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Genetically-based trait variation within a foundation tree species influences a dominant bark lichen

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ABSTRACT

Lichens frequently exhibit preference for tree species, however, tree traits that influence preference also vary intraspecifically. We hypothesized that genetically-based trait variation within *Populus angustifolia* affects bark lichens. To test this hypothesis, we quantified the lichen *Xanthomendoza galericulata*, and factors that could influence its distribution, including photosynthetically active radiation, bark roughness, bark condensed tannins, bark nitrogen and bole circumference on replicated *P. angustifolia* genotypes in a common garden. Several key findings emerged: (1) Tree genotype explained one-third of the variation in *X. galericulata* cover (broad-sense heritability: $H^2 = 0.32$); (2) Bark roughness, condensed tannins and bole circumference varied among tree genotypes ($H^2 = 0.25–0.35$); (3) Structural equation modelling suggested that bark roughness is the genetically-based trait that positively influences *X. galericulata*, and that bark roughness is positively influenced by bole circumference. This is the first study to link genetically-based trait variation in a foundation tree species to variation in the cover of a dominant lichen.

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Introduction

Lichens are composite organisms composed of a fungus with a green algal and/or cyanobacterial partner. Lichens colonize all major terrestrial substrata (e.g., rock, dead wood, living plants, soil) where they fill a diverse range of niches (Brodo 1973; Hale 1974). Due to their photosynthetic, and in some cases nitrogen-fixing, capabilities, they provide important energy and nutrient inputs into a variety of terrestrial

ecosystems around the globe (Brodo et al. 2001). Lichens serve as food or habitat for organisms ranging from vertebrates to microarthropods (Maser et al. 1985; Meier et al. 2002). In addition to lichenized fungi, which represent more than one-fifth of the approximately 74 000 described fungal species (Hawksworth 2001), a diversity of nonlichenized fungal lineages have evolved to occupy the unique microhabitats of lichen thalli (Arnold et al. 2009). Because of their ubiquity, diverse and important ecological niches, and role as

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evolutionary cradles for other organisms, it is important to understand the factors that determine lichen distributions.

Lichens that live on or in the bark of trees are known to vary in their affinities for tree species (Culberson 1955; Adams & Risser 1971; Johansson & Ehrlén 2003). For example, six of 17 lichen species in a boreal forest ecosystem occurred exclusively on *Populus tremula* and were absent on an adjacent angiosperm and conifer tree species (Uliczka & Angelstam 1999). Variation in lichen abundances among different tree species is likely due in part to traits such as bark texture and chemistry, or environmental variables, such as light availability, that may be differentially influenced by tree species (Culberson 1955; Brodo 1973). Although there is much focus on patterns of lichen distributions among tree species, lichen abundances are also known to vary among individual trees within species (e.g., Gustafsson & Ericson 1995; Ellis & Coppins 2007; Boudreault et al. 2008). However, it is unknown how much intraspecific variation in tree traits such as bark texture, tree size, bark chemistry, and the lichens they influence, is due to genotypic differences among individual trees.

Many ecological systems are governed by foundation species that structure communities by creating locally stable conditions and modulating fundamental ecosystem processes (Dayton 1972; Ellison et al. 2005). Ecosystems are frequently defined by one or more foundation species that provide habitat for entire communities (Ellison et al. 2005; Whitham et al. 2006, 2008). A growing body of evidence indicates that genetically-based trait variation within foundation species of terrestrial and aquatic habitats affects the distributions of associated species, including taxa as diverse as foliar arthropods, gut flora, soil microbes, marine invertebrates and mycorrhizal fungi (Maddox & Root 1987; Zoetendal et al. 2001; Reusch et al. 2005; Schweitzer et al. 2008; Sthultz et al. 2009). These associated taxa can exhibit broad-sense (Fritz & Price 1988; Bailey et al. 2006) and narrow-sense (Maddox & Root 1987) heritabilities among plant genotypes. This body of research demonstrates that variation in traits of foundation species creates a range of ecologically and evolutionarily important genetically-based interactions among organisms that influence the distributions of a diverse array of taxa. Despite progress in this area of research, there is still little understanding about the influence of genetically-based trait variation within foundation species on associated organisms that are not dependent on the foundation species for energy, such as bark lichens and other epiphytic vegetation.

Lichens are sensitive to substratum characteristics (Brodo 1973) and frequently live in association with foundation species; we therefore predict that they should respond to trait variation among replicated genotypes of a foundation tree species. To test this prediction we examine the distribution of a dominant bark lichen, *Xanthomendoza galericulata*, on replicated genotypes of a foundation species, *Populus angustifolia* (narrowleaf cottonwood), using a common garden. The use of a common garden enabled us to control confounding effects of environment and tree age, in order to evaluate the strength of *P. angustifolia* genotype on *X. galericulata* distribution. *Populus angustifolia* is a widespread foundation species of mid and upper elevation interior western North American riparian habitat (Eckenwalder 1984). Genetically-based trait variation within *P. angustifolia* influences ecosystem processes and

a phylogenetically diverse community of associated organisms; consequently, *P. angustifolia* is becoming a model species for community genetics research (Whitham et al. 2008). We focused on *X. galericulata* because it is a broadly distributed bark lichen in western North America (Lindblom 2006), that is dominant at our study site. Furthermore, preliminary sampling indicated that the cover of other bark lichen species correlated positively with *X. galericulata* cover, suggesting that *X. galericulata* distributions are indicative of broader lichen community patterns (Lau et al. 2010; L.J. Lamit unpublished data). Therefore, *X. galericulata* represents a useful taxon with which to begin evaluation of tree genotype effects on lichens, and epiphytic vegetation in general. We specifically hypothesized that *X. galericulata* cover differs among replicated *P. angustifolia* genotypes, and that variables that may influence *X. galericulata*, including tree traits and light availability (which may be affected by tree traits), also vary among *P. angustifolia* genotypes. We used structural equation modelling (SEM) to assess the hypothesis that genetically variable tree traits (e.g., bole circumference, bark roughness, and condensed tannins) influence *X. galericulata* cover, and may therefore be mechanistic links between *X. galericulata* and tree genotype.

Methods

Study system and sampling design

This study was conducted in a *Populus* common garden located at the Ogden Nature Center in Ogden, Utah, USA. The garden was planted in 1991 with trees propagated from cuttings collected randomly from nearby riparian stands along the Weber River, and was approximately 16 yr old during the time of this study. The garden included genotypes of *P. angustifolia*, *P. fremontii* and their natural hybrids planted in a randomized design to minimize environmental influences. We focused our study on 25 unique *P. angustifolia* genotypes, each of which was replicated two to nine times, for a total of 89 individual trees. Reanalysis of tree genotype data from Martinsen et al. (2001), based on 35 codominant restriction fragment length polymorphism markers, verified that these trees represent *P. angustifolia* genotypes with no significant introgression of *P. fremontii* alleles (M. Zinkgraf unpublished data). Soils in the garden were coarse-loams, common in low elevation riparian systems (Schweitzer et al. 2008). Understory vegetation was dominated by exotic and ruderal forbs and grasses (L.J. Lamit et al. unpublished).

Xanthomendoza galericulata cover was measured within a vertical quadrat, 10 cm wide by 1 m tall, which originated at ground level on the north side of each tree trunk. Lichen specimens were identified using published and unpublished keys, including Lindblom (2004, 2006), as well as through morphological comparison with specimens from Arizona State University, New York Botanical Garden, and the University of Colorado herbaria. We deposited representative specimens of *X. galericulata* from our study in the Deaver Herbarium at Northern Arizona University.

Many factors can influence bark lichens. We chose to focus on a small number of factors that we hypothesized to be important in our system and that may be influenced by tree

genotype, including physical and chemical bark traits. Bark texture may affect the ability of lichen propagules to adhere and germinate on tree trunks, and may influence evaporation rates and moisture levels that influence lichen functioning (Brodo 1973; Palmqvist 2000). To quantify bark texture we made a dichotomous distinction between rough bark, which is furrowed and/or coarsely textured, and smooth bark, which is not furrowed or coarsely textured. Bark texture was measured in the same quadrats used for lichen quantification and expressed as a % cover of rough bark. Bark chemistry has many dimensions, but it was not within the scope of this study to measure all chemicals in bark. We focused on bark condensed tannins (CTs) because plant secondary compounds have antifungal properties (Grayer & Harborne 1994) and were hypothesized to influence epiphytic lichens (Williams & Sillett 2007). Furthermore, CTs have strong genetically-based influences on other organisms and processes within this system (Whitham et al. 2006, 2008). We also measured bark nitrogen (N) because *Xanthomendoza* and related genera are considered nitrophilic (Hale 1974) and N is also important to photosynthesis (Palmqvist 2000). We hypothesized that *X. galericulata* would respond positively to increases in bark N among genotypes. For CT and N analyses, at least four small pieces of lichen-free bark, up to 1 mm deep, were collected along the length of the outer edge of each lichen quadrat. Samples were flash frozen between blocks of dry ice, freeze-dried, ground in a Wiley mill using a 40-mesh screen, and then subsampled for CT and total N analysis. Condensed tannins were quantified using the acid butanol assay described by Porter et al. (1986) with purified *P. angustifolia* leaf CT as the standard. Total N was determined in a CE Elantech Flash EA1112 C:N analyzer (CE Elantech Inc, Lakewood, NJ) using atropine as a standard.

Two other variables that have been shown to be important to lichens were measured. Photosynthetically active radiation (PAR) is not a tree trait in itself but may be influenced by variation in tree traits, such as size, and is important for photosynthesis and thallus hydration (Palmqvist 2000). Photosynthetic active radiation was measured with a LI-COR LI-250A light meter between 11:30 am and 2:30 pm on June 2nd and 3rd, within 2 weeks after the summer solstice. Measurements were taken immediately adjacent to the north side of each tree trunk at 20, 40, 60 and 80 cm above the soil surface, and averaged per tree. Tree size may influence the other variables we measured and research in natural stands has found it to be an important correlate with lichens (Johansson & Ehrlén 2003; Boudreault et al. 2008). We used the circumference of the base of each tree's bole as an indicator of tree size instead of diameter at breast height because some trees had more than one trunk at breast height. It is important to note that because this study was conducted in a common garden, all trees were the same age and therefore differences in size among genotypes were primarily a function of genetics.

Statistical analyses

Our first set of analyses was aimed at uncovering effects of *P. angustifolia* genotype on *X. galericulata* cover, as well as the measured tree traits and PAR. Restricted maximum likelihood (REML) was used to estimate broad-sense heritability (H^2), representing the proportion of variation in a response variable

explained by differences among tree genotypes (Conner & Hartl 2004), and a likelihood ratio test was used to test for tree genotype as a predictor (Shaw 1987). For all analyses, data on *X. galericulata* cover and PAR were log transformed, data on bole basal circumference were square root transformed and data on bark CT were rank transformed. Analyses were conducted in R 2.8.1 (R Development Core Team 2008) using the package lme4.

We examined the relationships among *X. galericulata* cover and the variables that differed among tree genotypes – bole basal circumference, rough bark cover and bark CTs (see Results) – with structural equation modelling (SEM) in the program Amos 5 (SmallWaters Corp, Chicago, IL). Structural equation modelling combines path analysis and factor analysis to allow the user to analyze data as a system of interrelated variables (Grace 2006). We used SEM to identify potential mechanisms by which genetically-based tree traits influenced *X. galericulata* cover, and to factor out the effects of measurement error on our estimates of *X. galericulata* cover. Fig 1 outlines our hypothesis of the mechanisms linking tree genotype to its effects on tree traits and their subsequent influence on *X. galericulata* cover. We hypothesized that rough bark cover would positively affect the cover of *X. galericulata*, and bark CTs would have a negative effect on *X. galericulata*. We further hypothesized that rough bark cover would have an effect on bark CT due to potential differences in chemistry between rough and smooth barks. Furthermore, bark CT and roughness should be affected by a tree's basal circumference because of tradeoffs between tree growth and resource allocation to defensive chemistry (Stevens et al. 2007), and larger trees are likely to have greater cover of rough bark (L.J. Lamit personal observation). Finally, we hypothesized that variation among tree genotypes in these traits causes differences in *X. galericulata* cover among tree genotypes, however, due to low within-genotype replication we were unable to incorporate *P. angustifolia* genotype as a categorical variable into the SEM model. Therefore, our model was specifically focused on

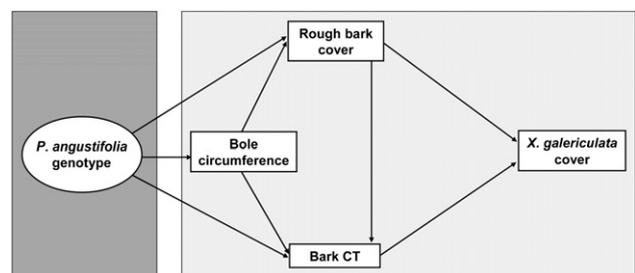


Fig 1 – Conceptual model outlining our hypothesis that *Populus angustifolia* genotype identity (dark grey box) influences the tree traits (arrows connecting dark grey box and light grey box), which then interact with each other and influence *Xanthomendoza galericulata* cover (light grey box). Heritability analyses show that these traits, and *X. galericulata* cover, vary among *P. angustifolia* genotypes (see results). We focus our structural equation modelling on understanding the interrelationships among the genetically-based variables in the right side of the diagram only (light grey box).

how the genetically-based tree traits interrelate and affect *X. galericulata* cover, but could not statistically link these traits to tree genotype within the SEM.

Measurement error for *X. galericulata* cover was accounted for in the SEM by representing actual *X. galericulata* cover as a latent variable (an unmeasured variable represented by at least one indicator) and adjusting its error variance (Grace 2006). Repeated measurements of *X. galericulata* cover were performed on 21 trees and used to calculate reliability of cover estimates. The reliability estimate was used to calculate the error variance term of the latent variable that represented the actual cover of *X. galericulata* (Grace 2006). Error variance calculations were conducted in R 2.8.1.

We arrived at our final SEM through a two-stage process. First, we ran the model and examined *P*-values associated with individual paths, removing statistically insignificant paths. Second, two model fit tests were performed and examined for consensus support. Maximum likelihood chi-square and root mean square error of approximation (RMSEA) tests were used to determine model fit (Grace 2006). *P*-values associated with both tests are the probabilities that the model fits the data, thus higher *P*-values are desirable.

Results

Lichen cover and tree traits among *P. angustifolia* genotypes

Xanthomendoza galericulata cover varied among *P. angustifolia* genotypes (Table 1; Fig 2). Broad-sense heritability estimates indicated that tree genotype explained 32 % of the variation in the cover of *X. galericulata* in the common garden. Mean *X. galericulata* cover ranged from nearly zero to approximately 40 % among genotypes (Fig 2). This consistent variation is strong evidence that the genetic identity of a tree influences a dominant lichen species intimately associated with its bark.

Of the four measured tree traits (i.e., bark N, bark CT, bole basal circumference, and bark roughness), three differed among tree genotypes, and PAR was not affected by *P. angustifolia* genotype (Table 1). Broad-sense heritability estimates indicated that 35 % of the variance in rough bark cover was explained by genotype (range of genotype means = 14.5–65.5 % cover), 31 % of the variance in bark CT was explained by genotype (range of

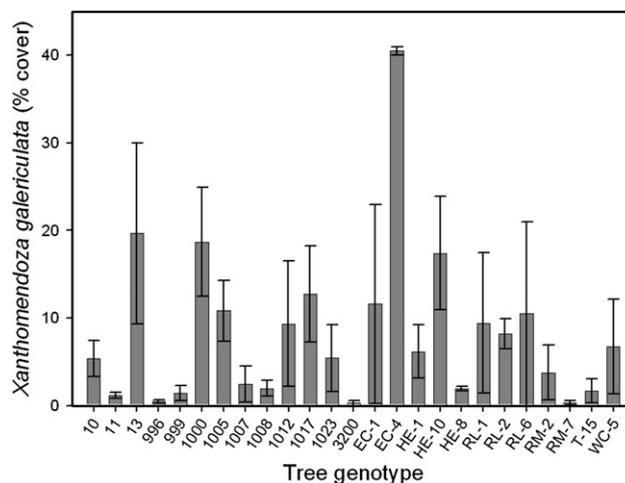


Fig 2 – Non-transformed *Xanthomendoza galericulata* cover (mean ± SEM) on replicated *Populus angustifolia* genotypes.

genotype means = 1.68–5.38 % dry weight), and 25 % of the variance in bole basal circumference was explained by tree genotype (range of genotype means = 48.26–309.88 cm) (Table 1). There was no evidence that bark N (total range = 0.39–1.30 % dry weight) or PAR (total range = 83.28–2103.28 $\mu\text{mol s}^{-1} \text{m}^{-2}$) differed consistently among tree genotypes (Table 1) and therefore we excluded PAR and bark N from subsequent analyses.

Linking genetically variable tree traits and lichens

Structural equation modelling identified tree traits that likely serve as mechanistic intermediates linking *X. galericulata* to *P. angustifolia* genotype (Fig 3). Before running the final model fit analyses, bark CT was removed from the model because the paths leading into bark CT from bole circumference and bark roughness, as well as the path leading from bark CT to *X. galericulata* cover, had path coefficients less than 0.15 and high *P*-values; furthermore, only 2 % of the variation in bark CT was explained (data not shown). The structure of the final model, which lacked bark CT, matched the empirical data (i.e., there was good model fit) and 64 % of the variation in *X. galericulata* cover was explained by the final model (Fig 3). Factoring out measurement error greatly increased the model's ability to explain *X. galericulata* cover (Fig 3). Although our model fit tests indicate good model fit, due to *post-hoc* exploration, future studies are required to confirm our final model.

Our SEM suggested that the genetically-based trait (as determined by broad-sense heritability analyses) bark roughness had a strong effect on *X. galericulata* cover (Fig 3). The relationship between bark roughness and *X. galericulata* was positive, which supported our hypothesis that coarsely textured *P. angustifolia* bark facilitates *X. galericulata* establishment and growth. The cover of rough bark is in turn positively related to the genetically-based trait bole basal circumference, whose variation was not confounded by age in this study, supporting our hypothesis that larger trees of the same age tend to have rougher bark. This suggests that these

Table 1 – Broad-sense heritability (H^2) for *Xanthomendoza galericulata* cover, tree traits and photosynthetically active radiation among replicated *Populus angustifolia* genotypes, as well as the associated chi-square value and *P*-value for the log-likelihood ratio test

	H^2	χ^2	<i>P</i>
<i>Xanthomendoza galericulata</i> (% cover)	0.32	9.92	0.002
Photosynthetically active radiation ($\mu\text{mol s}^{-1} \text{m}^{-2}$)	0.00	0.00	1.000
Rough bark (% cover)	0.35	15.17	<0.001
Bark condensed tannin concentration (% DW)	0.31	10.01	0.002
Bark nitrogen concentration (% DW)	0.03	0.15	0.704
Bole basal circumference (cm)	0.25	10.50	0.001

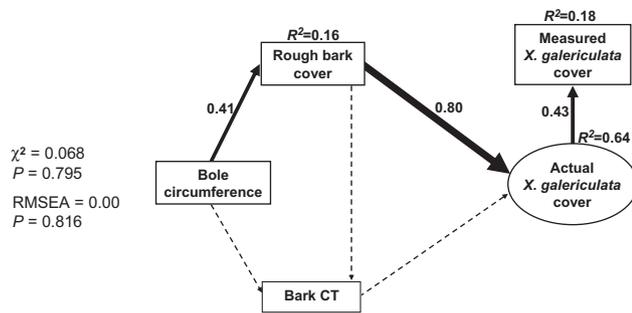


Fig 3 – The final structural equation model shows good fit with the data, and links *Xanthomendoza galericulata* cover to the genetically-based traits, bole basal circumference and bark roughness. This lends support to the hypothesis that bark roughness, partially through the influence of bole basal circumference on bark roughness, may be the genetically-based trait linking *Populus angustifolia* genotype to *X. galericulata* cover. Rectangles represent measured variables, the oval represents an unmeasured latent variable, arrows represent hypothesized causal influences, and dotted arrows represent non-influential paths absent from the final model. Numbers associated with arrows are standardized path coefficients and indicate the strength of each relationship. Path arrow widths are scaled to reflect values of associated path coefficients. The model fit statistics associated with the maximum likelihood chi-square and Root Mean Square Error of Approximation (RMSEA) tests are presented on the left side of the figure.

two genetically-based tree traits interact to influence the quantity of *X. galericulata* on a tree's trunk.

Discussion

Patterns and mechanisms: linking lichen cover to tree genetics

For the first time, we show that a dominant bark lichen is influenced by genetically-based trait variation in a foundation tree species (Figs 2 and 3; Table 1). Broad-sense heritability estimates indicate that differences among tree genotypes explain one-third ($H^2 = 0.32$) of the variation in *X. galericulata* cover (Table 1). To our knowledge, lichen abundances have previously been shown to differ only among tree species and not among tree genotypes. For example, Culbertson (1955) concluded that within the floristic region of northern Wisconsin, USA, tree species is the most important factor influencing the distribution of epiphytic vegetation (including lichens) on tree bark. If sensitivity to fine-scale genetically-based trait variation is common, studies that do not incorporate genotype may be missing important ecological patterns. This is supported by Crutsinger et al. (2006), who showed that the effect size of patch level genotypic diversity in *Solidago altissima* on associated arthropods is comparable to the effect size of plant species diversity in a grassland ecosystem.

Bark roughness varies among *P. angustifolia* genotypes and is strongly positively correlated with *X. galericulata* cover (Table 1, Fig 3). Bark texture may affect the ability of lichen propagules to settle on a tree during dispersal, or influence propagule germination and thallus growth by altering evaporation and available moisture (Brodo 1973). Bark texture, and other physical bark traits, likely have important influences on patterns of lichen specificity among tree species (Brodo 1973; Uliczka & Angelstam 1999; Williams & Sillett 2007), and are also linked to variation in lichen distributions among individuals within tree species growing in natural stands (Ellis & Coppins 2007; Boudreault et al. 2008). Here we have shown that intraspecific variation in bark roughness has a genetic basis and is in-part influenced by differences in growth rate among genotypes (as indicated by differences in bole basal circumference), suggesting that of the measured predictors, bark roughness is the most likely mechanistic link between *X. galericulata* and tree genotype. However, bark roughness may also correlate with other characteristics of bark relevant to lichens, including exchangeable cations and pH, and future research should explore more traits.

The other variables measured are not good candidates as mechanisms linking tree genotype and *X. galericulata*. Bark N and PAR do not vary consistently among *P. angustifolia* genotypes (Table 1), and we therefore did not include them in further analyses. Bark CTs vary among *P. angustifolia* genotypes (Table 1), however SEM indicated that bark CTs have no influence on *X. galericulata* cover. We originally hypothesized that bark CTs should adversely affect *X. galericulata* because many plant secondary chemicals have antifungal properties (Grayer & Harborne 1994). Although this hypothesis was not supported, bark CTs may influence other lichen species and relationships between lichens and plant secondary chemistry deserve further investigation.

Trophic relations and tree genetics

We have shown that a primary producer is sensitive to intraspecific genetically-based trait variation of a foundation tree species. Many studies have shown that organisms such as plant associated arthropods (e.g., Maddox & Root 1987; Bailey et al. 2006), and in some cases nonlichenized fungi (e.g., Elamo et al. 1999; Sthultz et al. 2009), respond to genetic variation in foundation species. However, in most cases these organisms are intimately dependent upon the foundation species for energy, while lichens are not. This key difference creates a fundamentally different relationship between trees and lichens, and illustrates the point that effects of quantitative trait variation in a foundation species can extend to associated primary producers. If shown to commonly occur, this may have important implications for energy flow, community dynamics and succession (e.g., Proffitt et al. 2005; Crutsinger et al. 2008; Lau et al. 2010).

The effect of variation in genetically-based plant traits on associated organisms can cascade to higher trophic levels (Bailey et al. 2006) and this may be true for lichens as well. We examine the overall effects of tree genetics on lichens without focusing on potential changes in the dynamics occurring between the mycobiont and photobiont. Genetic effects on lichen photobionts may cascade to mycobionts.

Examining the relative abundance or biomass of photobiont to mycobiont in future studies may uncover hidden trophic interactions within the lichen thallus that are affected by tree genetics. Other organisms, including microarthropods, and lichenicolous and endolichenic fungi, that consume energy fixed by lichen photobionts (Meier et al. 2002; Arnold et al. 2009), may also be affected by variation in lichen abundance or the relative biomasses of the photobiont and mycobiont in a thallus.

Implications for evolution and conservation

Genetically-based variation within species is necessary for evolution by natural selection to occur (Conner & Hartl 2004), and here we have shown that *X. galericulata* is sensitive enough to variation within a foundation species to show measurable broad-sense heritability among tree genotypes. We hypothesized that the relationship between *X. galericulata* and their *P. angustifolia* substrata is asymmetrical. There is probably little or no direct selective pressure on the trees for more or less lichen cover. However, *P. angustifolia* traits that influence lichens may have important functions besides their influence on *X. galericulata* or may be genetically linked to other important traits. If there is selection on these *P. angustifolia* traits, *X. galericulata* may be affected by evolutionary processes occurring within *P. angustifolia*. This possibility highlights the importance of incorporating an evolutionary perspective into community ecology (Whitham et al. 2006, 2008).

The question remains whether the influence of *Populus* genetic variation on lichens is strong enough to influence lichen evolution. *Xanthomendoza galericulata* colonizes a range of tree species, and results from studies of genetic differentiation of widely distributed lichen taxa on more broad scales of substratum (e.g., rock vs bark, among tree species) are mixed (Lindblom & Ekman 2006; Werth & Sork 2008; Mattsson et al. 2009). Therefore, *X. galericulata* may or may not have an evolutionary response to fine-scale trait differences among *P. angustifolia* genotypes. However, in some ecosystems *Populus* spp. harbour unique and rare lichen species that do not tend to associate with other tree species (e.g., Uliczka & Angelstam 1999; Hedenäs & Ericson 2003). The mycobionts or photobionts of lichens specialized on *Populus* may show strong responses to differences among tree genotypes and experience sustained effects of selection by *Populus* genotypes. Although we are unaware of any studies that document adaptive genetic differentiation among lichens on individual tree genotypes, recent studies by Evans et al. (2008) have experimentally demonstrated such adaptive differentiation with the specialized gall-forming mite, *Aceria parapopuli*, on *Populus*.

Conservation goals frequently focus on rare species. However, to sustain the ecological integrity and evolutionary processes in ecosystems, the importance of conserving foundation species, which are often common, is becoming increasingly apparent (Ellison et al. 2005; Whitham et al. 2006). Our study, in conjunction with others, points to the need to preserve genetic diversity within foundation species because organisms as seemingly uncoupled from them as lichens are affected by their genetics.

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