formation, probability of population extinction, and the intrinsic rate of population increase,  $r$ , are strongly affected by cottonwood genotype. Furthermore, in the wild and in common garden studies, Whitham et al. (1999) and McIntyre and Whitham (2003) found evidence of pronounced differences in mite performance among *Populus angustifolia* × *P. fremontii* F<sub>1</sub> type hybrid genotypes, and Evans et al. (2008) found that tree genotype can drive the local adaptation of mite populations. In the present study, we examined the abundance of *Aceria parapopuli* on different F<sub>1</sub> hybrid type genotypes in a common garden over 8 years that encompassed a record drought and wet years. These data allowed us to quantify the relative magnitudes of the effects of tree genotype and yearly abiotic variation on the population size of *A. parapopuli*.

## Materials and methods

*Aceria parapopuli* Kiefer (Acari: Eriophyidae) is widely distributed and attacks the buds of North American *Populus* species and their naturally occurring hybrids to form woody, cauliflower-like galls (Kiefer 1940; Drouin and Langor 1992; Amrine and Stasny 1994; Baker et al. 1996). Mites disperse by crawling among branches within a tree and are wind-dispersed among trees (Sabelis and Brouin 1996). They are capable of long-distance, passive dispersal (Zhao and Amrine 1997; Bergh 2001). In natural F<sub>1</sub> hybrid stands along the Weber River, the number of mite galls per tree ranges from 0 to 50,000, and trees ranging from the most resistant to the most susceptible grow next to one another (Whitham et al. 1999; Fig. 1a).

To address the relative influences of tree genotype and yearly abiotic variation, we surveyed the number of *A. parapopuli* galls on F<sub>1</sub> type hybrid cottonwoods (*P. angustifolia* × *P. fremontii*) growing in a common garden in Ogden, UT (as described in McIntyre and Whitham 2003).



**Fig. 1** **a** Observed number of galls per whole tree at four sites along the Weber River, UT; data from Whitham et al. (1999). **b** Observed counts of galls per tree (lower 3 m only) for each genotype in the common garden

Because galls remain on the twigs for several years, the year the galls were formed can be determined by counting back the number of bud scars from the current year’s growth (McIntyre and Whitham 2003). Each of the 18 F<sub>1</sub> hybrid genotypes in the common garden is represented by 1–10 replicates (mean = 3.7, median = 2.5 replicates/genotype). We only counted galls on the lower 3 m of the trees, the height limit at which galls could be accurately dated. Thus, our dataset includes the number of galls per tree (lower 3 m) each year from 1998 to 2005 for each F<sub>1</sub> hybrid tree in the garden (Fig. 1b; 536 observations, 8–80 observations per genotype).

We used a hierarchical Bayesian analysis to model mite population size on each tree *i* of genotype *m* in each year *t*. Our approach differs from a standard generalized linear model in that we allow for additional sources of variation. Thus, we include not only random effects on individual genotypes but also extra-Poisson variation in the counts themselves. This variation is taken up by a latent variable  $\theta_{imt}$ , the underlying intensity of the Poisson process that results from sources of variation not represented by fixed and random effects. In effect, this model acknowledges that the model is an approximation. This approach allows incorporating variability at multiple scales to account for differences among individual genotypes and years (Clark and LaDeau 2004; Helms and Hunter 2005; Clark 2007). The number of mite galls on a given tree *i* of genotype *m* during year *t* ( $y_{imt}$ ) was modeled as

$$y_{imt} \sim \text{Poisson}(\theta_{imt})$$

where  $\theta_{imt}$  is the Poisson mean for tree *i* of genotype *m* during year *t*. The individual tree means were modeled as:

$$\begin{aligned} \ln(\theta_{imt}) &= \alpha_0 + \beta_i + \alpha_1 K_t + \alpha_2 Z_m + \varepsilon_{imt} \\ &= \mathbf{x}_j \mathbf{a} + \beta_i + \varepsilon_{imt} \end{aligned}$$

where  $\alpha_0$  is the intercept,  $K_t$  and  $Z_m$  are indicators for year *t* and genotype *m*, and  $\alpha_1$  and  $\alpha_2$  are the respective parameters, with Gaussian (on a log scale) priors  $N(\alpha|a_\alpha, V_\alpha)$ .  $\beta_i$  is the random effect of individual *i*, which is normally distributed with a mean of 0 and variance  $\tau^2$ , has an Inverse Gamma prior  $IG(\tau^2|a_\tau, b_\tau)$ , and describes the variance among individual trees (of the same genotype). In the second line, fixed effects are combined into the vector of indicators  $\mathbf{x}_j$  and parameters  $\mathbf{a}$ , each of length 27, to include all years and genotypes. The  $\mathbf{x}_j$  can be stacked to produce an *n* by 27 matrix  $\mathbf{X}$  of 1’s and 0’s identifying each observation with the year and tree genotype. Column 1 is the intercept (all 1’s), columns 2–9 represent the years, and columns 10–27 represent the genotypes. Each fixed factor has one level represented by all 0’s, with the effect of these levels incorporated into the intercept term. The error  $\varepsilon_{imt}$  is

Gaussian  $N(\varepsilon|0, \sigma^2)$ , with an Inverse Gamma prior for  $\sigma^2$   $IG(\sigma^2|a_\sigma, b_\sigma)$ . The full model is

$$\begin{aligned} p(\theta, \alpha, \mathbf{V}_\alpha, \beta, \tau^2, \sigma^2 | \mathbf{Y}, \mathbf{X}, a_\tau, b_\tau, a_\sigma, b_\sigma) \\ \propto \text{Pois}(y_{imt} | \theta_{imt}) \times N(\ln \theta_{imt} | \mathbf{X} \mathbf{a} + \beta_i + \varepsilon_{imt}) \\ \times N_{27}(\alpha | \mathbf{a}_\alpha, \mathbf{V}_\alpha) \times N(\beta | 0, \tau^2) \times IG(\tau^2 | a_\tau, b_\tau) . \\ \times N(\varepsilon_{imt} | 0, \sigma^2) \\ \times IG(\sigma^2 | a_\sigma, b_\sigma) \end{aligned}$$

Gaussian priors (on a log scale) were specified for all fixed effects with means  $a_\alpha = 0$  and variances  $V_\alpha = 3$ . Weak Inverse Gamma hyperpriors were given for the variances [ $\tau^2 \sim IG(5, 1.6)$  and  $\sigma^2 \sim IG(5, 1.6)$ ].

A second model, “genotype × year interaction,” was also evaluated which included genotype by year interaction terms, because the genotypes may respond differently among years. These interaction term effects are not estimable for genotypes represented only once. We therefore removed these genotypes and ran the analysis with the remaining 12 genotypes.

We used a third model, “genotype and climate,” to compare the relative effects of tree genotype and three specific abiotic variables on mite gall abundance. Winter minimum temperatures can affect the mean population dynamics of arthropods (Régnière and Bentz 2007). Because Eriophyid egg production and development are affected by temperature (Chandrapatya and Baker 1986), mean temperature during the growing season in year *t* – 1 may affect gall abundance in year *t* if there are more or fewer mites within galls to attack new buds the following spring. Plant vigor or chemical defenses may be affected by water availability (Price 2003), so the amount of precipitation in year *t* – 1 may affect the ability of mites to successfully attack new buds in year *t*. Therefore, we tested (1) minimum winter temperature in year *t*, (2) mean temperature June–September in year *t* – 1, and (3) cumulative precipitation June–May of year *t* – 1. We used climate data from the National Climate Data Center recording station at the Ogden Sugar Factory, the closest station to our common garden (~3.2 km distant; [www.ncdc.noaa.gov](http://www.ncdc.noaa.gov)). The model was similar to the “genotype and year” model above, except that  $\mathbf{X}$  represents the *n* × 19 design matrix with column 1 as the intercept, columns 2–16 representing tree genotype (0 or 1), and columns 17–19 the continuous climate variables.

The analysis was performed in R v. 2.10.1 (R Development Core Team 2009) with a Markov chain Monte Carlo method using a Gibbs sampler with an imbedded Metropolis step (Clark and LaDeau 2004; Clark 2007). Posterior distributions were sampled using 200,000 steps through the sampler, with a burnin of 20,000. Convergence was assessed using visual inspection of each Gibbs chain. See the

Online Resource for a detailed explanation of the sampler. We attempted to use DIC (Spiegelhalter et al. 2002) to compare the alternative models. However, estimating the effective number of parameters is erratic (Gelman and Hill 2007), and the approach did not work here. Regardless, all models supported the same conclusions.

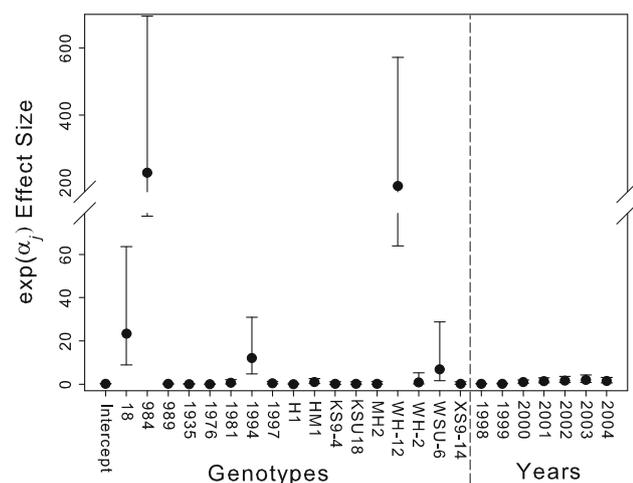
## Results

### Genotype and year model

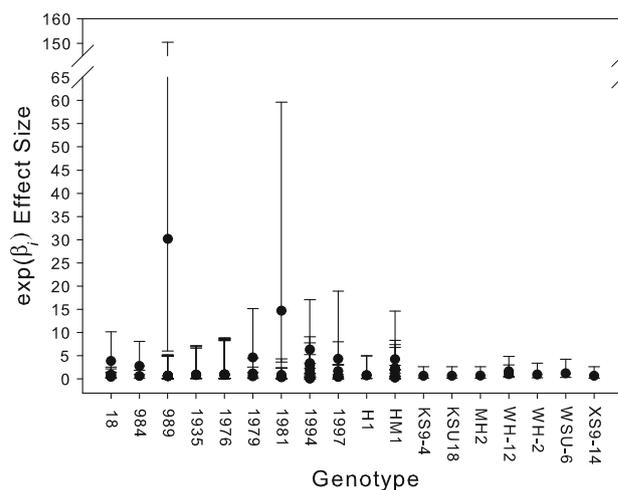
Parameter estimates of the effect of individual *Populus* F<sub>1</sub> hybrid genotypes ( $\alpha$ 's) on *A. parapopuli* gall abundance varied greatly (Fig. 2). Bayesian posterior mean estimates of  $\alpha$  (on a linear scale) for genotypes with no observed galls (e.g., genotype 1935) are nearly 0, while estimates for genotypes with many galls (e.g., WH12) are positive (range: 0.0043–229; Fig. 2). The 95% credible intervals tended to be larger for those tree genotypes with many observed galls, because there was more variation compared to those trees with no galls ever observed. The 95% credible intervals were non-overlapping for many genotypes, supporting our hypothesis that tree genotype has strong effects on the population sizes of *A. parapopuli*.

Posterior estimates of individual tree effects ( $\beta$ 's) ranged from near 0 to over 30 (linear scale). The 95% credible intervals do not overlap for several individual trees, indicating some variation among replicates of genotypes (Fig. 3; Online Resource Table S4).

While tree genotype has strong effects on *A. parapopuli*, estimates of  $\alpha$  were similar across years (Fig. 2). Parameter



**Fig. 2** Exponentiated effect sizes for genotype and year effects on the number of mite galls per tree. The effects of tree genotype 1979 and year 2005 are incorporated into the intercept term, and thus not represented independently. Points represent posterior means, and bars signify 95% Bayesian credible intervals



**Fig. 3** Individual tree effect sizes (exponentiated) for each tree of a given genotype from the “Genotype and year” model. Results from the “Genotype and climate” and “Genotype  $\times$  year” models are similar, and thus not shown. Points represent posterior means, and bars signify 95% Bayesian credible intervals

estimates for 1998 and 1999 were lower than those for 2000 on. This could be due to population growth in the garden (McIntyre and Whitham 2003). After 1999, estimates of  $\alpha$  across years were similar indicating stable population sizes among years.

In summary, effects of year were much smaller than effects of genotype. Posterior genotype  $\alpha$  means (linear scale) ranged from 0.0043 to 229, while year  $\alpha$ 's ranged only from 0.133 to 1.895 (Fig. 2; Online Resource Table S1). The 130-fold greater range among genotypes than years suggests that the variation among tree genotypes has stronger effects on the population sizes of *A. parapopuli* than yearly abiotic variation across 8 years.

The second model, “genotype  $\times$  year interaction,” yielded estimates of genotype, year, and individual tree effects similar to the “genotype and year” model (see Online Resource Tables S2 and S4). Additionally, this model evaluated genotype by year interaction terms; however, posterior 95% credible intervals all overlapped, indicating that we could not detect genotype  $\times$  year effects (see Online Resource Table S2).

The third model, using yearly climate variables, yielded similar results. Tree genotype effects were similar to the estimates from the genotype and year model (Online Resource Table S3). Effects of minimum winter temperature, mean growing season temperature, and precipitation on gall abundance were negligible. As before, the genotype effects were much larger than the climatic effect. Posterior estimates of individual tree effects ( $\beta$ 's) were similar to those in the “Genotype and year” model (see Online Resource Table S4).

## Discussion

Long-term studies that specifically quantify the relative importance of genetic factors in relation to abiotic factors are critical to understanding what influences herbivore populations (Hunter and Price 1992; Whitham et al. 2006). Despite the clear impacts of both plant genetic and yearly abiotic variation, these two key influences have rarely been compared using long-term datasets. *Aceria parapopuli* population size was affected by both host tree genotype and yearly abiotic variation, but the variation among genotypes was 130-fold greater than the variation among years (Fig. 2), even while climate varied from moist to severe drought ([www.ncdc.noaa.gov/oa/climate/research/drought/palmer-maps](http://www.ncdc.noaa.gov/oa/climate/research/drought/palmer-maps)). Furthermore, year effects differed only between the first 2 years and subsequent years, among which mite population sizes were constant. We found no evidence of genotype by year interactions, indicating that the effects of individual genotypes are similar in different years. Thus, our findings indicate a central role of genotypic variation in the population sizes of *A. parapopuli*, and support other studies that have shown the importance of individual host variation for herbivore population dynamics (Underwood and Rausher 2000; McIntyre and Whitham 2003; Helms and Hunter 2005).

Climate-related variables that we did not examine may be influencing gall abundances; however, we selected variables with demonstrable effects in other systems, and which, based on the natural history of *A. parapopuli*, we thought would have the largest influence in this study system. Other abiotic factors, such as soil nutrient levels, could play important roles in herbivore abundances through effects on plants (e.g., Ritchie 2000) and could interact with plant genotype. Our surveys minimized this possibility through the experimental common garden design, but we found non-overlapping 95% credible intervals for several individual trees ( $\beta$ 's; Fig. 3; Online Resource Table S4). Such effects could represent an abiotic factor that varies throughout the garden and which is consistent through time. However, it is important to note that these effects are still much smaller, with less variation, than the observed genotype effects. Thus, this reinforces the conclusion that tree genotype is much more important than annual or within-site abiotic variation in determining mite gall abundances.

The finding of stronger variation among tree genotypes than among years must necessarily be restricted to the garden environment in which the observations were made. However, two lines of evidence argue that these results are relevant to other sites throughout the Weber River. First, the trees used in this common garden were collected from throughout a 13-km stretch of the Weber River (described in McIntyre and Whitham 2003). Second, trees within this

stretch range from the most resistant to the most susceptible, often growing next to one another in the same natural stands. Using data from Whitham et al. (1999) and an overdispersed poisson model with sites as fixed effects, similar to the models described above, we investigated site effects on the number of galls per whole tree. The 95% credible intervals were overlapping for all sites, while most of the variation is found within sites (Online Resource Table S5; Fig. 1a). Therefore, the range of susceptible to resistant trees observed in the common garden likely represents the range of variation found within natural stands, and while we have not characterized abiotic variation among stands in the wild, this analysis indicates that there is no systematic difference in the number of galls per tree among stands (Fig. 1). We argue, therefore, that the findings of this study for *A. parapopuli* in a common garden across years are relevant to the scale of variation observed along the river among years.

The mechanisms by which individual genotypes affect *A. parapopuli* are unknown, but we hypothesize that genetically-based defensive chemistry (Rehill et al. 2006), sink-source relationships (Larson and Whitham 1991, 1997), phenology (Floate et al. 1993), and/or plant vigor (Price 1991) may play central roles. While less important than tree genetic variation for *A. parapopuli*, abiotic factors can affect herbivores directly or indirectly by modifying host plant quality (Kingsolver 1989; Ritchie 2000; Bale et al. 2002). We examined three climate variables that seemed likely to influence mite populations, yet found no or minimal effects on gall abundances compared to tree genotype. As an endophagous, gall-forming arthropod, *A. parapopuli* may be more likely than free-feeders to experience strong tree genotypic effects. However, Price and Hunter (2005) found extremely large climatic effects for an endophagous sawfly, and Maddox and Cappuccino (1986), Louda and Collinge (1992), and Helms and Hunter (2005) found plant genotypic effects for free-feeding herbivores. Additionally, Keith et al. (2010) found tree genotype effects for a large number of species, including free-feeding and galling herbivores, as well as predators and parasites. Thus, while gall-forming arthropods are intimately tied to their host plants (Stone and Schönrogge 2003) and may be especially likely to experience strong genotypic effects, free-living arthropods are potentially also subject to such strong genotypic effects.

Evolutionary, conservation, and climate change implications

The central importance of host genotype for the population dynamics of a dependent herbivore has important evolutionary and conservation implications. The abundance of *A. parapopuli* galls was strongly affected by tree genotype,

with some genotypes supporting no galls and others supporting many. When patches differ strongly from one another, selection by these differences may lead to local adaptation of herbivores even at fine spatial scales (Karban 1989; Mopper 1996; Egan and Ott 2007). *Aceria parapopuli* can be adapted to individual trees (Evans et al. 2008); therefore, the large genotypic effects observed in this study may make such adaptation more likely. From a conservation perspective, persistence of *A. parapopuli* depends not only on the occurrence of cottonwood trees, which are common in many riparian areas, but on the occurrence of particular tree genotypes. Because variation in quality or herbivory has been documented among individual plants in a wide range of systems (Coley 1983; Underwood and Rausher 2000; Helms and Hunter 2005; Whitham et al. 2006; Crawford et al. 2007), this may be a general principle. Paradoxically, this leaves *A. parapopuli* vulnerable to any abiotic factor that causes mortality in cottonwoods, despite being relatively unaffected by climatic variation itself. Regional warming has increased mortality rates throughout the western United States of many dominant forest trees (van Mantgem et al. 2009); thus, climate change has the potential to affect the distribution and survival of species that depend upon a subset of their hosts' genotypes. While the relative contributions of tree genotype and environmental variation have not been widely examined, this study and others (Whitham et al. 2003, 2006; McIntyre and Whitham 2003) argue that the conservation of genetic variation in common foundation species is important for conserving dependent community members (Whitham et al. 2010).

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