

Leaf phenology mediates provenance differences in herbivore populations on valley oaks in a common garden

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Abstract. 1. Plants from different populations often display a variation in herbivore resistance. However, it is rarely understood what plant traits mediate such differences.

2. It was tested how leaf phenology affects herbivore populations in a 15-year-old common garden of valley oaks (*Quercus lobata* Née) with different populations and maternal parents from throughout the *Q. lobata* range.

3. The abundance of leaf miners (*Stigmella* sp. Shrank) and leaf phenology of oaks in the common garden was measured.

4. Leaf miner abundance varied among provenance locations (population), but not among maternal parents within populations. Leaf phenology varied by provenance location and maternal parent, and trees that leafed out earlier accrued higher leaf-miner abundance. Path analysis indicated that leaf phenology was the likely driver of provenance and parental differences in resistance to leaf miners.

5. Understanding population differences is particularly important when considering transport of genotypes for ornamental or restoration purposes. The present study suggests that similarity in leaf phenology may be one factor that could be used to find genotypes with a similar herbivore resistance to local genotypes.

Key words. Folivory, leaf mine, local adaptation, provenance, *Quercus*.

Introduction

Across populations, plants differ in numerous traits and ecological interactions. Heritable differences in plant traits can exist locally, among populations, and between regions (Linhart & Grant, 1996; Geber & Griffen, 2003; Savolainen *et al.*, 2007). It is important to understand the variability in plant traits across populations for two reasons. First, variability in plant traits can lead to differences in long-term fitness and demographic success. In particular, local adaptation, the increase in fitness of locally adapted genotypes in their home environments, can be mediated by numerous plant traits (Kawecki & Ebert, 2004). Second, the traits that particular plant genotypes express can have cascading effects on higher trophic levels (Whitham *et al.*, 2003; Crutsinger *et al.*, 2006). For example, *Populus* genotypes

house unique communities of arthropods (Wimp *et al.*, 2005), pathogens (Busby *et al.*, 2013), and birds (Dickson & Whitham, 1996).

Herbivore resistance, defined as any suite of traits that reduces herbivore damage in a common environment, often varies between populations and between genetically different individuals (Agrawal *et al.*, 2002; Núñez-Farfán *et al.*, 2007). Herbivore resistance is likely one of the most important traits in determining the cascading effects of the plant genotype on higher trophic levels, as herbivores are a direct energetic link between plants and consumers. Herbivore resistance, however, is a complex trait. Resistance can be imparted by chemical traits, such as diverse secondary metabolites, defensive enzymes, and low nutritional value; physical traits such as trichomes, toughness, and turgidity; and phenological traits such as the timing of leaf set and leaf drop (Stamp, 2003). Most of these types of traits display some degree of heritability, and there is considerable interest in which plant traits mediate population differences in resistance to herbivores (Wimp *et al.*, 2005). In particular, while

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understanding the heritability of herbivore-resistance traits in long-lived plants is difficult, it is also particularly important because many long-lived plants, especially trees, are associated with large herbivore communities.

Leaf phenology is an important plant trait that conveys resistance against folivores in annual and deciduous plants, and may be a particularly viable candidate for mediating population differences in herbivore resistance. Early season herbivores have a finite window of opportunity for leaf set and the ensuing build-up of leaf secondary metabolites in which they can exploit leaf material (Feeny, 1970). As such, many herbivores colonise individual plants with particular leaf phenologies, where in some cases this leads to earlier and in other cases later leafing plants accumulating more herbivore damage (van Asch & Visser, 2007). Moreover, leaf and flower phenology varies dramatically across the range of many plants (Hendry & Day, 2005), where the flowering date of several European tree species differed by more than 70 days between southern and northern sites (Chuine *et al.*, 2000).

Leaf phenology has been shown to be an important determinant of leaf miner abundance of oaks (Mopper & Simberloff, 1995; Pearse & Karban, 2013). Leaf miners are found in various families of Lepidoptera, Diptera, Hymenoptera, and Coleoptera (Connor & Taverner, 1997). These herbivores are often host specialists or oligophages (Connor *et al.*, 1980), and eggs are often deposited in the early season by adults that emerged from pupae in the litter layer (Connor *et al.*, 1983). Some species are multivoltine (Connor *et al.*, 1994), but their late-season abundance can still correlate with early season phenological events (Pearse & Karban, 2013).

In this study, we looked for population and parental differences in resistance to leaf mining herbivores, and we assessed whether leaf phenology might mediate those differences in resistance. We established a common garden of valley oak (*Quercus lobata* Née) individuals reared from acorns collected across the range of the species. When plants were 15 years old, we surveyed the abundance of leaf-mining herbivores [*Stigmella* sp. (Lepidoptera)] on those individuals as well as leaf phenology in order to test whether: (i) heritable variation in herbivore resistance exists between provenance localities (populations) and between sibling groups within populations; (ii) variation in leaf phenology exists between provenance localities (populations) and between sibling groups within populations; and whether (iii) differences in resistance are mediated by differences in phenology among populations and sibling groups.

Methods

Natural history, acorn collection, and common garden management

The present study was conducted at a common garden of valley oaks established at Sedgwick Preserve, CA, USA (34.6983°N, 120.0409°W). The common garden site was in an open grassland and oak savanna habitat. *Quercus lobata*, a deciduous oak species endemic to California, is the dominant tree within 500 m of the site, although blue oak (*Q. douglasii* Hook. & Arn.) and coast live oak (*Q. agrifolia* Née) are common elsewhere on



Fig. 1. A map of oak provenance localities (stars) and common garden location (Sedgwick) in California. Shaded areas represent the distribution of *Quercus lobata*. County boundaries are shown for reference. Localities: San Fernando: 34.143°N, 118.762°W; Sedgwick: 34.698°N, 120.041°W; Hastings: 36.385°N, 121.551°W; Orinda: 37.883°N, 122.190°W; Cone Grove: 40.168°N, 122.135°W.

the preserve. The understory vegetation consists of native and non-native grasses and forbs such as *Avena barbata* Pott ex Link, *Bromus hordeaceus* L., *Erodium* sp., *Eschscholzia californica* Cham., *Lactuca serriola* L., *Lolium multiflorum* Lam., *Lupinus* sp., and *Stipa pulchra* (Hitchc.) Barkworth. A short (1.5 m) fence enclosed the site, which excluded cattle, but did not exclude other mammalian herbivores such as deer, gophers, mice, and jackrabbits.

The methods of garden establishment and management are described in detail elsewhere (Sage *et al.*, 2011). In October to November 1997, mature acorns were collected from five localities spanning the latitudinal range of valley oak (Fig. 1). Acorns were taken directly from maternal trees or the ground under maternal trees in situations where maternity was unambiguous.

At the common garden, a grid was established where *Q. lobata* were planted with 2-m spacing. To establish each individual, we germinated four acorns from a given maternal tree in buried baskets at each grid intersect (Sage *et al.*, 2011). After 7 months, in cases of multiple germinants, we randomly chose a single individual and removed all others. Placement of individuals was randomised with respect to the maternal parent (and thereby site of origin). We established 3–8 individuals per maternal tree with 11 maternal trees per site resulting in 325 individuals. In the subsequent 15 years, 22 individuals died resulting in a total of 303 individuals in the present study. Mortality resulted in a loss of no more than eight individuals of a provenance locality or two individuals of a maternal parent.

We scored the size of seedlings in September 2012. The height of *Q. lobata* individuals ranged from 20 to 350 cm, where all but two larger sapling individuals were at the late seedling stage

(described in Pearse *et al.*, 2014). This stage of development is especially important to the overall fitness of this species because the seedling-sapling transition limits *Q. lobata* recruitment in oak savanna habitats (Tyler *et al.*, 2006; Davis *et al.*, 2011). Late-stage oak seedlings may persist at Californian sites for decades without substantial above-ground growth or mortality (Koenig & Knops, 2007); accordingly, we observed no seedling to sapling transitions from 2012 to 2014. Mammalian herbivory is thought to be a major factor in reducing the above-ground growth of late-stage seedlings and limiting the transition to the sapling stage (Griffin, 1971; Davis *et al.*, 2011). Mammalian herbivory (likely deer, jackrabbit, and ground squirrel) was common at the site, but was difficult to score quantitatively.

Insect and phenology surveys

We conducted surveys of endophagous insects on *Q. lobata* individuals on 15–16 September 2012. Specifically, we comprehensively surveyed the damage caused by leaf miners and galls with visual surveys of leaves. For consistency, each individual tree was surveyed for a minimum of 1 min, and larger individuals received longer search times when necessary. Counts typically saturated after a 30-s search. Abundance estimates of endophagous insects are possible because they are based on the lasting, and readily identifiable leaf mines and galls caused by different insect species. We divided mines into serpentine mines caused by *Stigmella* sp. (Nepticulidae: Lepidoptera), blotch mines caused by *Cameraria* cf. *lobatiella* Opler and Davis (Gracillariidae: Lepidoptera), and unknown or ambiguous mines. Galls [caused by cynipid gall wasps *Andricus confertus* McCracken and Egbert, *Andricus fullawayi* Beutenmueller, *Andricus kingi* Bassett, *Andricus quercuscalifornicus* (Bassett), *Antron douglasii* (Ashmead), and *Neutoterus saltatorius* (Edwards)] occurred at the site, but were rare. Species assignment was made based on standard entomological texts (Needham *et al.*, 1928; Russo, 2006; Powell & Opler, 2009).

We scored leaf phenology of each individual on 4 April 2014, which was roughly in the middle of the leaf set (Ducousso *et al.*, 1996). Leaf development (leaf set) was scored qualitatively on a 0–3 scale where: 3 was no leaf set; 2 had burst buds present, < 5% partially expanded leaves, no fully expanded leaves; 1 had partially expanded leaves common > 5%, < 5% fully expanded leaves; 0 was fully expanded leaves common > 5%. Although leaf phenology was measured after damage estimates, the order of leaf set among *Q. lobata* individuals is concordant among years, such that an individual that sets leaf before the population mean in 1 year will do so in subsequent years (Koenig *et al.*, 2012). Surveys of herbivore abundance and leaf phenology were conducted blind with reference to provenance and maternal parent by the senior author.

Statistical analysis

We explored a few simple correlations within our data (e.g. *Stigmella*: *Cameraria* mine abundance and mine abundance: distance from the common garden) using Pearson's correlations. In initial tests, we detected a pattern of spatial clustering of tree volume within our common garden (Moran's

$I=0.007$, $P=0.02$). The abundance of leaf miners and leaf phenology, standardised by tree volume, were not spatially clustered, however (leaf miner Moran's $I=0.003$, $P=0.14$; leaf phenology $I=0.0002$, $P=0.42$). Thus, spatial clustering of tree volume – probably as a result of micro-topographical gradients – is not a confounding factor in our trait analyses as populations and family groups were also not spatially clustered.

We estimated broad sense heritability (H^2) as V_G/V_T (i.e. trait variance explained by maternal family divided by total trait variance). Because it is unclear to what degree gene flow exists between localities, we calculated H^2 in two ways: (i) across maternal families among all localities and (ii) within each locality. Because we sampled across the majority of the range of *Q. lobata*, the trait variance in this study is probably representative of the entire species. We did not include plant height as a covariate in calculating H^2 , as we considered size variation a biologically meaningful contributor to trait variance.

We assessed the significance of provenance and maternal parent using linear mixed models. Maternal parent and provenance locality were considered nested random factors (Table S1). In all models, plant size (volume, calculated with the shape of a cone: height \times radius² \times $\pi/3$) was considered a continuous covariate.

We explored whether leaf phenology and leaf mine abundance varied by site or maternal parent using identical models, only with leaf phenology as a continuous response variable. Because phenology was measured as ordinal interval data, we first tested the effect of phenology on leaf-miner abundance as a categorical variable. Leaf miner abundance varied strongly between phenology categories [likelihood ratio (LR)=16.7, $P<0.001$], and phenology was treated as a continuous variable in all further tests.

We assessed the fit and significance of models by comparing a full model to an identical model that lacked the key factor using a likelihood ratio test (Table S1). Using these models, we conducted a path analysis to determine whether leaf phenology could mediate provenance locality and parental effects on leaf-miner abundance (Mitchell, 2001). Parental effects in this analysis represent maternal variation within a site of origin, as variation owing to site of origin was accounted for as a random effect in those models. All models used to construct the path diagram are listed in Table S1.

After square-root transformation of leaf miner counts, all models conformed to assumptions of homoscedasticity and normality. Two trees were outliers in terms of size (i.e. they had transitioned to small saplings). Initial analyses conducted with and without these outlier trees yielded qualitatively identical results, so we present analyses including those two individuals.

Linear models were calculated in R using package *nlme* for mixed models and *ape* for calculation of Moran's I (Paradis *et al.*, 2004; Pinheiro *et al.*, 2009; R Core Development Team, 2012).

Results

Abundance of leaf miners by site of origin and parent

We detected 3505 leaf mines, accounted for by two main types. Serpentine mines caused by *Stigmella* sp. accounted for

71% of all leaf mines. Blotch mines caused by *Cameraria* cf. *lobatiella* accounted for 14% of all leaf mines. The remaining 15% of mines were of ambiguous morphology and could not be readily identified. The abundance of *Cameraria* mines was highly correlated with *Stigmella* mines ($r = 0.45$, $P < 0.001$), and the direction of trends for *Cameraria* mines followed *Stigmella* mines. Thus, we focus on *Stigmella* leaf mines here because they were most abundant and easily identified. Larger individuals had more *Stigmella* mines (LR = 10.6, $P = 0.001$) such that 0.948 *Stigmella* mines were added for every additional 1000 dm³ of tree volume. Tree size (volume) did not differ significantly between populations (LR > 0.1, $P = 0.99$) nor did it differ between maternal families (LR > 0.1, $P = 0.99$). We used tree size as a covariate in all subsequent analysis except for heritability, and we standardised mine abundance by tree size in graphs using the relationship described above.

The broad sense heritability (H^2) of susceptibility to *Stigmella* leaf miners across all sites was 0.25. When accounting for tree-size effects on leaf miners, the abundance of *Stigmella* mines varied by population (LR = 4.7, $P = 0.029$, Fig. 2a), but not by maternal parent within a population (LR = 1.8, $P = 0.17$), suggesting that there was heritable variation in the susceptibility to leaf miners between, but not within, sites. There was a trend for *Q. lobata* originating from sites more distant from the common garden to have fewer *Stigmella* mines, but the trend was not significant ($r = -0.82$, $n = 5$, $P = 0.087$). Within each site, the broad sense heritability of susceptibility to *Stigmella* leaf miners ranged from 0.14 to 0.44 (Table S2).

Leaf phenology by site of origin and parent

The broad sense heritability (H^2) of leaf phenology across sites was 0.41. Leaf set phenology varied significantly by population (LR = 17.4, $P < 0.001$, Fig. 2b), with trees from the two most northern sites (Cone Grove and Orinda) leafing out earlier than trees from more southern sites. Leaf phenology also varied by maternal parent within a population (LR = 25.9, $P < 0.001$), suggesting that there were heritable differences in leaf phenology both between and within sites. Within each site, the broad sense heritability of leaf phenology ranged from 0.20 to 0.41 (Table S2). Leaf phenology showed a non-significant trend with plant size in which trees that were larger set leaf earlier (LR = 3.51, $P = 0.061$).

Phenology mediates site of origin effect on leaf miners

Considering all individuals, trees that set leaf earlier in the spring accumulated more *Stigmella* mines ($r = -0.26$, $P < 0.001$). This effect remained significant after accounting for tree size, site of origin, and maternal parent effects (LR = 14.5, $P < 0.001$, Fig. 3). Indeed, leaf phenology accounted for the majority of the variation in *Stigmella* mine abundance that was explained by site of origin or maternal parent, suggesting that leaf phenology was the primary driver of population and maternal family differences in leaf mine abundance (Fig. 4).

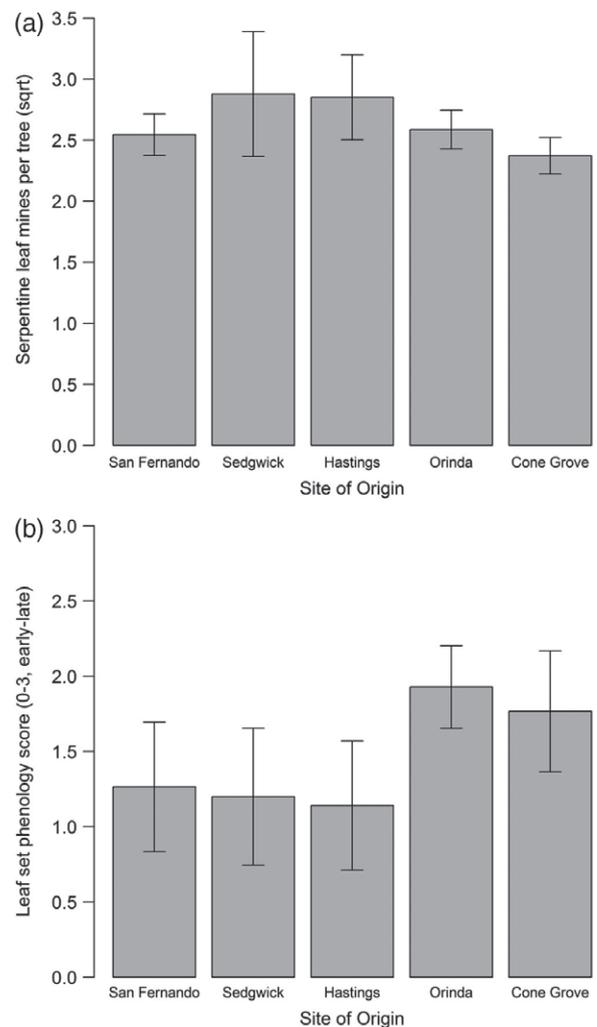


Fig. 2. (a) Number of *Stigmella* (serpentine) leaf mines on *Quercus lobata* by site of origin. Mine estimates were standardised to the size of the tree. (b) Leaf set phenology (scored early-late: 0–3) of *Q. lobata* by site of origin, standardised to the size of the tree. Sites are ordered south to north. Bars are the mean \pm SD.

Discussion

Our results support the hypothesis that variation in herbivore resistance between *Q. lobata* populations is mediated by differences in leaf phenology. Leaf phenology varied both by provenance locality and by the maternal parent within a locality. At the same time, trees that set leaf earlier accrued higher abundances of leaf miners.

The timing of leaf set has been shown to be an important determinant of herbivore abundance in numerous systems, and it may be particularly important in oaks. In a survey of herbivore damage to naturally occurring mature *Q. lobata* at a single site, herbivore damage was greater on trees that set leaf earlier in the season (Pearse *et al.*, 2015). Similar trends were found previously with winter moth damage to *Quercus robur* L. (Hunter, 1992; Tikkanen & Julkunen-Tiitto, 2003; van Asch *et al.*, 2007).

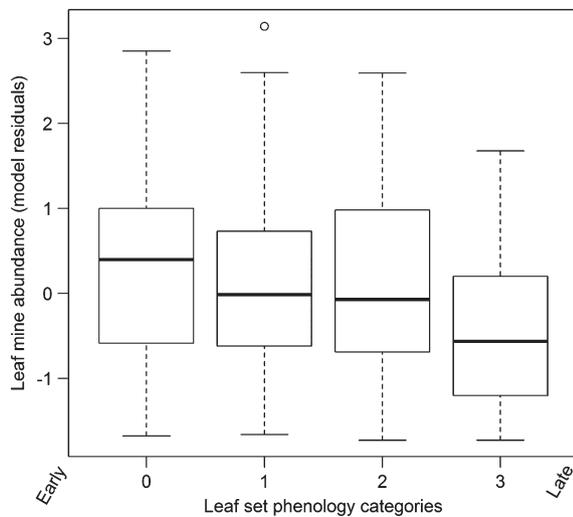


Fig. 3. Residuals of leaf mine abundance controlling for tree volume on *Quercus lobata* with different phenologies (scored early-late: 0–3). The thick line represents the median value of leaf set (residuals). The differences in leaf mine abundance varied highly significantly by phenology category ($P=0.0001$).

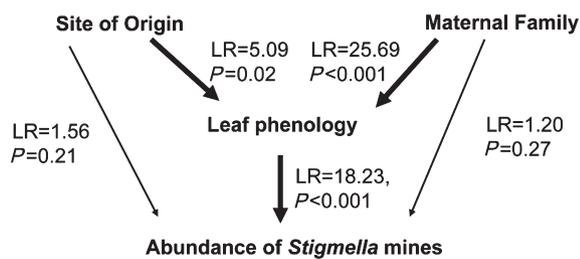


Fig. 4. Path diagrams testing the hypothesis that the effects of site of origin and maternal parent on leaf mine abundance were mediated by leaf phenology. The effects of maternal family in this case are analysed across all sites as opposed to being nested within a site. LR = likelihood ratio. Thicker arrows indicate a significant path.

In a common garden of numerous oak species, those species that set leaf earlier also accrued higher abundances of leaf miners (Pearse & Karban, 2013), although other aspects of leaf phenology also correlated with miner abundance. In contrast, in *Quercus geminata* Small, a southeastern North American oak, trees that set leaf later accrued greater populations of the leaf miner *Stilbosis quadricustatella* (Chambers) (Mopper & Simberloff, 1995).

In addition to oaks, the timing of leaf set has been shown to be a major determinant of herbivore abundance or damage in numerous other systems including coniferous (Chen *et al.*, 2003) and tropical trees (Aide, 1993). A relationship between phenology of herbivore damage is not universal, however, as spring phenology has been shown to have little effect on other herbivores in studies of both oaks (Crawley & Akhteruzzaman, 1988; Connor *et al.*, 1994) and conifers (Watt & McFarlane, 1991). One confounding factor in examining the effects of spring phenology on herbivore damage is that early-emerging leaves

will be available to herbivores for a longer period of time than late emerging leaves at any given sampling date. While most studies (including this one) cannot distinguish the effects of time of leaf availability from the effects of leaf set date *per se*, the single study that attempted to disentangle these effects found evidence for an effect of leaf set irrespective of time of leaf availability in mature *Q. lobata* trees (Pearse *et al.*, 2015).

The majority of heritable variation to herbivore resistance in *Q. lobata* was found among populations, as opposed to within populations. This is again consistent with the hypothesis that leaf phenology mediates differences in herbivore resistance in *Q. lobata*, because leaf phenology also varied significantly among populations (Fig. 2b).

The geographical scale of variation in herbivore resistance clearly varies between systems. For example, in milkweed (*Asclepias*), resistance to monarch butterflies (*Danaus plexippus* Linnaeus) and aphids (Aphidae) varied between populations, although it is unclear how much heritable variation was present within populations (Woods *et al.*, 2012). Heritable variation in resistance to herbivores was found in *Datura* both within and between populations (Fornoni *et al.*, 2003). In the *Q. lobata* we studied, there was no evidence for variation in resistance to leaf miners within populations, but substantial variation between populations.

The scale at which variation in resistance occurs probably depends on the type of traits that determine resistance. For example, if specialised plant traits mediate resistance with few pleiotropic effects, then patterns of resistance might follow patterns of herbivore pressure or factors that prohibit tolerance (Núñez-Farfán *et al.*, 2007; Pearse & Hipp, 2012). Moreover, if there are tradeoffs between resistance and growth or reproduction, there may be adaptive variation in resistance over small geographical distances.

In contrast, if traits that mediate resistance pleiotropically affect a broad suite of a plant's interactions with its environment, then these traits may be more constrained by the other selection pressures imposed upon them than by herbivores. We posit that this is the case in our system. Gene flow in *Q. lobata*, a wind-pollinated tree, can occur over multiple kilometres (Abraham *et al.*, 2011), and genetic variation between populations occurs mostly at large spatial scales and across climatic gradients (Gugger *et al.*, 2013), so it is likely that resistance alleles can easily travel between populations. However, we found that resistance was mediated by leaf phenology, which also affects a plant's resource acquisition, competitive ability, reproduction, and stress avoidance (Polgar & Primack, 2011). These other selection pressures probably constrain phenology, and thereby leaf miner resistance, at broad geographical scales.

The present study only provides preliminary evidence about local adaptation between leaf miners and valley oaks because conclusive evidence for local adaptation requires common gardens at multiple sites. The present results are consistent with previous work on the subject, however. Leaf miner populations on *Q. geminata* become highly differentiated and quickly adapt to local tree individuals (Mopper *et al.*, 2000). Consistent with this result, there was a trend for trees from more distant *Q. lobata* populations to accrue fewer leaf mines, although the pattern was not significant. This suggests that oak phenology may cause a

geographical cline in selection for leaf miner phenology. The complementary pattern, that is, local adaptation in *Q. lobata* for resistance against local leaf miners, is less likely to be true in our study, as local populations accumulated the most leaf miners. Again, previous studies have found the resistance traits mediating leaf mining to be linked to leaf phenology and likely to be under selection by agents other than herbivores (Mopper & Simberloff, 1995).

We found heritable variation in resistance to herbivores between populations that was driven by leaf phenology. Because herbivores are an important component of biodiversity and a key energetic link between plants and higher trophic levels, these population-level differences in herbivore resistance suggest an advantage to using locally adapted oaks for restoration efforts.

Conservation of higher trophic levels, such as herbivores, is a goal of many plant restoration efforts. Herbivores are an important component of biodiversity and are the energetic link between plants and higher trophic levels. Oaks are a foundational species harbouring a substantial portion of biodiversity in many ecosystems (Pavlik *et al.*, 1991). Moreover, while non-outbreak herbivores, such as leaf miners, may reduce the fitness of individual oak trees (Marquis & Whelan, 1994; Pearse *et al.*, 2015), they rarely cause mortality or interact negatively with humans (Costello *et al.*, 2011; Herrmann *et al.*, 2012). Past studies have shown that local environmental factors shape the diversity of herbivores on *Q. lobata* (Herrmann *et al.*, 2012). Consistent with the community genetics hypothesis, we found that provenance effects influence herbivore populations on planted *Q. lobata* via differences in leaf phenology.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/een.12219

Table S1. A description of models compared with test key hypotheses.

Table S2. Broad sense heritability (H^2) for leaf set phenology and leaf mine abundance within five provenance localities of *Q. lobata*.

References

- Abraham, S.T., Zaya, D.N., Koenig, W.D. & Ashley, M.V. (2011) Interspecific and intraspecific pollination patterns of valley oak, *Quercus lobata*, in a mixed stand in coastal central California. *International Journal of Plant Sciences*, **172**, 691–699.
- Agrawal, A.A., Conner, J.K., Johnson, M.T.J. & Wallsgrove, R. (2002) Ecological genetics of an induced plant defense against herbivores: additive genetic variance and costs of phenotypic plasticity. *Evolution*, **56**, 2206–2213.
- Aide, T.M. (1993) Patterns of leaf development and herbivory in a tropical understory community. *Ecology*, **74**, 455–466.
- van Asch, M. & Visser, M.E. (2007) Phenology of forest caterpillars and their host trees: the importance of synchrony. *Annual Review of Entomology*, **52**, 37–55.
- van Asch, M., Tienderen, P.H., Holleman, L.J.M. & Visser, M.E. (2007) Predicting adaptation of phenology in response to climate change, an insect herbivore example. *Global Change Biology*, **13**, 1596–1604.
- Busby, P.E., Newcombe, G., Dirzo, R. & Whitham, T.G. (2013) Genetic basis of pathogen community structure for foundation tree species in a common garden and in the wild. *Journal of Ecology*, **101**, 867–877.
- Chen, Z., Clancy, K.M. & Kolb, T.E. (2003) Variation in budburst phenology of Douglas-fir related to western spruce budworm (Lepidoptera: Tortricidae) fitness. *Journal of Economic Entomology*, **96**, 377–387.
- Chaine, I., Belmonte, J. & Mignot, A. (2000) A modelling analysis of the genetic variation of phenology between tree populations. *Journal of Ecology*, **88**, 561–570.
- Connor, E.F. & Taverner, M.P. (1997) The evolution and adaptive significance of the leaf-mining habit. *Oikos*, **79**, 6–25.
- Connor, E.F., Faeth, S.H., Simberloff, D. & Opler, P.A. (1980) Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology*, **5**, 205–211.
- Connor, E.F., Faeth, S.H. & Simberloff, D. (1983) Leafminers on oak: the role of immigration and in site reproductive recruitment. *Ecology*, **64**, 191–204.
- Connor, E.F., Adams-Manson, R.H., Carr, T.G. & Beck, M.W. (1994) The effects of host plant phenology on the demography and population dynamics of the leaf-mining moth, *Cameraria hamadryadella* (Lepidoptera, Gracillariidae). *Ecological Entomology*, **19**, 111–120.
- Costello, L.R., Hagen, B.W. & Jones, K.S. (2011) *Oaks in the Urban Landscape: Selection, Care, and Preservation*. University of California Agricultural and Natural Resources Publication 3518. University of California, Richmond, California.
- Crawley, M.J. & Akhteruzzaman, M. (1988) Individual variation in the phenology of oak trees and its consequences for herbivorous insects. *Functional Ecology*, **2**, 409–415.
- Crutsinger, G.M., Collins, M.D., Fordyce, J.A., Gompert, Z., Nice, C.C. & Sanders, N.J. (2006) Plant genotypic diversity predicts community structure and governs an ecosystem process. *Science*, **313**, 966–968.
- Davis, F.W., Tyler, C.M. & Mahall, B.E. (2011) Consumer control of oak demography in a Mediterranean-climate savanna. *Ecosphere*, **2**, art108.
- Dickson, L.L. & Whitham, T.G. (1996) Genetically-based plant resistance traits affect arthropods, fungi, and birds. *Oecologia*, **106**, 400–406.
- Ducousso, A., Guyon, J.P. & Krémer, A. (1996) Latitudinal and altitudinal variation of bud burst in western populations of sessile oak (*Quercus petraea* (Matt) Liebl). *Annals of Forest Science*, **53**, 775–782.
- Feeny, P. (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology*, **51**, 565–581.
- Fornoni, J., Valverde, P.L. & Núñez-Farfán, J. (2003) Quantitative genetics of plant tolerance and resistance against natural enemies of two natural populations of *Datura stramonium*. *Evolutionary Ecology Research*, **5**, 1049–1065.

- Geber, M.A. & Griffen, L.R. (2003) Inheritance and natural selection on functional traits. *International Journal of Plant Sciences*, **164**, S21–S42.
- Griffin, J.R. (1971) Oak regeneration in the upper Carmel Valley, California. *Ecology*, **52**, 862–868.
- Gugger, P.F., Ikegami, M. & Sork, V.L. (2013) Influence of late Quaternary climate change on present patterns of genetic variation in valley oak, *Quercus lobata* Née. *Molecular Ecology*, **22**, 3598–3612.
- Hendry, A.P. & Day, T. (2005) Population structure attributable to reproductive time: isolation by time and adaptation by time. *Molecular Ecology*, **14**, 901–916.
- Herrmann, D.L., Pearse, I.S. & Baty, J.H. (2012) Drivers of specialist herbivore diversity across 10 cities. *Landscape and Urban Planning*, **108**, 123–130.
- Hunter, M.D. (1992) A variable insect-plant interaction: the relationship between tree budburst phenology and population levels of insect herbivores among trees. *Ecological Entomology*, **17**, 91–95.
- Kawecki, T.J. & Ebert, D. (2004) Conceptual issues in local adaptation. *Ecology Letters*, **7**, 1225–1241.
- Koenig, W.D. & Knops, J.M.H. (2007) Long-term growth and persistence of blue oak (*Quercus douglasii*) seedlings in a California oak savanna. *Madrono*, **54**, 269–274.
- Koenig, W.D., Funk, K.A., Kraft, T.S., Carmen, W.J., Barringer, B.C. & Knops, J.M.H. (2012) Stabilizing selection for within-season flowering phenology confirms pollen limitation in a wind-pollinated tree. *Journal of Ecology*, **100**, 758–763.
- Linhart, Y.B. & Grant, M.C. (1996) Evolutionary significance of local genetic differentiation in plants. *Annual Review of Ecology and Systematics*, **27**, 237–277.
- Marquis, R.J. & Whelan, C.J. (1994) Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology*, **75**, 2007–2014.
- Mitchell, R.J. (2001). Path analysis. *Design and Analysis of Ecological Experiments* (ed. by S.M. Scheiner and J. Gurevitch), pp. 217–234. Oxford University Press, New York, New York.
- Mopper, S. & Simberloff, D. (1995) Differential herbivory in an oak population: the role of plant phenology and insect performance. *Ecology*, **76**, 1233–1241.
- Mopper, S., Stiling, P., Landau, K., Simberloff, D. & Van Zandt, P. (2000) Spatiotemporal variation in leafminer population structure and adaptation to individual oak trees. *Ecology*, **81**, 1577–1587.
- Needham, J.G., Frost, S.W. & Tothill, B.H. (1928) *Leaf-Mining Insects*. The Williams and Wilkins Company, Baltimore, Maryland.
- Núñez-Farfán, J., Fornoni, J. & Valverde, P.L. (2007) The evolution of resistance and tolerance to herbivores. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 541–566.
- Paradis, E., Claude, J. & Strimmer, K. (2004) APE: analyses of phylogenetics and evolution in R language. *Bioinformatics*, **20**, 289–290.
- Pavlik, B.M., Muick, P.C., Johnson, S.G. & Popper, M. (1991) *Oaks of California*. Cachuma Press, Los Olivos, California.
- Pearse, I.S. & Hipp, A.L. (2012) Global patterns of leaf defenses in oak species. *Evolution*, **66**, 2272–2286.
- Pearse, I.S. & Karban, R. (2013) Leaf drop affects herbivory in oaks. *Oecologia*, **173**, 925–932.
- Pearse, I.S., Griswold, S., Pizarro, D. & Koenig, W.D. (2014) Stage and size structure of three species of oaks in central coastal California. *Madrono*, **61**, 1–8.
- Pearse, I.S., Funk, K.A., Kraft, T.S. & Koenig, W.D. (2015) Lagged effects of early-season herbivores on valley oak fecundity. *Oecologia*, **178**, 361–368.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & The R Core Development Team. (2009) *nlme: Linear and Nonlinear Mixed Effects Models*. R package, version 3.1-93.
- Polgar, C.A. & Primack, R.B. (2011) Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytologist*, **191**, 926–941.
- Powell, J.A. & Opler, P.A. (2009) *Moths of Western North America*. University of California Press, Berkeley, California.
- R Core Development Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria [WWW document]. URL <http://www.R-project.org/> [accessed on 15 October 2012].
- Russo, R. (2006) *Field Guide to Plant Galls of California and Other Western States*. University of California Press, Berkeley, California.
- Sage, R.D., Koenig, W.D. & McLaughlin, B.C. (2011) Fitness consequences of seed size in the valley oak *Quercus lobata* Née (Fagaceae). *Annals of Forest Science*, **68**, 477–484.
- Savolainen, O., Pyhäjärvi, T. & Knürr, T. (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 595–619.
- Stamp, N. (2003) Out of the quagmire of plant defense hypotheses. *Quarterly Review of Biology*, **78**, 23–55.
- Tikkanen, O.P. & Julkunen-Tiitto, R. (2003) Phenological variation as protection against defoliating insects: the case of *Quercus robur* and *Operophtera brumata*. *Oecologia*, **136**, 244–251.
- Tyler, C.M., Kuhn, B. & Davis, F.W. (2006) Demography and recruitment limitations of three oak species in California. *Quarterly Review of Biology*, **81**, 127–152.
- Watt, A.D. & McFarlane, A.M. (1991) Winter moth on Sitka spruce: synchrony of egg hatch and budburst, and its effect on larval survival. *Ecological Entomology*, **16**, 387–390.
- Whitham, T.G., Young, W.P., Martinsen, G.D., Gehring, C.A., Schweitzer, J.A., Shuster, S.M. *et al.* (2003) Community and ecosystem genetics: a consequence of the extended phenotype. *Ecology*, **84**, 559–573.
- Wimp, G.M., Martinsen, G.D., Floate, K.D., Bangert, R.K. & Whitham, T.G. (2005) Plant genetic determinants of arthropod community structure and diversity. *Evolution*, **59**, 61–69.
- Woods, E.C., Hastings, A.P., Turley, N.E., Heard, S.B. & Agrawal, A.A. (2012) Adaptive geographical clines in the growth and defense of a native plant. *Ecological Monographs*, **82**, 149–168.

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