Investigating ecological variation and statistical tools for testing ecological hypotheses

By

Clay J. Morrow

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The dissertation is approved by the following members of the Final Oral Committee:
- Richard L. Lindroth, Professor, Entomology and Forest and Wildlife Ecology
- Anthony R. Ives, Professor, Integrative Biology
- Cécile Ané, Professor, Statistics
- Claudio Gratton, Professor, Entomology
- Philip Townsend, Professor, Forest and Wildlife Ecology

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Introduction

Variation is a fundamental component of ecological systems and understanding its sources and consequences is crucial for understanding these systems. Biological diversity is an example of an ecologically relevant, and important, consequence of variation. Species diversity, for example, is a key indicator of ecosystem health (Cardinale et al. 2002; Cook-Patton et al. 2011; Grace et al. 2016; Grossiord 2020). Environmental variation, another key ecological driver (Frank and Inouye 1994; Brown et al. 1995; Ettema and Wardle 2002; Wright et al. 2005; Kolb et al. 2007), determines what types of organisms and communities can exist across space and time. Phenotypic variation allows organisms to utilize different resources and occupy different niches, which over evolutionary time drives speciation (Schluter 2001; Milá et al. 2007; Nakazato et al. 2008; Pfennig et al. 2010; Seddon et al. 2013). Ultimately, then, biological diversity is driven and maintained by genetic variation, environmental interaction, and the resulting phenotypic expression.

Intraspecific variation, that which occurs within species, is emerging as a greater effector of ecological systems than previously understood. Impacts of intraspecific variation on entire communities and ecosystem processes can be comparable or greater than those of variation among species (Des Roches et al. 2018; Koricheva and Hayes 2018). Large intraspecific effects seem to be especially common in plants (Siefert et al. 2015; Koricheva and Hayes 2018; Westerband et al. 2021) because of the importance of plants to the systems in which they exist and their capacity for variation. Community and ecosystem genetics, the facet of ecology that investigates the sources and impacts of intraspecific genetic variation, has largely focused on plants for this reason (Crutsinger et al. 2006; Johnson et al. 2006; Shuster et al. 2006; Whitham et al. 2006, 2020; Schweitzer et al. 2008; Crutsinger 2016; Gehring et al. 2017; Barker et al. 2019b, a). The evidence increasingly shows that genetic variation in a single species can have far-reaching consequences for ecosystems. This is especially true of the effects that foundation species have on associated populations and communities (Bailey et al. 2005; Lamit et al. 2011; Gehring et al. 2017; Barker et al. 2019b; Whitham et al. 2020).

Ecological variation is rarely entirely random, and it is important that scientific investigations account for the underlying structure in ecological systems. Characteristics of individuals within populations and of species within communities often covary with their genetic relationships or group membership (Schweitzer et al. 2004; Bangert et al. 2006; Hayes 2013; Zhang et al. 2021). These characteristics often also covary with spatial and temporal variation (Winemiller 1990; Soininen 2016; Boyce 2018). Researchers engaged in designing experiments, testing hypothesis, or conducting associative analyses in ecological systems must carefully consider covariation structure to ensure accurate conclusions. The costs of not adequately accounting for genetic, temporal, or spatial covariance range from loss of statistical power at best to complete invalidation of statistical models. Clearly, it is important for researchers to be aware of and account for the many sources of variation in their systems and to account for relationships between and among those sources.

This research aims to answer ecological questions concerning variation while testing and using statistical tools that account for genetic, temporal, and spatial covariance structure. The first three chapters focus on intraspecific variation in the context of plant-insect interactions. These chapters involve the study species *Populus tremuloides*, which exhibits exceptional variation and interacts strongly with its various associated insect herbivores. The fourth chapter takes a step back from this system and addresses spatial and temporal variation broadly on a much larger scale – regional, continental, and global maps.

This work also takes two different approaches to scientific research. The first two chapters outline studies conducted on real systems in the lab and field. This approach allows for testing hypotheses in the natural systems that the hypotheses are about. By contrast, the latter two chapters outline simulation studies. This approach allows comparison and validation of the statistical tools used to test hypotheses in a controlled way and under known conditions. Simulation studies are valuable tools for verifying that a method works as expected, for testing how robust a method is to various assumptions, and by simplifying a study system to its most basic mechanistic components of interest.

In chapter one, I quantified and evaluated the effects of intraspecific variation of *P. tremuloides* (aspen) on the generalist herbivore *Lymantria dispar*. The general pattern of plant traits worldwide suggests that resource-acquisitive plants, optimized for fast-growth, have higher nutritional value for herbivores and are less defended than slower-growing, resource-conservative plants. I tested the hypothesis that *L. dispar* larvae, allowed to feed on aspen leaves, would perform better on resource-acquisitive aspen genotypes than on resource-conservative genotypes. I also hypothesized that larvae would preferentially feed upon genotypes with more resource-acquisitive strategies. I designed and conducted a pair of bioassays, one testing larval preference and the other testing larval performance on genotypes with varying strategies.

The second chapter investigates the effects of genetic and phenotypic aspen variation on insect communities. I hypothesized that aspen genes contribute to shaping insect communities (i.e., as an extended phenotype). I quantified the phenotypic variation of aspen as well as variation among aspen-associated insect communities. I compared tree traits and insect communities among aspen genotypes and determined which traits and community aspects were genetically heritable. I then related insect community metrics to tree traits to determine which traits were most influential. Finally, I identified individual genes that were associated with tree traits and community metrics.

The third chapter evaluates the accuracy of the mixed effects genomic association model developed to conduct the analyses in chapter two. I designed and executed a simulation study, based on the aspen-herbivore system, to compare the statistical properties of various genomic association methods. The mixed model method I propose (and use in Ch. 2) uses computational advancements to detect genetic associations with extended phenotypes more accurately than the other commonly used methods

The fourth and final chapter evaluates the robustness and accuracy of a novel statistical method, PARTS (Partitioned Autoregressive Time Series analysis), for conducting map-level hypothesis tests of spatial and spatiotemporal datasets. I developed and deployed a software package in the R statistical programming language that contains tools for implementing this method. I then used these tools to design and conduct a simulation study testing the method under various conditions. Finally, based on the results from the simulation study, I evaluate the method’s applicability to real world data.

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Chapter 1

Intraspecific variation in plant economic traits predicts trembling aspen resistance to a generalist insect herbivore

Authors: Clay J. Morrow, Samuel J. Jaeger, and Richard L. Lindroth

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Abstract

Patterns of trait expression within some plant species have recently been shown to align with the leaf economics spectrum paradigm. Resistance to herbivores is also expected to covary with leaf economics traits. We selected 36 mature *Populus tremuloides* genotypes in a common garden to assess whether aspen leaf economics patterns follow those observed among species globally. We also evaluated leaf economics strategies in the context of insect resistance by conducting bioassays to determine the effects of plant traits on preference and performance of *Lymantria dispar.* We found that: 1) intraspecific trait patterns of *P. tremuloides* parallel those exhibited by the interspecific leaf economics spectrum, 2) herbivores preferred leaves from genotypes with resource-acquisitive strategies, and 3) herbivores also performed best on genotypes with resource-acquisitive strategies. We conclude that a leaf economics spectrum that incorporates defense traits is a useful tool for explaining intraspecific patterns of variation in plant strategies, including resistance to herbivores.

Introduction

Plants exhibit phenotypic variation, both within and among species, that results in variable resistance to phytophagy. Metabolic, allocational, and genetic tradeoffs between growth and defense traits contribute to this variation and have been well-documented (Züst et al. 2015; Züst and Agrawal 2017; Heckman et al. 2019). Growth and defense traits, however, do not exist in isolation. Rather, they are single components of larger phenotypic expression networks. Patterns of trait covariation are typically complex, with tradeoffs occurring among multiple traits simultaneously (Züst and Agrawal 2017; Cole et al. 2021). Accordingly, hypotheses addressing variation in plant defense strategies, especially those that incorporate growth-defense associations, would benefit by considering co-expression of resistance and non-resistance traits alike.

Plant traits are intercorrelated in predictable ways across a broad array of species, worldwide. Mass-based rates of photosynthesis are positively associated with leaf nitrogen and phosphorous content, dark respiration, and specific leaf area (SLA). Developed by Wright et al. (2004), the leaf economics spectrum (LES) summarizes these patterns as a tradeoff between resource-conservative and resource-acquisitive strategies of adaptation across biomes and has proven useful for predicting the distribution of plant traits and fitness (Donovan et al. 2011; Reich 2014). Differentiation of plant strategies arises partly because of investment costs associated with one trait or function over another. Allocation tradeoffs extend to plant defense. Predictions that plants in resource-poor environments should grow slowly and invest in defense traits (Coley et al. 1985; Coley 1987) have been generally supported (Endara and Coley 2011). As a consequence, slow-growing plants are expected to sustain less herbivore damage than their fast-growing counterparts (Price 1991; Herms and Mattson 1992). Recognition of the ubiquity of growth-defense tradeoffs and the importance of herbivore resistance to plant fitness has led to the recent incorporation of defense traits, specifically phytochemical resistance, into the LES paradigm (Agrawal 2020).

If increased growth is associated with decreased herbivore resistance, then herbivores should both prefer and perform best on growth-optimized plants (Levins and MacArthur 1969; Price 1991; Mayhew 1997). This means that insect preference and performance should be aligned and that growth-associated plant traits drive these outcomes. Little evidence exists, however, that insect preference and performance are linked to each other or to plant growth in general. Some sessile insects, which are closely associated with their host plants, do exhibit a preference-performance linkage (e.g., Fritz et al. 2000). Additionally, Gripenberg et al. (2010) demonstrated a link between ovipositional preference and offspring survival across 21 plant-insect systems. Yet, studies of preference-performance relationships have been limited in scope and evidence of a broad linkage remains largely inconsistent. For example, investigations of insect preference and performance within the same experimental system are uncommon and host selection behaviors other than oviposition preference have rarely been considered (Gripenberg et al. 2010). Moreover, although many studies have focused on the relationship between plant growth and defense, and implications thereof for herbivores, research directly comparing insect performance to plant growth was relatively scarce a decade ago (Cornelissen et al. 2008; Gripenberg et al. 2010) and has not increased appreciably since.

The capacity to explain plant variation and herbivore resistance with a small number of LES traits is appealing, but may be scale-dependent. The applicability of the LES across taxonomic and ecological scales has been assessed in several recent studies. Anderegg et al. (2018) found that some leaf economics traits exhibited different correlations when compared within versus among species (962 genera). They concluded that, due to phenotypic plasticity, the LES may not be indicative of plant strategies at smaller taxonomic scales. Agrawal (2020) found similar inconsistencies in *Asclepias* across populations, species, and environmental gradients; at some scales, no LES correlations were found. It remains unclear under what conditions patterns of intraspecific trait co-expression differ from patterns among species. Phenotypic variation within plant species, and effects on their communities and ecosystems, can be substantial in certain systems (Des Roches et al. 2018; Koricheva and Hayes 2018; Westerband et al. 2021). Co-expression of plant phenotype and its impact on herbivores is key to understanding intraspecific strategies of resistance.

This research used an ecologically and economically important tree-insect system to investigate the impacts of trait co-expression on resistance to herbivores. Trembling aspen (*Populus tremuloides*) is a foundation tree species with an expansive range across northern and western North America (Mitton and Grant 1996). The species has exceptional levels of phenotypic variation in growth and defense traits (Mitton and Grant 1996; Cole et al. 2021), and tradeoffs thereof, making it an ideal candidate for linking plant growth, leaf economics patterns, and resistance to defoliators. A key defoliator, *Lymantria dispar* (formerly known as “gypsy moth” and now as “spongy moth”) is an invasive forest insect (McManus and Csóka 2007), for which aspen is a preferred host (Liebhold et al. 1997). Trembling aspen express a wide range of heritable variation in phytochemical defense that reduces performance of *L. dispar* (Hemming and Lindroth 2000; Osier et al. 2000; Donaldson and Lindroth 2007). This experimental system, therefore, provided an ideal opportunity to assess the utility of the LES at the intraspecific level. The trade-offs, across multiple traits, exhibited by aspen are complex and age-dependent (Cole et al. 2016, 2021; Cope et al. 2019), but whether overall trait expression is consistent with LES patterns is unknown. The system also provided a unique opportunity to test the preference-performance linkage with an herbivore underrepresented in prior research. *Lymantria dispar* are mobile, leaf-chewing, generalist lepidopterans and exhibit host selection as larvae (Doane and McManus 1981). These types of insects are largely absent from the preference-performance literature (Gripenberg et al. 2010).

This study evaluated the LES paradigm, including chemical defense traits, at the intraspecific level and assessed its ability to explain preference and performance patterns of *L. dispar* on trembling aspen. We addressed the following questions: 1) Are patterns of intraspecific trait expression consistent with predictions of the LES? 2) Do herbivores preferentially feed on aspen with resource-acquisitive strategies? 3) Are herbivores advantaged by feeding on resource-acquisitive plants over resource-conservative plants?

Materials and methods

To investigate the effects of leaf economics strategies on resistance to herbivory, we conducted two concurrent bioassays comparing larval preference and performance among aspen clones with varying intrinsic growth rates. We assessed host selection and growth of larvae as indicators of aspen resistance, as both metrics influence *L. dispar* fitness. We selected aspen clones to represent a wide range of variation in growth over a six-year period, thereby enhancing the probability of detecting intraspecific patterns of leaf economics traits and their effects on larval preference and performance.

Aspen genotype selection

This study used 36 aspen genotypes from a common garden population of 492 genotypes. We established the garden by collecting rootstock from throughout

Wisconsin (358 km latitude range, 186 km longitude range) and planting root sprouts with 2.5 × 2.5 m spacing at the University of Wisconsin-Madison Arlington Agricultural Research Station (43.32°N latitude, 89.33°W longitude) in 2010. One year prior to the study reported here, we selected experimental genotypes to maximize variation in growth over the garden's 7-year life. To achieve desired variation, we randomly selected twelve genotypes, with three replicate trees, from each of the bottom, middle and top deciles of the experimental population's growth distribution and classified them as low-, moderate- and high-growth genotypes, respectively.

Insect bioassays

We performed two bioassays to evaluate *L. dispar* preference for, and performance on, aspen genotypes from different growth classes. We obtained multiple *L. dispar* egg masses from the USDA APHIS insect production facility (Buzzards Bay, MA), incubated (25-18°C, 50-70% humidity, 16:8 L:D cycle), hatched, and reared them to third and fourth instars for use in bioassays. Larvae were fed a standardized diet of non-experimental *P. tremuloides* leaves and *L. dispar* wheat germ diet (MP Biomedicals) prior to experimental deployment.

Preference bioassays were designed to test host selection of *L. dispar* larvae in response to aspen phenotype. We maintained third instars (69-90 mg) without food for 24 hours preceding the experiment, after which time they were placed individually into petri dishes (15 cm diameter) with two leaves. Dishes contained pairs of leaves such that larvae had a choice between genotypes from different growth classes (i.e., low vs moderate, low vs. high, moderate vs. high). We replicated each growth class pairing with 12 distinct genotype pairs, for a total of 36 dishes in the bioassay. We replicated each genotype twice and assigned genotype pairs randomly. Larvae fed freely within dishes for 60 hours.

Leaves used in the preference bioassays were obtained from a single representative tree for each genotype. On the morning that trials were begun, we collected a single proleptic short shoot from each tree and kept them refrigerated until use. Two bioassay leaves were randomly selected from each shoot, weighed, and measured for specific leaf area (SLA). We inserted petioles of the bioassay leaves through a hole punched into lids of 2.0 mL microcentrifuge tubes containing water and placed them into their experimental dishes prior to larval introduction. We then developed genotype-specific water content calibrations with remaining short shoot leaves by comparing leaf weights before and after vacuum drying. We estimated initial dry mass of bioassay leaves by subtracting genotype-specific water content from initial leaf weights. We measured final dry mass of bioassay leaves upon conclusion of the trials.

At the end of the preference bioassays, we removed larvae and leaves from dishes and determined genotype preference by comparing the mass consumed from each leaf (i.e., $finalmass - initialmass$). We used the proportional consumption of a leaf by a larva as our metric of preference (i.e., $leafmassconsumed \div totalmassconsumed$) We then created a genotype-specific preference index by averaging preference for each genotype across dishes in which they occurred.

Performance bioassays were designed to assess the growth of *L. dispar* larvae in response to aspen growth strategy. The experiment followed a nested factorial design where three replicate trees of 12 genotypes were nested within each of the three growth classes for a total of 108 trees. We selected and weighed sets of ten newly molted third instars and deployed them to trees in the common garden. Fine mesh bags, secured with zip ties, contained larvae on northeast-facing branches at approximately 1.4 m above ground. After ten days, we collected, counted, sexed (Lavenseau 1982), vacuum dried, and weighed surviving larvae. As a performance metric, we estimated average relative growth rate (RGR) for larvae on each tree with the formula $(finalmass - initialmass) \div (initialmass \times 10days)$. We estimated initial dry mass of larvae from fresh weights with the formula $initialaggregateweight \div 10larvae \times 0.13mg + 0.27mg$, as determined via calibration from additional third instars from our colony. Immediately before deployment of larvae, we collected four to six mature leaves from each experimental branch for quantification of morphological and phytochemical traits.

Phenotypic trait measurements

We quantified aspen growth rates to evaluate their relationship with expression of other traits and resistance to herbivores. We calculated growth metrics for each of two time periods. First, a long-term growth metric was calculated to assess the relationship of phenotypic traits measured in 2018 to the average annual growth of trees over the preceding eight years. Long-term growth was measured as basal area increment (BAI) averaged over the eight-year life of the trees ($BAI = (\pi r_{2018}^2 - \pi r_{2010}^2) \div 8$; measured at stem base in 2010 and 1.4 m above ground in 2018).

Second, a short-term growth metric was calculated to evaluate the relationship of phenotypic traits measured in 2018 to the growth rates of trees in that same year. We used relative growth rate ($RGR_{st} = ln\ (\pi r_{2018}^2 \div \pi r_{2017}^2)$; Hunt 1982) as our short-term metric, as it accommodates for variation in tree size at the beginning of the one-year period (2017-2018). The long-term growth metric (BAI) was not relativized because initial sizes did not vary significantly in 2010. RGR_{st} is a log-transformed ratio of diameters and accounts for the exponential growth exhibited by aspen (Supp. Fig. 1).

We also quantified leaf morphological and chemical traits to evaluate their effects on herbivore resistance and their relationships with growth. We used leaves collected during the performance bioassays for quantification of leaf traits for all experimental trees. We first measured leaf area with a *LI-COR 3100* area meter. Next, we vacuum dried, weighed, and ground leaves (ball mill) for phytochemical analyses. We measured salicinoid phenolic glycosides as chemical resistance traits in this study because of their documented deleterious effects on *L. dispar* and other Lepidoptera (Donaldson and Lindroth 2007; Lindroth and St. Clair 2013). Condensed tannins, which do not negatively impact lepidopterans, were not measured. We extracted salicinoids from leaf tissue into methanol and quantified them by UPLC mass spectrometry (Rubert-Nason et al. 2017). Our chemical standards for salicinoid analyses consisted of commercially available salicin and lab-purified salicortin, tremulacin, and tremuloidin. We measured nitrogen concentrations with a ThermoFlash carbon/nitrogen elemental analyzer. All chemical concentrations are expressed as a percentage of leaf dry weight. Finally, we calculated specific leaf area by dividing total leaf area by total mass of all leaves collected from a tree.

Statistical analyses

To test the hypothesis that *L. dispar* larvae should prefer resource-acquisitive aspen, we performed multifactor analysis of variance (ANOVA) and pairwise t-tests comparing the mass consumed between leaves within dishes in the preference bioassays. All treatment specifications (dish treatment, genotype identity, and growth class) were included as factors in both analyses. We then performed multiple linear regression analysis relating a leaf's preference index with aspen phenotype to determine which traits best explain larval preference.

To test the hypothesis that *L. dispar* larvae should grow faster on resource-acquisitive aspen genotypes, we performed further multi-factor ANOVAs and pairwise t-tests of performance assay data, comparing larval relative growth rates among aspen growth classes and genotypes. We also performed multiple linear regression analysis of larval relative growth rates to determine which traits best explain larval performance.

Finally, we conducted a redundancy analysis (RDA) to investigate the effects of aspen phenotype on herbivore resistance. RDA is a constrained ordination that partitions variation of a multivariate regression. We used larval growth on, and preference for, genotypes as our multivariate response indicative of resistance. We included genotype averages of all traits as predictors. We assessed variation in larval metrics attributable to variation in trait expression using the RDA loadings. We also graphically assessed alignment of intraspecific trait variation with the LES.

All statistical analyses were performed using the R statistical software package (R Core Team 2020). We used a significance threshold of 0.05 for all hypothesis tests and considered results marginally significant for P-values between 0.05 and 0.10. We performed stepwise selection to obtain linear models that best explain (i.e., lowest AIC) insect metrics with tree traits and growth class. We also calculated adjusted R^2 (R^2_{adj}) to assess overall fit of the selected models. RDA was performed using the *rda* function from the *vegan* R package and statistical significance was determined via permutation test (Oksanen et al. 2020).

Results

Here, we first present variation observed among growth classes for each aspen trait. Next, we explore resistance to *L. dispar* by comparing insect metrics among aspen growth classes and genotypes, and by assessing associations between insect metrics and plant traits. Finally, we describe correlated patterns of leaf economics traits among genotypes and their associations with herbivore resistance.

Aspen trait variation

Trait expression differed among aspen genotypes from the three different growth classes. Of all traits measured, only BAI differed among all three growth classes (Figure 1A). Genotypes in the high-growth class had slightly lower RGR_{st} than those in the low-growth class, indicating that average long-term aspen growth was not a strong indicator of short-term growth (Figure 1B). Of the four salicinoids, salicortin and tremulacin were most abundant and concentrations of both were lowest for high-growth genotypes (Figure 1D-E). In contrast, tremuloidin concentrations were very low, but were higher among high-growth genotypes than among low-growth genotypes (Figure 1F). Salicin concentrations were similarly low but did not differ among growth classes (Figure 1C). Notably, one low-growth genotype had extraordinarily high concentrations of all four salicinoids when compared with other low-growth genotypes (Figure 1C-F). Nitrogen did not differ among growth classes (Figure 1G) and had the lowest variation of any trait. SLA was lower for low-growth genotypes than for high-growth genotypes (Figure 1H).

Herbivore resistance bioassays

Larvae preferred to feed on leaves from fast-growing aspen (Figure 2). Aspen growth class and genotype affected preference independent of treatment combination (Supp. Table 1). Larvae consumed twice as much tissue from high-growth than from low-growth genotypes, and 53% more from high-growth than from moderate-growth genotypes. Larvae did not discriminate between low-growth and moderate-growth genotypes. BAI and total salicinoids were positively and negatively associated with leaf consumption, respectively (Table 1, Supp. Figure 2). Together, these traits best explained larval preference for a genotype ($R^2_{adj} = 0.23$), with salicinoids explaining more than BAI (Table 1).

Larvae also performed well on fast-growing aspen (Figure 3). Larvae grew faster on high-growth genotypes than on moderate-growth genotypes. Interestingly, larval growth rates were intermediate, and most variable, on low-growth genotypes. SLA and tremulacin were positively and negatively associated with larval growth, respectively (Table 2, Supp. Figure 3). These traits, along with growth class, best explained variation in larval performance ($R^2_{adj} = 0.38$) and SLA explained the most (Table 2). Increased nitrogen was also associated with increased larval growth (Supp. Figure 3G) but the strong correlation between nitrogen and SLA (Table 3) made their effects largely redundant.

Leaf economics trait patterns

Aspen genotypes exhibited trait correlations consistent with growth-resistance tradeoffs and LES patterns (Table 3). BAI was negatively correlated with salicortin and positively correlated with SLA. Short-term aspen RGR_{st} was not significantly correlated with long-term BAI or any other traits. Salicortin and tremulacin were strongly positively correlated, as were salicin and tremuloidin. SLA was positively correlated with both tremuloidin and nitrogen.

Redundancy analysis revealed that trait patterns consistent with leaf economics strategies were associated with resistance to herbivory, and that genotypes exhibited substantial variation in these strategies both within and among aspen growth classes (Figure 4). The primary RDA axis, which accounts for twice the variation explained by the secondary RDA axis, aligns with the LES for the traits measured (RDA loadings found in Supp. Table 2). Larval preference and performance were not strongly correlated (Table 3) and were affected differently by aspen traits. Larval preference for aspen genotypes was most closely associated with high BAI and low levels of the salicinoids salicortin and tremulacin. In contrast, larval performance (growth rate) was determined by levels of tremulacin and nitrogen, as well as SLA. These multivariate results align with those from univariate analyses of the two bioassays. Aspen traits explained 35% of the variation in *L. dispar* resistance, of which salicortin and BAI explained the most (Supp. Table 3).

Growth class alone was not a reliable predictor of LES patterns. Although high-growth genotypes were more likely to align with resource-acquisitive patterns than those in other classes, this tendency was too weak to be differentiable (Figure 4). High levels of genotypic variation within growth classes contributed to substantial phenotypic overlap among classes.

Discussion

This research aimed to evaluate the LES paradigm at the level of intraspecific trait variation, and its potential to explain insect herbivore resistance. Our results demonstrate that the paradigm can indeed be useful for explaining intraspecific variation in plant strategies. Fast-growing genotypes had higher SLA, higher foliar nitrogen concentrations, and lower foliar salicinoid concentrations, matching a resource-acquisitive strategy in the LES paradigm. As a result, these genotypes experienced low herbivore resistance, when compared with genotypes matching more resource-conservative strategies. No strong insect preference-performance linkage was found, and aspen traits affected the two indicators of herbivore resistance somewhat differently. Larvae preferred to feed on aspen with low salicinoid concentrations and fast growth. Larvae also performed well on aspen with low salicinoid concentrations, but performance was primarily associated with nitrogen and SLA. Generally, the primary RDA axis of aspen traits aligned well with patterns expected for a defense-integrated LES, making it a useful proxy for the paradigm. In summary, leaf economics traits were useful indicators of plant resistance strategies.

Observed trait patterns within *P. tremuloides* align with those found among species worldwide. Intraspecific LES patterns have been demonstrated in a variety of species (e.g., common reed: Hu et al. 2015; coffee: Martin et al. 2017). Yet, recent comparisons of the LES across diverse ecological and taxonomic scales reveal that trait correlations can be scale-dependent. For example, in their meta-analysis of 2,031 species, Anderegg et al. (2018) found that, although directions remain consistent, magnitudes of trait correlations with LMA (i.e., $\frac{1}{SLA}$) and nitrogen vary among taxonomic scales. In another study, Grady et al. (2013) showed that conservative leaf economics traits were associated with fast growth of *Populus fremontii* in hot environments. Other research also shows that conformation with LES patterns can depend upon spatial scales (Messier et al. 2017). We could not evaluate spatial dependence but trait patterns driven by genetics are unlikely spatially structured in Wisconsin aspen due to lack of population structure (Cole 2005; Barker et al. 2019b).

This work also reveals that incorporation of defense traits can benefit assessments of the LES at the intraspecific level. Recent research shows that plant defense is correlated with traditional LES traits within and among species. For example, *Helianthus* defense is correlated with interspecific LES strategy (Mason and Donovan 2015). Similarly, across species of spiny plants, physical defenses are associated with leaf productivity, whereas chemical defenses are not (Armani et al. 2020). Both chemical and physical defense traits are correlated with LES traits within *Asclepias syriaca*, but not among different *Asclepias* species (Agrawal 2020). In short, a growing body of literature suggests that the utility of incorporating herbivore defense into the LES paradigm is species- or context-specific. A major limitation of a defense-integrated LES paradigm is the sheer diversity of defense types, which makes comparisons across species challenging. Even so, because herbivores are ubiquitous and formative components of plant communities, incorporation of herbivore defense traits will likely enhance the value and function of LES models.

Our results show that not only are defense traits associated with leaf economics strategies, but so too are defense outcomes. While it is clear that intraspecific plant strategies result in tradeoffs between growth and defense traits in many systems (Endara and Coley 2011; Züst and Agrawal 2017), to our knowledge, none of the recent evaluations of plant defense and the LES include measures of resistance outcomes. Covarying effects of plant traits on herbivore fitness are well known (e. g., Simpson and Raubenheimer 2001) and defense traits are particularly well-studied (e.g., Gong and Zhang 2014). Of the four aspen salicinoids evaluated in this study, the compounds that occur in the lowest concentrations - salicin and tremuloidin - have low biological activity (but see Cook et al. 2003). The more abundant salicortin and tremulacin are much more biologically active, due to the presence of cyclohexenone and benzoyl functional groups (Lindroth et al. 1988; Boeckler et al. 2011). Consistent with that information, our results show that salicortin and tremulacin were the salicinoids most strongly linked to herbivore performance and LES traits. This work further establishes how defense traits can be integrated across a spectrum of intraspecific functional strategies, and the consequences thereof for trophic interactions.

Intraspecific covariation in defense and conventional LES traits has important ecological and evolutionary consequences in aspen and other *Populus* species. Foliar nitrogen and salicinoids govern the preference, performance, distribution, and abundance of herbivorous insects, as well as their rates of defoliation (Donaldson and Lindroth 2007; Falk et al. 2018). They also influence the structure of herbivorous insect communities (Bangert et al. 2006; Barker et al. 2018, 2019a) and dynamics of multi-trophic interactions (Bailey et al. 2006). More recently, work with experimental aspen stands documented that intraspecific competition alters the consequences of genotypic growth-defense tradeoffs, leading to divergent genetic architecture of aspen populations (Cope et al. 2021).

The relationship between host plant selection and performance of insect herbivores remains equivocal. The most comprehensive meta-analysis of preference-performance relationships to date found that survival, but not weight or development time, are associated with host preference (21 comparable plant-insect systems; Gripenberg et al. 2010). For *L. dispar* and numerous other insects, however, preference and performance appear unrelated (e.g., Valladares and Lawton 1991; Underwood 1994; Fritz et al. 2000).

Lymantria dispar larvae engage in host plant selection by dispersing from unsuitable hosts (Capinera and Barbosa 1976; Lance and Barbosa 1981). These decisions appear to be made primarily in response to chemical defenses; Solari et al. (2002) found that *L. dispar* larvae respond strongly to deterrent stimuli (i.e., nicotine) but not to classical nutrition stimuli. Our work reaffirms these findings. *Lymantria dispar* selected hosts according to salicinoid concentrations and largely ignored performance-associated nutrients (i.e., nitrogen).

In conclusion, our work reveals that the leaf economics spectrum can be useful for describing patterns of association among plant functional traits, - including herbivore resistance traits - at the intraspecific level. In trembling aspen, genotypes of resource acquisitive plants tended to have high specific leaf area, high nitrogen concentrations, and low salicinoid concentrations compared with resource-conservative genotypes. This trait combination elicited higher herbivore preference, and performance, relative to insects on resource-conservative plants. Patterns of phenotypic relationships identified in this research suggest that growth-associated plant traits are associated with susceptibility to herbivore attack.

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Author's contributions: CJM, SJJ, and RLL conceived and designed the experiments. RLL secured funding. CJM and SJJ conducted fieldwork, lab work, and analyzed the data. CJM and RLL wrote the manuscript.

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Tables

Table 1: Best model (lowest AIC) for explaining larval preference for aspen genotypes. Rows represent model terms. Columns represent regression coefficients, standard error of the coefficients, regression t-statistics, type II sum of squares, degrees of freedom, F-statistics (SS/MSE), and corresponding P-values. The P-value for the t- and F-statistics are identical.

	Coef	SE	t	SS	df	F	P
(Intercept)	0.64	0.17	3.8				0.0005
BAI	0.02	0.02	1.8	0.23	1	3.4	0.0758
Total salicinoids	-0.06	0.02	-2.6	0.45	1	6.5	0.0154

Table 2: Best model (lowest AIC) for explaining larval growth performance for aspen genotypes. Formatting follows from Table 1. Values for moderate and high growth classes are relative to that of the low growth class, which is captured by the intercept term. ANOVA results for Growth class factor: SS = 0.17, Df = 2, F = 2.6, P = 0.090.

	Coef	SE	t	SS	df	F	P
(Intercept)	0.25	0.27	0.9				0.362
SLA	3.88	1.07	3.6	0.43	1	13.1	0.001
Tremulacin	-0.07	0.04	-1.7	0.10	1	3.0	0.091
Class:mod	-0.16	0.08	-2.1				0.043
Class:high	-0.03	0.08	-0.4				0.728

Table 3: Correlation matrix for aspen traits and larval metrics among genotypes. Column and row headings correspond to basal area increment; short-term relative growth rate of aspen; concentrations of salicin, salicortin, tremulacin, tremuloidin, and nitrogen; specific leaf area; larval relative growth rate; and larval preference. Cells represent Pearson's correlation coefficient and superscript symbols represent statistical significance (+: 0.05 < P < 0.1, *: 0.01 < P < 0.05, **: P < 0.01).

	BAI	RGR_{st}	Salicin	Salicortin	Tremulacin	Tremuloidin	N	SLA	larval RGR
RGR_{st}	-0.29^{+}								
Salicin	0.21	-0.05							
Salicortin	-0.40^{*}	0.17	-0.04						
Tremulacin	-0.28^{+}	0.18	0.25	0.90^{**}					
Tremuloidin	0.30^{+}	-0.08	0.90^{**}	-0.18	0.13				
N	0.17	-0.30^{+}	0.31^{+}	-0.27	-0.18	0.30^{+}			
SLA	0.40^{*}	-0.21	0.32^{+}	-0.22	-0.15	0.40*	0.50^{**}		
larval RGR	0.23	-0.20	-0.03	-0.31^{+}	-0.30^{*}	0.10	0.40^{*}	0.50^{**}	
larval pref.	0.40^{+}	-0.21	-0.2	-0.40^{*}	-0.40^{*}	-0.21	0.06	0.05	0.23

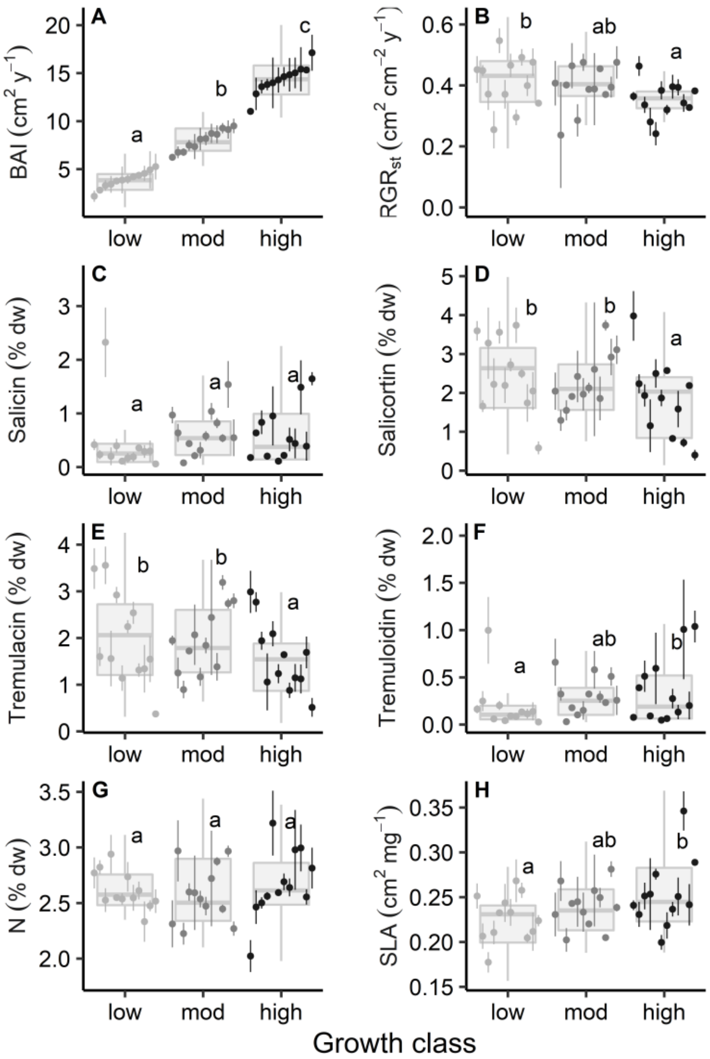


Fig. 1: Trait variation among *Populus tremuloides* growth classes. Points represent genotype means for each trait and error bars represent +/- 1 standard error. Boxes show quartiles for each growth class and whiskers show the range, excluding outliers. Lower case letters represent statistically distinct groupings among growth classes (Tukey’s least significant difference). Phytochemical concentrations are expressed as percent dry weight. Genotypes are shown in order of ascending BAI for all panels.

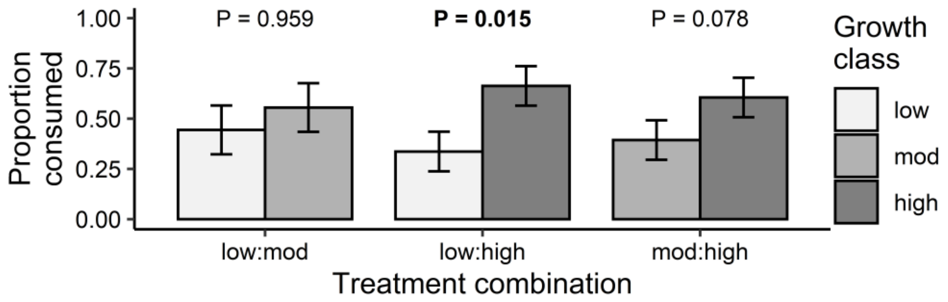


Fig. 2 Feeding preferences of larval *Lymantria dispar* for pairwise combinations of aspen leaves from low, moderate, and high growth classes. Bars represent leaf mass consumed from a leaf within a dish, as a proportion of total tissue consumed. Error bars represent +/- 1 standard error and P-values correspond to pairwise t-tests.

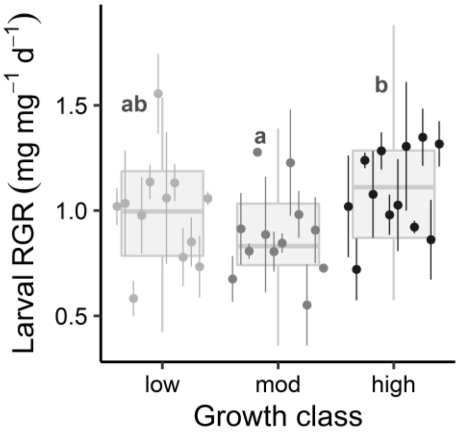


Fig. 3: Variation in larval growth rate among aspen growth classes. Formatting follows from Fig. 1.

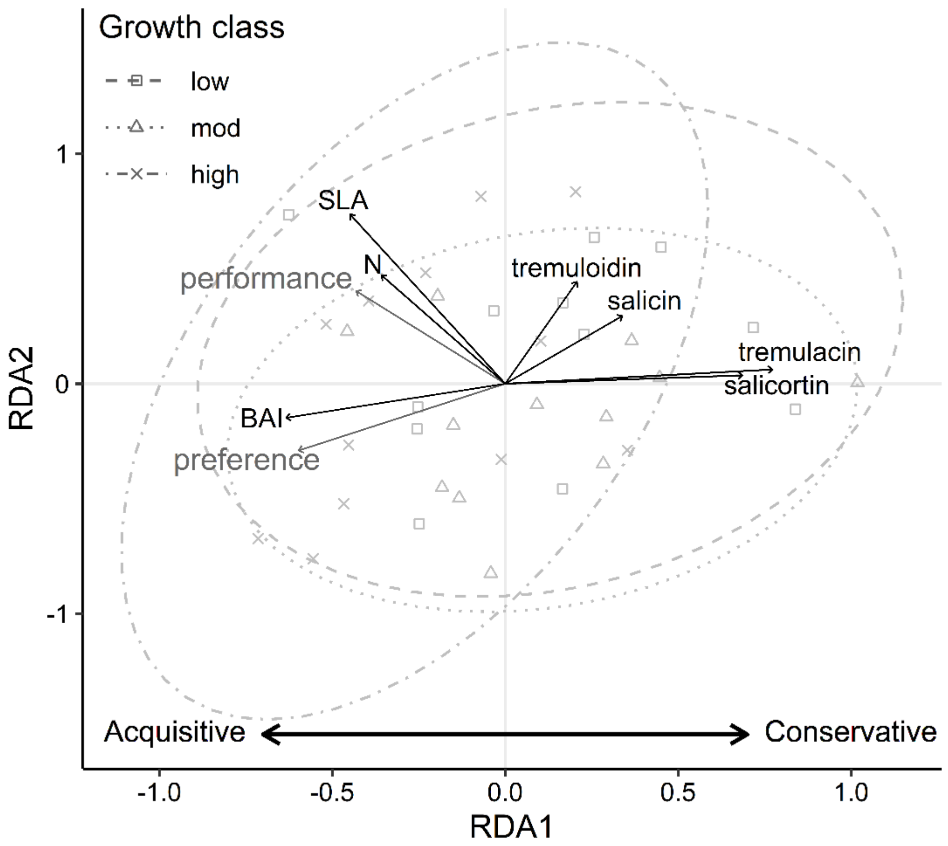


Fig. 4: RDA plot of insect responses (gray vectors) and tree trait predictors (black vectors). Angles between vectors are approximately proportional to correlations between variables (90°: none, > 90°: negative, < 90°: positive) but see Table 3 for true correlations. Points represent genotypes. Ellipses encompass the expected phenotypes of each growth class. Axis RDA1 accounts for 24.2% of variation in larval responses and RDA2 accounts for 11.0%. Black arrows at the bottom of the plot represent the LES.

Supplemental Tables

Supp. Table 1: Results from multi-factor ANOVA of larval preference by experimental treatment. Column headings correspond to degrees of freedom, sum of squares, mean squares, F-statistic, and P-value, respectively. This analysis shows that preference was independent of dish treatment combination, indicating that comparison across dishes is appropriate.

	df	SS	MS	F	P
Growth class	2	0.74	0.37	3.7	0.04
Genet	33	5.55	0.17	1.7	0.07
Treatment combination	2	0.27	0.14	1.4	0.27
Residuals	34	3.40	0.10		

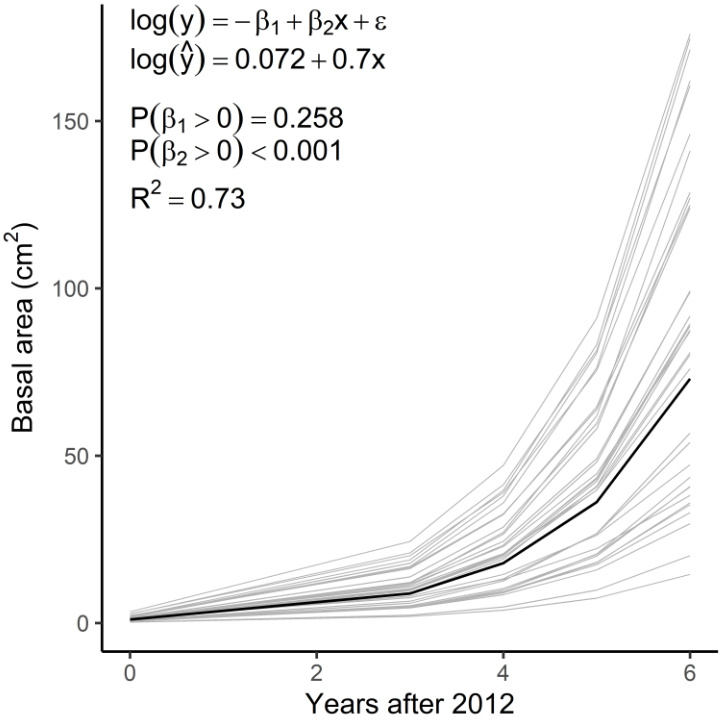
Supp. Table 2: RDA variable loadings. Rows represent all variables included in the RDA. The larval metrics ‘preference’, and ‘performance’ comprised the multivariate response. Columns represent the RDA ordination axes (RDA1, RDA2) and principal component axes (PC1, PC2).

variable	RDA1	RDA2	PC1	PC2
Preference	-0.60	-0.29	0.97	-0.14
Performance	-0.43	0.40	0.20	0.67
BAI	-0.63	-0.15	0	0
Salicin	0.34	0.29	0	0
Salicortin	0.69	0.04	0	0
Tremulacin	0.77	0.06	0	0
Tremuloidin	0.21	0.44	0	0
N	-0.36	0.47	0	0

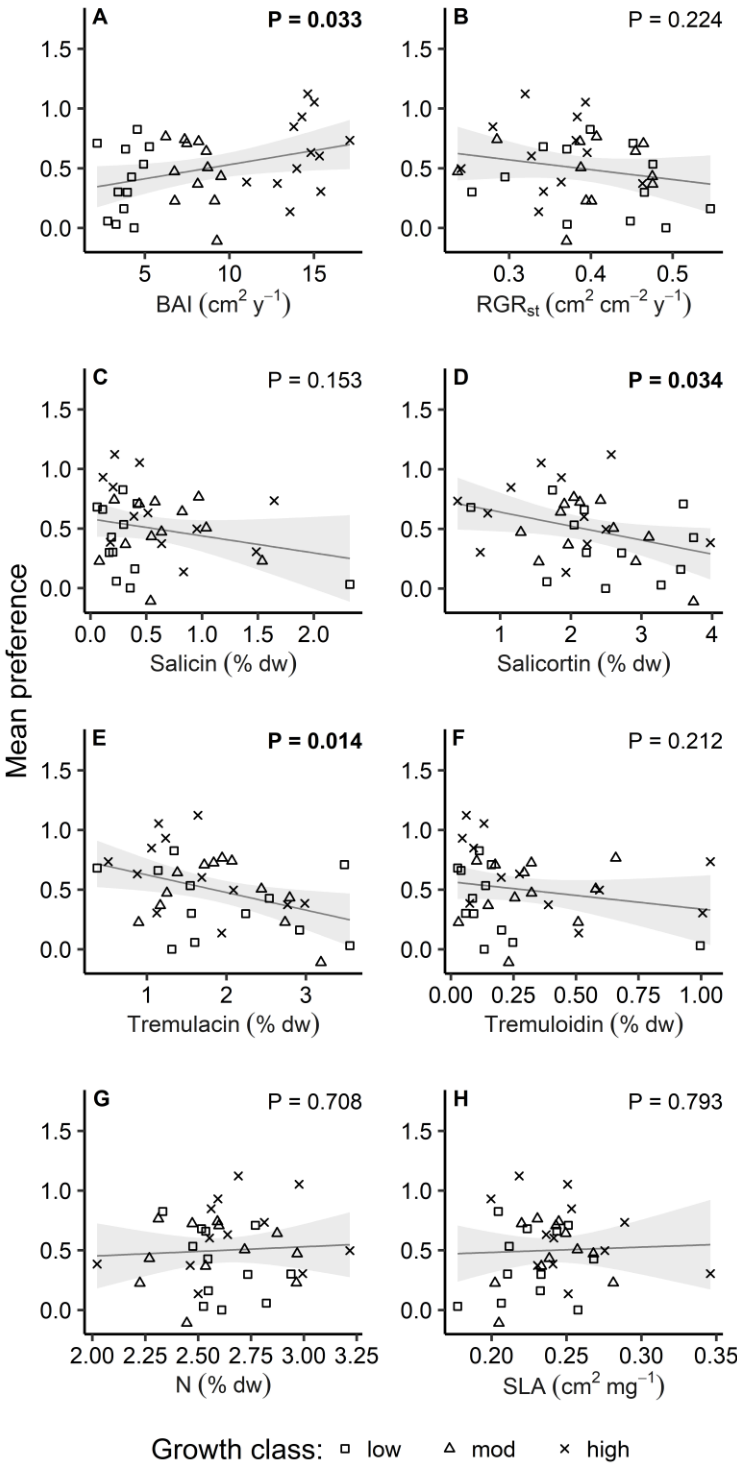
Supp. Table 3: RDA ANOVA-like table showing variance partitioning for effects of tree traits on larval preference and performance. Columns represent the source of variation, degrees of freedom, variance explained, proportion of total variance, proportion of explained variance, permutation test F-statistic, and P-value. Values in this table were derived from a permutation test with 1000 iterations.

source	df	var	var prop	prop explained	F	P
BAI	1	0.0089	0.062	0.065	2.7	0.08
Salicin	1	0.0054	0.037	0.040	1.6	0.20
Salicortin	1	0.0171	0.119	0.124	5.2	0.01
Tremulacin	1	0.0013	0.009	0.009	0.4	0.67
Tremuloidin	1	0.0057	0.040	0.042	1.7	0.20
N	1	0.0065	0.046	0.048	2.0	0.13
SLA	1	0.0057	0.040	0.041	1.7	0.19
Residual	28	0.0926	0.647			

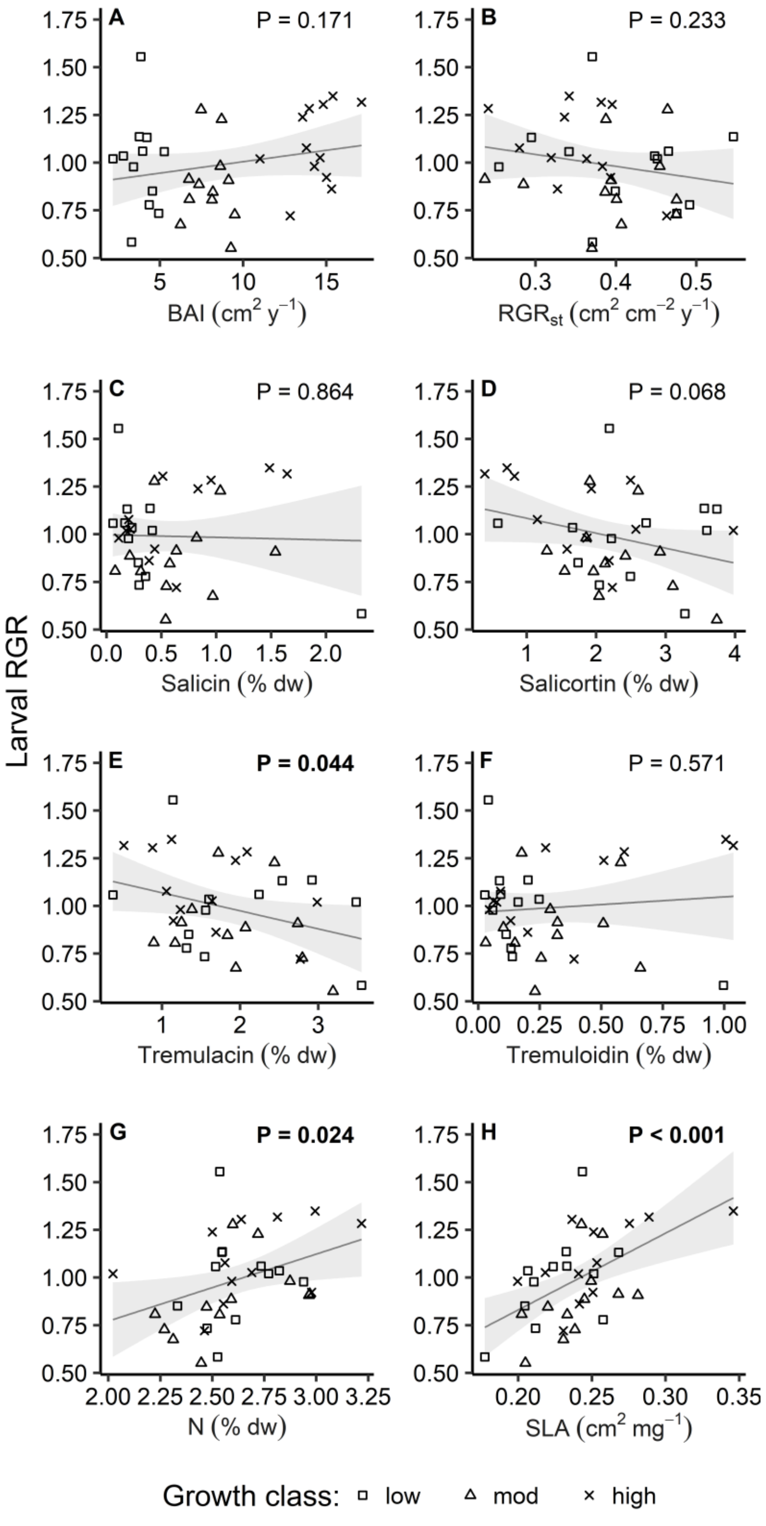
Supplemental Figures



Supp. Fig 1: Six-year growth, in terms of basal area, of 36 aspen genotypes used in this study. Discrete exponential growth curves are shown in gray for each genotype. The black line represents the average growth curve of all genotypes. Text in the upper left corresponds to this average growth curve and denotes: the exponential model, the parameter estimates for the fitted model, P-values for parameter estimates, and overall fit.



Supp. Fig. 2: Bivariate correlations between herbivore preference and aspen traits. Points represent genotype averages. Gray lines and error bars represent the bivariate linear regression line and standard error. P-values correspond to t-tests



Supp. Fig. 3: Bivariate correlations between herbivore performance and aspen traits. Formatting follows from Supp. Fig. 2.

Chapter 2

Genomic variation in aspen underlies variation in insect communities

Authors: Clay J. Morrow, Jennifer Lind-Riehl, Christopher T. Cole, Kennedy Rubert-Nason, Richard L. Lindroth

Abstract

Plant intraspecific variation, driven by genetic variation, plays an important role in shaping communities of associated organisms. Community genetics research aims to understand the causes of intraspecific variation and their effects on extended phenotypes such as community structure and diversity. To better understand the linkages between plant genes, phenotypes, and insect communities, we quantified natural intraspecific variation in a common garden of aspen, *Populus tremuloides,* and assessed its implications for associated communities of insect herbivores. We also aimed to identify gene variants linked to insect extended phenotypes, using a genomic association model with improved statistical properties over traditional methods. We found that communities of insect herbivores were heritable, and that structure and diversity of insect communities responded to aspen trait expression. Specialist herbivores *Harmandia sp.*, *Zeugophora scutellaris*, *Phyllocolpa sp.*, and *Chaitophorus populicola* were the most heritable insect species, while phenology, defense chemistry, reproduction, and leaf morphology were the most heritable tree traits. We identified 73 genes associated with budbreak timing, extrafloral nectary density, and flower production. We also identified an additional 15 genes associated with incidence of *Ectoedemia populella*, *Paraleucoptera albella*, *Zeugophora scutellaris*, and *Gluphisia septentrionis*. The genes associated with *E. populella* are especially relevant because their known functions correspond to physiological mechanisms that galling insects exploit. We conclude that intraspecific variation, complex patterns of phenotypic expression, and complex genetic architecture plays an important role in shaping aspen-associated communities of insect herbivores.

Introduction

Intraspecific trait variation can have far-reaching and impactful consequences that extend beyond populations to communities and ecosystems. On average, 25% of the total trait variation within plant communities is attributable to intraspecific variation (Siefert et al. 2015). The ecological impacts of intraspecific variation can be comparable to those of among-species diversity (Des Roches et al. 2018; Koricheva and Hayes 2018), especially in plants. For example, intraspecific variation in expression of secondary metabolites influences herbivore abundance and performance (e.g., Strauss and Agrawal 1999; Donaldson and Lindroth 2007) and can ultimately lead to differences in diversity and structure of associated insect communities (Bangert et al. 2006; Wimp et al. 2007; Poelman et al. 2009). Many other studies have similarly shown a link between genetic variation and communities of arthropods and fungi (e.g., Johnson and Agrawal 2005; Gosney et al. 2014, 2017, 2021; Barbour et al. 2016; Jiang et al. 2021), which in turn has consequences for entire ecosystems and evo-evolutionary dynamics. For example, genetic variation within a population of piñon pine resulted in differential associations with ectomycorrhizal fungi that affected drought tolerance among individuals (Gehring et al. 2017). Over time, and after a severe drought, the population evolved toward phenotypes that facilitated fungal communities that provide drought tolerance to their hosts (Gehring et al. 2017; Whitham et al. 2020). The effects plants have on their environment that differ with genotype are known as extended phenotypes (Flinn and Dawkins 1984; Whitham et al. 2003). Research into the underlying genetic variation has been increasing in plant systems (Westerband et al. 2021), where the effects appear common and ecologically relevant.

Despite the many advances of community genetics over recent decades, much remains unknown about the genomic mechanisms that shape intraspecific variation and, ultimately, extended phenotypes. Until recently (e.g., Westerband et al. 2021), few studies had investigated the relative importance of different traits in shaping extended phenotypes (Crutsinger 2016) and the interconnections among genes, phenotypes, and extended phenotypes remain broadly elusive. An outstanding criticism levied against community genetics research is that genotypes are often hand-selected and may not be representative of natural diversity (Hersch-Green et al. 2011; Crutsinger 2016). Finally, minimal research has investigated which specific genes govern ecologically relevant intraspecific variation and extended phenotypes. While important discoveries of genetic links have been made (e.g., with microflora [Horton et al. 2014] and invertebrate communities [Barker et al. 2019]), research in this area remains scarce. Understanding not only how associated communities differ among plant genotypes, but also the roles that genes and traits play to shape those communities, can elucidate the importance of genomic variation in maintaining diverse and resilient ecosystems. Furthermore, discoveries of genetic links to communities have important implications for allied disciplines such as conservation biology and ecosystem management.

Community genetic effects most likely occur in species that have high levels of heritable trait variation, are associated with diverse communities, and for which particular functional traits have large impacts on those communities (Whitham et al. 2006; Crutsinger 2016). Trembling aspen (*Populus tremuloides* Michx.) and related *Populus* species are ideal organisms to study in a community genetics context because they satisfy all three criteria. They exhibit substantial variation across a wide range of traits, many of which are genetically heritable (Cole et al. 2021); they are associated with biologically diverse communities that are also heritable (Whitham et al. 2006; Bangert et al. 2008); and much of their considerable phenotypic diversity occurs in ecologically relevant traits that drive these associations (Hwang and Lindroth 1997; Lindroth and St. Clair 2013). Collectively, these qualities in aspen can have profound effects on their communities, and explain why aspen is a foundation species throughout its expansive North American range (Madson 1996; Rogers et al. 2020). Aspen and other *Populus* have also been important models in plant-insect interaction research, in part due to their quantitative variation in chemical defense (Lindroth and St. Clair 2013; Barker et al. 2019a). Similarly, *Populus* is a model organism for genomic research (Yang et al. 2009; Constabel and Lindroth 2010) and for biology in general (Jansson and Douglas 2007). A wealth of quality genomic information is therefore available for aspen, relative to other tree species.

To better understand the links between genes, traits, and communities, this study investigated the effects of naturally-occurring intraspecific plant variation on associated insect communities among aspen genotypes in a common garden. We aimed to identify three distinct links: those between plant phenotypes and insect communities, those between plant genes and plant phenotypes, and those between plant genes and insect communities. We quantified insect communities and plant traits within the garden and investigated their relationships. We then fit a genome wide association model, improved from previous published studies, to identify potentially relevant genes. This work builds on previous studies of this system (Lind-Riehl et al.; Barker et al. 2019b) and addresses the following questions: 1) Are communities of aspen-associated herbivores genetically heritable? 2) Do heritable aspen traits contribute to shaping herbivore communities? 3) Do specific aspen genes contribute to shaping herbivore communities?

Materials and Methods

To evaluate the influence of aspen genotype and phenotype on associated canopy insect communities, we surveyed insects, measured tree traits, and conducted genomic analyses on aspen in a common garden. We estimated broad sense heritability of both tree traits and insect community metrics. We assessed potential phenotypic drivers of insect communities by associating community metrics with tree traits. Finally, we genetically sequenced all genotypes in our population and identified genomic associations with community metrics and with community-associated tree traits.

Experimental aspen population

The aspen population used in this study consisted of 1,568 experimental trees representing 492 genotypes. The common garden was established with sprouts propagated from roots collected from genotypes occurring naturally throughout Wisconsin (358 km latitude range, 186 km longitude range). In 2010, trees were planted in a 2.5 × 2.5 m grid in an incomplete randomized block design with four blocks. Trees from the outer perimeter of the garden were excluded from the study to guard against edge effects. The garden is located at the University of Wisconsin-Madison Arlington Agricultural Research Station (43.32°N, 89.33°W). Additional information about the setup, location, plot details, and source genotypes are documented by Barker et al. (2018, 2019b).The experimental population exhibits substantial phenotypic variation in diverse traits, including growth, chemical defense, reproduction, and phenology (Cole et al. 2021). The garden has been colonized by a diverse assemblage of tree-feeding insects, as first documented by (Barker et al. 2018).

Herbivore communities: extended phenotype

Over the course of two years, we conducted four total insect surveys to quantify herbivore communities occurring on individual aspen trees, and to compare the communities among genotypes and in relation to tree traits. Due to the magnitude of the survey efforts, we restricted them to the lower third of the canopy to reduce total survey time and within-survey temporal variation. We identified and counted insect herbivores and ants. Because of substantial variation in tree size, and to avoid biasing insect counts toward larger trees, we surveyed for durations approximately proportional to tree size. These sampling times were determined via rarefaction methods one week prior to the first survey event. Rarefaction revealed that no additional species were found beyond three, five, and ten minutes of sampling for the shortest (< 4m), intermediate (4-8m), and tallest (> 8m) trees sampled (10 each), respectively. Trees were then assigned survey times from three to ten minutes, according to diameter. These assignments ensured that approximately 75% of the lower canopy was sampled for each tree. Surveys occurred in mid-June and early-August of 2016 and 2017. We surveyed north to south, by experimental block, and each survey lasted ten days.

We quantified insect communities using diversity and structure metrics for each tree. We estimated species abundance, species richness, species evenness, and Shannon index as metrics of diversity (Hill 1973). We used species incidence, indicative of community composition, as a metric of community structure. We also used the first two axes of a non-metric multi-dimensional scaling ordination, based on Bray-Curtis community dissimilarities, as multivariate community metrics (adapted from Barker et al. 2019b). Because most insect species were very rare, this research focused on common insects that occurred on at least five percent of trees in any of the four survey events. Community analyses focused on these species and the two most common functional groups (free-feeding insects and leaf-modifying insects).

Aspen traits: phenotype

We quantified aspen traits that were expected to influence insect communities. These included phytochemistry, leaf morphology, tree size, tree phenology, and reproduction.

Immediately following each insect survey, we collected leaves to measure phytochemical and morphological traits. We collected four leaves, semi-randomly, from each cardinal direction of the lower canopy (16 per tree). Leaves were digitally scanned, vacuum dried, weighed, ground with a ball mill, and aliquoted for chemical analyses. We included four phytochemical metrics in this study: condensed tannin (CT) concentration, salicinoid phenolic glycoside (PG) concentration, nitrogen (N) concentration, and carbon-nitrogen ratio (C:N). We extracted CTs into acetone and quantified them via absorbance at 550 nm, using standards purified from aspen following Hagerman and Butler (1980). We extracted PGs into methanol and quantified them via UPLC mass spectrometry (Rubert-Nason et al. 2018). Commercially available salicin and lab-purified salicortin, tremulacin, and tremuloidin served as standards. We report PGs as the sum of those four compounds. Salicortin and tremulacin comprised >90% of the total PG pool; details on quantitative variation in individual compounds are provided by Cole et al. (2021). A ThermoFlash carbon/nitrogen elemental analyzer was used to determine N and C:N. All chemical concentrations are expressed as a percent of dry leaf weight (%

dw). Using a *LI-COR 3100* area meter, we calculated average leaf area ($ALA = total\ leaf\ area \div no.\ leaves$) and specific leaf area ($SLA = total\ leaf\ area \div total\ leaf\ mass$). Using digital leaf scans, we quantified the density of extrafloral nectaries ($EFN = no.\ nectaries \div no.\ leaves$).

Unlike leaf traits, tree size, phenology, and reproduction were quantified only once per year. As metrics of tree size, we measured basal area ($BA = \pi r^2$; 1.4 m above ground; dm^2) and estimated volume ($Vol = diameter^2 \times height$; m^3) at the end of each growing season. At the beginning of each growing season, we tracked bud set stage and used polynomial regression to estimate onset of budbreak (BB) in degree days (dd; Lind-Riehl et al. *in review*). We also counted the number of twigs on which flowers occurred as a measure of reproduction. Because aspen flower early in the growing season, utilizing resources stored during the previous season, we counted flowers in the year following each insect survey.

Aspen genomics: genotype

We identified sources of genetic variation in our aspen population, via genomic markers, to associate with phenotype and extended phenotype. We conducted Illumina HiSeq (Shen et al. 2005) sequence capture genotyping, from 45,934 probes, for each genotype in the common garden. Probes were designed using full DNA transcripts to target the exome (Lin et al. 2018) and reads were aligned to *Populus tremula* v1.1 (Lind-Riehl et al. *in review*). Variant filtering removed all single nucleotide polymorphisms (SNPs) with more than 30% missing data. Genotypes with more than 20% missing data were also removed. A total of 113,674 SNPs remained after applying a minor allele frequency cut-off of 5% for genomic association analyses. All genomic sequencing, alignment, variant calling and filtering procedures are outlined in detail by Lind-Riehl et al. (*in review*), and Barker et al. (2019b).

We also used genomic information to verify genotype membership and sex, and to summarize heterozygosity. In 2018, genetic markers obtained via unique sequence repeat microsatellite genotyping (SSR; Rahman et al. 2000; Smulders et al. 2001) were evaluated with GenAlEx (Peakall and Smouse 2012; Politov et al. 2015) and verified with SNP and phenotype data. Consequently, genotype identifications of individual trees were updated relative to previous studies conducted in this garden (Barker et al. 2018, 2019b). Sex was determined from *Populus* sex marker TOZ19 (Pakull et al. 2015) and verified, when possible, with flowers. Average observed heterozygosity ($H_{obs} = heterozygous\ SSR\ alleles \div total\ SSR\ alleles$) across the SSR loci was also included as a genetic summary trait.

Statistical analyses

To ascertain whether insect communities were heritable, we estimated the relative contributions of genetic variation to phenotypic and community variation within the aspen population (broad-sense heritability (H^2)). We measured H^2 of aspen phenotypes and community extended phenotypes by partitioning variance components of random effects models. We parameterized these models with only random effects as predictors. Along with genotype, we also included statistical block, survey year, survey month, and distance from the plot border (edge distance) as environmental factors. This parameterization allowed us to separate genetic variation from environmental variation. Due to the strong influence of ontogeny on tree traits, we also included tree age as a predictor in phenotype models. We then calculated H^2 by dividing the genotype-associated variance component by the total phenotypic variance (i.e., $H^2 = \sigma_{genet} \div \sigma_{total}$; modified from Barker et al. 2019b). Linear random effects models were used to determine heritability of most traits, but one community metric (species incidence) was fit with logistic mixed effects models because of the binomial nature of this metrics. In all cases, we bootstrapped H^2 1000 times and calculated 95% confidence bounds. For the purposes of this study, we consider a phenotype or extended phenotype highly heritable, relative to other traits, when at least 50% of the variation in that characteristic is explained by genotype ($H^2 \geq 0.5$, bootstrapped average). We consider a characteristic moderately heritable if 20-50% of the variation is explained by genotype ($0.2 < H^2 < 0.5$) and weakly heritable if less than 20% is explained.

We used mixed effects models and redundancy analysis to determine the influence of aspen phenotype in shaping heritable components of insect communities. We performed exhaustive model selection to determine which traits to include (based on lowest AIC), as fixed effects in models for each common insect. Experimental block, survey year, survey month, genotype identity, and edge distance were included as random effects in all models. In all analyses pertaining to BA, a square root transformation was used (BAsqrt) to meet model assumptions. Volume and C:N were highly correlated with BAsqrt ($r = 0.94$) and N ($r = 0.95$), respectively. Thus, these redundant variables were omitted from statistical models to avoid multicollinearity. We report the standardized effect sizes of tree traits on community metrics derived from the selected models. We also used redundancy analysis (RDA), a multivariate regression tool, to evaluate the aggregate effects of aspen traits on herbivore community structure.

We then conducted genomic association analyses of tree traits and insect communities to identify underlying genes with links to community characteristics. We fit mixed effects models for each combination of SNPs and response variables (i.e., phenotype and extended phenotype). SNP genotype, coded as 0 for homozygous major, 1 for heterozygous, and 2 for homozygous minor, comprised the sole fixed effect in these models. Experimental block, survey year, survey month, genotype identity, and edge distance comprised the random effects. Models incorporating insect responses were fit with and without the explanatory tree traits as covariates. This approach allowed us to determine how much of the variation attributable to genomic variation could also be explained by phenotypic variation. These association models were improved from the earlier work of Barker et al. (2019b) on this system, by fitting a covariance matrix for the effects of each SNP in all of the models rather than fitting a common covariance matrix and regressing the best linear unbiased predictors for genotype effects against SNP data with simple linear regression. These improved models offer much better type I error control while maintaining sufficient power to detect the small effects expected of extended phenotypes (Ch. 3), but are much more computationally expensive. We used a Wald chi-squared test to determine the significance of SNP effects on responses and performed multiple test corrections by calculating Storey’s q-value (Storey 2003). A significance threshold of $q < 0.15$ was used to identify SNP associations. At this level, it is expected that fewer than 15% of the detected associations are false positives. Once significant SNPs were identified, we investigated known functions of genes in which these variants were located. Additionally, gene enrichment analyses (Lin et al. 2018) were conducted for the top 0.1% of SNPs (determined by uncorrected p-value). Gene enrichment can identify whether clusters of functionally related genes are associated with traits, even if each individual gene association was too weak to detect.

We also evaluated the probability that genomic associations may exist with community components, independent of whether they were detected via q-value. This probability was evaluated with Tukey's higher criticism test of p-value distributions (Wu et al. 2014; Donoho and Jin 2015). The higher criticism statistic (HC) was calculated as the square root of the number of tests (*n*) times the difference between the proportion of significant tests observed (ϕ) and the proportion expected if no associations exist, divided by the standard error (i.e., $HC = \sqrt{n}\frac{\phi - 0.05}{\sqrt{0.05 \times 0.95}}$). We then evaluated significance, for each response, by comparing HC to the standard normal distribution (Donoho and Jin 2015).

All statistical analyses were conducted using the R statistical software library (R Core Team 2020). Mixed models were fit using tools from the *lme4* package (Bates et al. 2015) and RDA was conducted using the *vegan* package (Oksanen et al. 2020).

Results

Here, we describe patterns and assess heritability among metrics of insect communities and aspen traits. We then explore the genomic and phenotypic mechanisms by which aspen may shape their associated insect communities.

Herbivore communities

Aspen-associated insect communities were diverse, and intraspecific variation among aspen substantially influenced diversity and structure of those communities (Figs. S1, S2, S3). We observed more than 100 total insect species and counted more than

640,000 individual insects during this project. From these, a total of 18 species of insects commonly occurred in each of the four insect surveys (Table 1). A species was considered common if it occurred on at least 5% of trees in any survey event. Only common insects were used in community analyses. Of the common insects, at least 14 were specialists of *Populus* or Salicaceae. Seven species were highly mobile, free-feeding herbivores and ten were sessile, leaf-modifying herbivores (i.e., leaf-gallers, leaf-miners, and leaf-rollers). The remaining insects were aphid-tending ants. In general, correlations among abundances of different species were relatively low (Fig. S4). The strongest correlation occurred between ants and the aphid species *C. populicola* ($r = 0.32$). Six of the seven free-feeding insect species were positively correlated with each other ($p < 0.05$), although most correlations were low (Fig. S4). Similarly, most leaf-modifying species were intercorrelated (Fig. S4).

Insect community composition was associated with aspen genotype (i.e., heritable) in our aspen population, but other community metrics were not. While alpha diversity of insect communities was relatively variable within the population (e.g., richness ranged from 0-14 species with an average of 5 species), this diversity was not strongly attributable to aspen genotype. Species richness, species evenness, Shannon diversity, total insect abundance, functional group abundance, functional group richness, and both multivariate community axes (MDS) were all weakly heritable ($H^2 < 0.2$; Fig. 1). On average, genotype accounted for only 7% of the variation in diversity metrics. Abundance of individual insect species was also weakly heritable for all but one species. Genotype accounted for only a small amount of the variation in common insect abundance overall (6%). Only one common species, *Phyllocolpa sp.*, was moderately heritable ($H^2 = 0.23$; Fig. 1). Community composition, by contrast, was more heritable. Incidence of five specialist insect species, *Harmandia sp.*, Coleophoridae *sp.*, *Z. scutellaris*, *Phyllocolpa sp.*, and *C. populicola*, was highly heritable (H^2 of 0.86, 0.53, 0.79, 0.78, and 0.88, respectively; Fig. 1). Six additional species, *E. populella*, *P. albella*, *P. populicola*, *C. stevensis*, Cicadamorpha *spp.,* and *G. septentrionis*, were moderately heritable (H^2 of 0.32, 0.39, 0.39, 0.29, 0.23, 0.25, respectively; Fig. 1). The remaining seven species were weakly heritable (Fig. 1). On average, variation among aspen genotypes accounted for an estimated 27.7% of the total variation in insect community composition, as assessed with species incidences.

Trait associations with insect communities

Aspen traits were also highly variable and strongly genetically heritable. Tree size, phytochemical composition, leaf morphology, reproduction, and phenology all varied substantially within the population (Fig. 2). Condensed tannin concentration was the most variable trait, ranging from 0.5% to 26.2% of leaf dry mass. Nitrogen concentration was the least variable trait, ranging from 1.4% to 3.4% of leaf mass (Fig. 2). All traits were at least moderately heritable ($H^2 > 0.2$; Fig. 1) and four traits - salicinoid phenolic glycoside concentration, extrafloral nectary density, budbreak timing, and flower production - were highly heritable (H^2 of 0.62, 0.67, 0.62, 0.50, respectively). Both ALA and CT concentration were narrowly excluded from the highly heritable classification (H^2 of 0.49 and 0.46, respectively). We excluded sex and heterozygosity from our heritability classifications because both traits are entirely genetically mediated (i.e., $H^2 = 1$; Fig.1) and, therefore, invariant within genotypes.

Diversity and function of insect communities were only moderately correlated with aspen traits. Tree size (BAsqrt) was moderately and positively correlated with species richness (Pearson's $r = 0.29$) and was most strongly associated with richness of free-feeding insects ($r = 0.25$). Tree size also exhibited a moderate positive correlation with species richness ($r = 0.29$). Conversely, condensed tannin concentration was negatively correlated with species richness ($r = -0.16$), primarily affecting leaf-modifying insects ($r = -0.16$). Condensed tannins were also negatively associated with abundance of leaf-modifying insects ($r = -0.22$) and were positively associated with species evenness ($r = 0.16$). SLA was associated with free-feeding insect richness ($r = 0.15$) and ALA was associated with abundance of leaf-modifying insects ($r = 0.16$). Shannon index was only weakly correlated with BAsqrt ($r = 0.12$). MDS axes were not correlated with any aspen traits.

Composition of insect communities was more strongly tied to aspen phenotype and each species was differentially affected by aspen traits. In the best models of species incidence (Fig. 3), BAsqrt was positively associated with all but one insect species, independent of other aspen traits and environmental factors. The exception was *C. populicola*, which was negatively associated with size. Averaged across species, increasing BAsqrt by one standard deviation (1.94 dm, which translates to BA = 3.76 dm^2) increased the probability of a common insect species occurring in a community by 31.3%. Effects of CT concentrations were mixed: incidence of four species was decreased by CTs while incidence of five species was increased. Somewhat surprisingly, increased PG concentrations resulted in *increased* incidence of seven species and decreased incidence of only one species. Most notably, increasing PG concentration by one standard deviation (2.97% dw) led to a 54% increased probability of *Z. scutellaris* occurring in a community. Foliar N concentrations, as well as ALA and SLA, had either positive or negative effects on many common insects. Terms for CTs, PGs, and SLA were all included in the best explanatory model for *Harmandia sp.*, but the magnitudes of these effects were too small to be functionally relevant (i.e., <0.001). EFN density weakly decreased incidence of three species and increased incidence of one species. Flower production was weakly associated with incidence of six species. Budbreak timing influenced incidence of 11 species and was negatively associated with four of them. Notably, budbreak timing that was delayed by one standard deviation (32.5 dd) resulted in a 55% increased probability of *Harmandia* sp. occurrence*.* Male aspen, which comprised 52% of the population, had increased incidence of two species, relative to females. H_{obs} was negatively associated with three species.

Redundancy analysis (Fig. 4) revealed that tree size, followed by budbreak timing, PG concentrations, and CT concentrations, most strongly shaped insect communities, accounting for 51, 16, 8, and 8% of the explained variation, respectively (Table 2). Overall, aspen traits explained an estimated 17.2% of the total variation in insect communities. Size, phenology, and defense chemistry together accounted for 83% of this explained variation.

Genomic associations with insect communities

We identified aspen genes associated with insect community composition but found no genomic associations with other community metrics. We identified 17 SNPs, within 15 unique genes, associated with insect community composition (i.e., species incidence; Table 3). The functions of these insect-associated genes are largely unknown, though some functional information is available. Three genes were associated with incidence of *E. populella* and appear to be involved in vacuolar functioning in *Arabidopsis* (Cui et al. 2014) programmed cell death in plants and animals (Osman et al. 2001; Avrova et al. 2004; Cui et al. 2017), and pectin structure in *Populus trichocarpa* (Bai et al. 2017). Six genes, involved primarily in cellular transport (Ward et al. 2009; Ostertag et al. 2013; Inada and Ueda 2014; Gu et al. 2016), and some of which may be defense-involved (Ascencio-Ibáñez et al. 2008; Gao et al. 2018), were associated with *P. albella*. Two genes were associated with *Z. scutellaris*, but little is known about their function. Three genes, two of which are likely regulatory (Zhao et al. 2003; Eyüboglu et al. 2007; Kong et al. 2007; Vaddepalli et al. 2011) and one of which is involved in flowering time (Weingartner et al. 2011), were associated with *C. stevensis.* One gene of little-known function was associated with *G. septentrionis*. No genomic associations were identified for common insect abundance or diversity, nor were associations found for functional group abundance or diversity.

In addition to this direct evidence of genomic associations with community composition, we also identified indirect evidence of genomic associations. Tukey's higher criticism tests showed that additional composition-associated genes remain unidentified (Table 3). This test, conducted on p-value distributions comprised of individual genomic association tests for each insect, revealed that five species are likely to have undiscovered associations. Genomic tests for *Coleophoridae sp.*, *Nematus sp.*, *Harmandia sp.*, *Phyllocolpa sp.*, and *C. populicola* had significantly more p-values below 0.05 than expected if no genomic associations truly existed with these species. Three of these species, *Harmandia sp.*, *Phyllocolpa sp.*, and *C. populicola* were among the four most heritable (i.e., strong genotypic effects) community members in our population (Fig. 1), which supports the hypothesis that genomic drivers for these species should exists.

We also identified genomic associations with some of the insect-associated aspen traits, providing a second indirect source of evidence for genomic effects on insect community composition. We found 110 SNPs, within 73 unique genes (Supp. Table 1), associated with three highly heritable aspen traits. Twenty-two SNPs were associated with budbreak timing, one was associated with extrafloral nectary density, and 87 were associated with flower production. These three traits were all associated with community composition, collectively influencing incidence of all 17 common herbivores (Fig. 3). In the clearest example linking genes-to-traits-to-communities, one gene associated with flower production (Potra002010g15755) was also the sole gene associated with *G. septentrionis*, and flower production was directly associated with *G. septentrionis* incidence in our genomic models (Fig. 3).

To assess the degree to which plant phenotypes mediate the link between genes and insect communities, genomic models of insect extended phenotypes were fit with and without aspen trait covariates. Comparisons between these model types for an insect species reveal phenotypic mediation. Within our aspen population, no SNPs were associated with any insect species once tree trait covariates were added to their genomic models. This result indicates that the detected plant genetic effects on insect community composition can be explained entirely by aspen phenotype.

Gene enrichment analyses identified no significant functional groupings of aspen genes among associations with phenotypes or extended phenotypes. No shared function was found among the top 0.1% of SNPs, for any trait or insect response.

Discussion

This work sought to link genes to traits, traits to insect communities, and genes to insects among trees with naturally occurring variation. Our findings support the notion that genetics of a single species can shape the communities with which it interacts. We found that herbivore communities differ among aspen genotypes and that the composition of those communities is genetically heritable. We also found that both community structure and diversity were shaped by heritable aspen traits. We identified 73 genes associated with those community-linked traits and another 15 genes directly associated with community composition. Finally, we discovered substantial evidence that additional community-associated genes remain undetected. These results demonstrate that intraspecific genetic variation plays an important role in maintaining diversity among plant-associated communities.

Community composition is a heritable extended phenotype

Relatively few studies investigating community heritability exist to date, but they suggest that heritability of community phenotypes is variable across systems and likely context-dependent. Among metrics of community structure, species richness and community dissimilarity tend to have the highest heritability (Shuster et al. 2006; Whitham et al. 2008; Bernhardsson et al. 2013). Our results, and those of Barker et al. (2018), differ from those preceding studies; total richness and functional group richness showed low heritability, and community dissimilarity (MDS) was non-heritable. This absence of heritability should perhaps not be surprising for our study, which was conducted over multiple seasons and years. Temporal variation in insect communities is largely unrelated to host genetics in many contexts.

While community genetics studies often evaluate the effects of intraspecific variation on the numbers of species and individuals occurring in communities, they rarely consider effects on *which* species occur. Occurrence of many species was highly heritable for this aspen population - more so than heritability of some tree traits. Indeed, community composition was much more heritable than other community metrics. Overall community diversity and function may not differ with genetic variation in aspen, but the members comprising those communities certainly do.

The most heritable insect species were specialist leaf-modifiers. Our finding that occurrence of the leaf-galling fly *Harmandia sp.* was highly heritable confirms results from a study that found abundance of galling insects was similarly heritable on *Populus tremula* (Bernhardsson et al. 2013). Free-feeding herbivores, which are less intimately associated with their host, were much less heritable. The one strong genotypic association with free-feeding herbivores was with the aphid *Chaitophorus stevensis.* This result corroborates similar findings for aphids in previous work (Zytynska and Preziosi 2011; Barker et al. 2018). In general, results from this and related work suggest that the heritability of community phenotypes is correlated with the degree of specialization and physical intimacy of insect-plant relationships.

Heritable traits are linked to composition and structure of communities

Across ecosystems, plant trait expression plays a major role in shaping communities and herbivores are particularly responsive (Stam et al. 2014). These traits are also often heritable. This study, supported by previous work in this system (Lind-Riehl et al. *in review*; Barker et al. 2018; Cole et al. 2021), clearly links community diversity and structure to genetically-mediated tree traits.

Foliar secondary chemistry was strongly associated with community composition and diversity, although with some counter-intuitive effects. Salicinoid phenolic glycosides (PGs) are known to have detrimental impacts on herbivores, especially Lepidopterans (Hemming and Lindroth 1995, 2000; Boeckler et al. 2016). For all but one species affected by PGs in this study, however, the relationship between PG concentration and incidence was positive. These insects were almost entirely specialists, which likely have developed resistance to aspen PGs. For example, *Chrysomela crotchi* metabolize PGs to produce salicylaldehydes for their own defense (Pasteels et al. 1983) and gregarious sawflies like *Nematus spp.* presumably exhibit similar defense co-opting (Boeve et al. 1992; Boeckler et al. 2011; Fernández et al. 2019). Similarly, condensed tannins (CTs) had positive impacts on half of the species they affected. This evidence, combined with the decreased diversity associated with CTs, indicates that the few insect species present on trees with high CT concentrations are particularly adapted to this secondary compound. In short, the common members of aspen-associated herbivore communities appear to be well-adapted to its chemical defenses, in contrast to less common, and generalist, herbivores (Lindroth and St. Clair 2013).

Ontogenetic trajectory plays another important role in shaping extended phenotype communities. Assemblages of common insects in this study were quite different from those observed in the same garden 2 years prior (Barker et al. 2018). For example, *Acronicta lepusculina*, *Choristoneura rosaceana*, *Phyllocnistis populiella*, and

Prodiplosis morrisi, which were common in 2014-2015, rarely occurred in 2016-2017. Conversely, *Choleophoridae sp.*, *Coccoidea sp.*, and *Chrysomela crotchi* were common only during 2016-2017. These differences are likely partially attributable to age-related (4-5 vs. 6-7 years old) changes in key aspen traits. In this later study, trees were much larger and had begun to reproduce, the canopy had closed, and foliage had lower secondary metabolite and higher nitrogen concentrations (Cole et al. 2021). These ontogenetic shifts expose herbivores to different tree phenotypes and environmental conditions (e.g., temperature, natural enemies), such that community composition changes over time.

This research focused primarily on bottom-up effects exerted by plants on insect communities, admittedly, a limited approach. Top-down factors are also integral to the mechanisms that shape herbivore communities. Of particular importance are the impacts of natural enemies, including predators and parasitoids, on insect herbivores (Carter and Rypstra 1995; Murphy 2004; Moreira et al. 2012; Long and Finke 2014; Becker et al. 2021). Physical structure of canopies and the microclimates they generate also have noteworthy effects on insect communities (Willmer 1982; Peng et al. 1992; Basset et al. 2001; Duffy et al. 2015; Lourenço et al. 2015). All told, top-down drivers are generally stronger than bottom-up effects for chewing, sucking, and gall-forming insects alike (Vidal and Murphy 2018), which indicates that such effects may interact with and obscure the impacts of phenotypic plant variation.

With that said, some top-down effects on herbivores are directly mediated by plants. For example, both predators and parasitoids are attracted to plant volatile organic compounds and to nectaries. Volatiles often signal to natural enemies that herbivores are present, increasing pressure on herbivores and decreased pressure on the plant (Benelli et al. 2017; Riddick 2020; Ahmed et al. 2022). Plant volatiles were not measured in this study but they likely play an important defense role in *Populus* (Isebrands et al. 1999; Clavijo Mccormick et al. 2014). Similarly, natural enemies can be attracted to – and benefit from – sugar sources produced at nectaries, which increases interactions with nearby herbivores (Heads and Lawton 1985; Rezende et al. 2014; Koptur et al. 2015). In our study, extrafloral nectaries were not associated with ants as expected and no other natural enemies were quantified. Extrafloral nectaries did, however, have negative effects on incidence of *Cicadamorpha spp., Coccoidea sp.,* and *P. populicola*. It is plausible that these impacts were mediated by natural enemies, attracted by the extrafloral nectaries. In any case, the field of community and ecosystem genetics would greatly benefit, in our estimation, from the inclusion of studies involving tri-trophic interactions (e.g., Mooney et al. 2012 and Abdala-Roberts et al. 2019) but with a genetic component.

Aspen genes are linked to community composition

Genotypic effects of plants on associated insects are common, but few previous studies have identified candidate genes associated with community phenotypes. *Populus* genes, specifically, have been associated with insect herbivore metrics, including damage rates (DeWoody et al. 2013; Zinkgraf et al. 2016) and community diversity (Bernhardsson et al. 2013). The 15 candidate genes identified by this study do not overlap with genes previously linked to aspen traits or community phenotypes (Lind-Riehl et al. *in review*; Barker et al. 2019b). While the functions of these 15 genes remain poorly understood overall, what is known aligns well with the ecological relevancy identified by this work.

A crucial step in uncovering genes-to-ecosystems links is to identify the impacts of genes on the target organism's environment, which includes associated communities. Our genomic analyses identified associations with the composition of insect communities. The most compelling direct evidence that aspen fit into this framework relates to the poplar petiole gall moth, *Ectoedemia populella*. We identified three genes associated with this species. The first gene, Potra000664g05124, has been linked to enzymes involved in structuring pectin in cell walls and is important for wood formation and vascular tissue in *Populus trichocarpa* (Bai et al. 2017). Galling insects like *E. populella* depend upon, and often manipulate, the morphology and physiology of their host (Larson 1998; Stone and Schönrogge 2003), processes likely influenced by plant structural enzymes. Potra000664g05124 has been similarly linked to interactions with parasitic cyst and root-knot nematodes (Wieczorek et al. 2014), which may interact with hosts in a manner mechanistically similar to *E. populella* (Oates et al. 2016). The homologous gene to Potra000664g05124 has also been linked to disease immunity in *Arabidopsis* (Bethke et al. 2016). The second gene associated with *E. populella* in our study, Potra001987g15625 is involved with vacuolar trafficking, biogenesis, and plant growth (Cui et al. 2014) as well as programmed cell death in *Arabidopsis* (Cui et al. 2017). The third gene, Ptra001905:g15122 has links to programmed cell death as well (Osman et al. 2001; Avrova et al. 2004). *Ectoedemia populella,* like most galling species, relies on the host's nutrient transport systems and photosynthetic products for nutrients. Programmed cell death is linked to oxidative stress in plants (Ramel et al.

2013; Sabater and Martín 2013; Laloi and Havaux 2015) and, unsurprisingly, *E. populella* has been shown to manipulate oxidative stress responses in *Populus* (Kot and Kmieć 2020). Clearly, these genes are ecologically relevant to E. populella and their implied relationships with this insect warrant further investigation. These results are promising for the genes to ecosystems framework: a gene that influences whether or not a particular species occurs in an ecological community will have ramifications for any ecological component that interacts with that species.

A more straightforward piece of evidence from this work connecting genes-to-traits-to-communities involves another species, *Gluphisia septentrionis*. The aspen gene Potra002010g15755 was associated with flower production in our population and with *G. septentrionis*, which itself was associated with flower production. Cumulatively, there is strong evidence that this gene influences the incidence of this species in communities. Why plant reproduction, and its associated genes, were positively correlated with a larval lepidopteran herbivore is unclear, but may be related to tradeoffs among growth, defense, and reproduction in aspen (Cole et al. 2021). In any case, both the genetic and phenotypic links between aspen and *G. septentrionis* were identified.

The sensitivity of genomic association mapping and the underlying genetic architecture of a population’s expressed traits strongly determine the capacity to detect genetic links with complex phenotypes and extended phenotypes. The models used in this study were designed to detect genetic associations with both plant traits and extended phenotypes. This method has improved Type I error control over traditional methods, a property that greatly reduces uncertainty but necessarily decreases the power to detect associations (Ch. 3). Our models, however, identified a similar number of associations to those previously identified for the same insects and metrics (Barker et al. 2019b). Our models also identified association patterns with tree traits that are similar to those obtained by a recent, more comprehensive genomic study of this system (Lind-Riehl et al. *in review*). Indeed, our higher criticism tests indicate that additional genetic drivers of extended phenotypes remain undetected. These tests revealed for five insect species that, among all genetic association tests, p-values trended lower than expected by random change. This situation arises when real effects exist, but the models are not sensitive enough to detect them: "although the evidence [of associations] may be cumulatively substantial, it is diffuse, individually weak, and affecting a relatively small fraction of the individual P-values" - Donoho and Jin (on HC test; 2015). Even heritability was not a reliable predictor of genomic effects. No specific gene associations were identified for three of the four most heritable herbivore species, while, in contrast, genetic links were identified for some species with only moderate heritability. These patterns are all consistent with a highly polygenic architecture, whereby many genes of small effect contribute to phenotypic expression.

A related study by our group previously recognized this phenomenon as affecting the expression of numerous aspen traits (Lind-Riehl et al. *in review*). It is no surprise that extended phenotypes, which are further removed from the genes and influenced by multiple polygenically controlled traits, would be susceptible to polygenic effects. In fact, many complex tree phenotypes are likely heavily polygenic. Tree traits are often associated with genes whose biological connections are vague (e.g., Bresadola et al. 2019; Chhetri et al. 2019; De La Torre et al. 2019), indicating that they are merely peripheral genes – which may be susceptible to evolution (Mähler et al. 2017) – and not core genes responsible for expression (Lind-Riehl et al. *in review*). While our method provides greater certainty over traditional methods regarding the identified associations, it is a single-marker analysis and therefore inadequate for detecting polygenic effects. Multi-marker methods have more power to detect small effects among multiple loci with correlated functionality (Bot et al. 2005; Homer et al. 2008; Li et al. 2011; Klasen et al. 2016). Both single-marker and multi-marker methods should be used in tandem to identify links to phenotypes with different types of genetic architecture. Where Crutsinger (2016) called for identification of specific genes associated with communities, our results indicate that identification of whole gene suites and their complex genetic architectures is also important. Furthermore, the framework put forth by Whitham and colleagues (Whitham et al. 2006, 2008), wherein relatively few genes should be associated with ecologically relevant extended phenotypes, has been verified in some important contexts but may be overly simplistic. While plant genes can clearly influence communities and ecosystems in meaningful ways, the underlying mechanisms are highly complex. Studies of community and ecosystem genetics need to shift towards identifying effects of variation across the *entire* genome, treating genes as the interdependent networks that they are, rather than focusing on isolated effects of individual genes.

Conclusions

Heritable intraspecific variation in plant traits, driven by genomic mechanisms, can shape the communities that interact with plants. Results from this research demonstrate that phytophagous insects respond to heritable variation in aspen traits to produce heritable extended phenotypes (aspen-associated insect communities). They provide strong evidence that specific aspen genes are associated with aspen phenotype and with composition of insect communities. There is also strong evidence that additional associated genes have gone undetected and further efforts (such as transcriptome analyses, gene network analyses, and multi-marker association mapping) are needed to detect them. Moving forward, research in community and ecosystem genetics should move beyond the assumption of simple expression architectures and implement state-of-the-art methods that consider complex interactions among genes, traits, and higher-level ecological structure and function. Nonetheless, this research demonstrates that intraspecific variation plays a role in fostering community diversity, with genes playing a major role. In much the same way that diverse plant communities promote diverse insect communities, diverse plant populations promote diversity in their associated insect communities.

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Tables

Table 1: Common insects, functional group, diet breadth, Tukey's HC statistic and associated p-value. Tukey's HC tests were performed on distributions of raw p-values from genomic association analyses.

Insect	Functl. group	Diet breadth	HC	p-value
Ectoedemia populella	Leaf modifier	*Populus* (Braun 1971)	4.302	<0.001
Harmandia sp.	Leaf modifier	*Populus* (Gagné 1989)	4.853	<0.001
Caloptilia stigmatella	Leaf modifier	Salicaceae (Noreika and Puplesis 1992)	-1.224	0.890
Coleophoridae sp.	Leaf modifier	unknown	2.608	0.005
Paraleucoptera albella	Leaf modifier	*Populus* (Heiman 2013)	0.648	0.259
Paraphytomyza populicola	Leaf modifier	*Populus* (Natural Resources Canada 2015)	0.846	0.199
Phyllonorycter tremuloidiella	Leaf modifier	*Populus*, *Salix* (Davis and Deschka 2001)	1.167	0.122
Tachyerges salicis	Leaf modifier	Salicaceae (Anderson 1989)	-0.394	0.653
Zeugophora scutellaris	Leaf modifier	*Populus*, *Salix* (Belov 2013)	4.809	<0.001
Phyllocolpa sp.	Leaf modifier	*Populus*, *Salix* (Eiseman 2010)	2.344	0.010
Chaitophorus populicola	Free feeder	*Populus* (Blackman and Eastop 2015)	5.328	<0.001
Chaitophorus stevensis	Free feeder	*Populus* (Blackman and Eastop 2015)	1.505	0.067
Cicadamorpha spp.[1]	Free feeder	unknown	1.137	0.128
Coccoidea sp.	Free feeder	unknown	1.514	0.065
Gluphisia septentrionis	Free feeder	*Populus* (McLeod 2005)	1.665	0.048
Nematus spp.[2]	Free feeder	Species specific (Sawflies.org 2021), likely Salicaceae (Malagón-Aldana et al. 2017)	2.246	0.012
Chrysomela crotchi	Free feeder	Salicaceae (Smereka 1965)	1.614	0.053
Formicidae	Aphid tender		0.028	0.489

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[1] Cicadamorpha spp. is a polyphyletic group containing functionally similar species from Cicadellidae and Membracidae

[2] The vast majority of *Nematus spp.* were one morphospecies, likely *Nematus oligospilus* (Malagón-Aldana et al. 2017)

Table 2: ANOVA-like table from a redundancy analysis of the effect of tree traits on insect communities, derived via permutation test with 1000 permutations.

	Df	Variance	F	p-value
BAsqrt	1	0.0289	50.093	0.001
CT	1	0.0043	7.516	0.001
PG	1	0.0043	7.439	0.001
N	1	0.0029	5.017	0.001
ALA	1	0.0030	5.221	0.001
SLA	1	0.0021	3.610	0.002
EFN	1	0.0007	1.236	0.229
Flowers	1	0.0006	0.985	0.436
Budbreak	1	0.0092	15.927	0.001
Sex	1	0.0006	1.088	0.355
Hobs	1	0.0005	0.823	0.607
Residual	476	0.2746		

Table 3: Genomic associations with insects[3].

Insect	SNP	Gene	Annotation	Effect	p-value	q-value
E. populella	Potra001987:15805	Potra001987g15625	vacuolar fusion protein MON1 homolog	-0.493	0.0000047	0.128
E. populella	Potra001987:16306	Potra001987g15625	vacuolar fusion protein MON1 homolog	-0.495	0.0000040	0.128
E. populella	Potra001905:22346	Potra001905g15122	oxysterol-binding family protein	0.517	0.0000021	0.128
E. populella	Potra000664:25828	Potra000664g05124	pectate lyase-like	-0.532	0.0000028	0.128
P. albella	Potra002350:11375	Potra002350g17933	probable voltage-gated potassium channel subunit beta	0.370	0.0000057	0.127
P. albella	Potra003977:65440	Potra003977g23930	probable magnesium transporter NIPA2/NIPA2 isoformX1	-0.373	0.0000014	0.117
P. albella	Potra000432:104584	Potra000432g02304	conserved oligomeric Golgi complex subunit 3-like	0.485	0.0000032	0.117
P. albella	Potra002902:3513	Potra002902g20271; Potra002902g35386	phosphate transporter PH01; Unknown	0.610	0.0000051	0.127
P. albella	Potra002165:8639	Potra002165g16720	delta(7)-sterol-C5(6)-desaturase-like	0.519	0.0000026	0.117
Z. scutellaris	Potra002388:21367	Potra002388g18183	Transmembrane Fragile-X-F-associated protein	0.543	0.0000026	0.140
Z. scutellaris	Potra000678:82497	Potra000678g05264	uncharacterized transporter YBR287W-like	0.435	<0.0000001	<0.001
C. stevensis	Potra003317:9694	Potra003317g21325	protein LATE FLOWERING-like	-0.345	0.0000043	0.129
C. stevensis	Potra003317:9705	Potra003317g21325	protein LATE FLOWERING-like	-0.350	0.0000035	0.129
C. stevensis	Potra000973:118740	Potra000973g08049	SKP1-like protein 21 isoform X1	0.297	0.0000049	0.129

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[3] Column descriptions: *Insect* is the common insect species; *SNP* is the SNP identifier: *Gene* is the gene identifier; *Annotation* is the short gene description; *Effect* is the standardized effect that a minor allele has on the incidence of the insect species when compared to the more dominant allele, as estimated with a logistic mixed effects model of genomic associations; *p-value* corresponds to the uncorrected p-value for the association test; and *q-value* corresponds to Storey's positive false discovery rate correction of the *p-value*.

C. stevensis	Potra001290:6891	Potra001290g11127	protein STRUBBELIG-RECEPTOR FAMILY 3 isoform X1	0.401	0.0000058	0.129
C. stevensis	Potra001290:6895	Potra001290g11127	protein STRUBBELIG-RECEPTOR FAMILY 3 isoform X1	0.401	0.0000058	0.129
G. septentrionis	Potra002010:112138	Potra002010g15755	serine/threonine-protein kinase rio1-like	0.496	0.0000010	0.112

Figures

(Starting on next page)

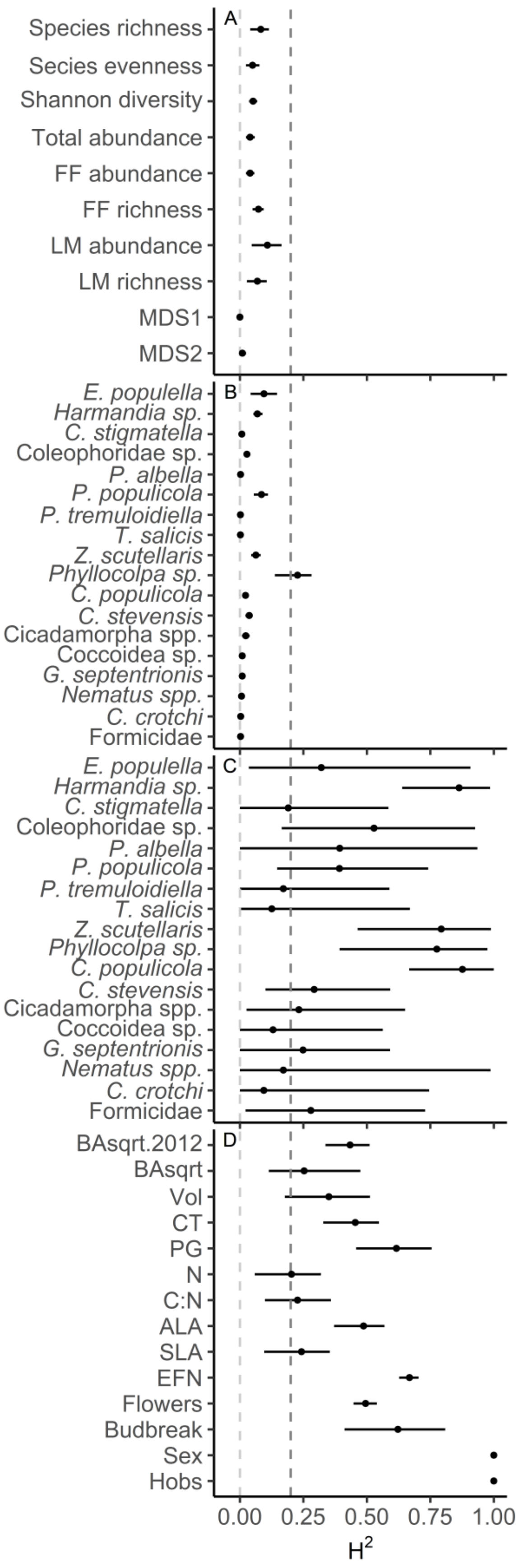


Figure 1: Bootstrapped heritability (H^2) estimates and asymmetrical 95% confidence intervals. Phenotype and extended phenotype along the y-axis are grouped into (A) community diversity metrics, (B) individual species abundance, (C) individual species incidence, and (D) aspen traits. LM: leaf-modifiers; FF: free feeders. BAsqrt.2012 represents the square-root of basal area in 2012.

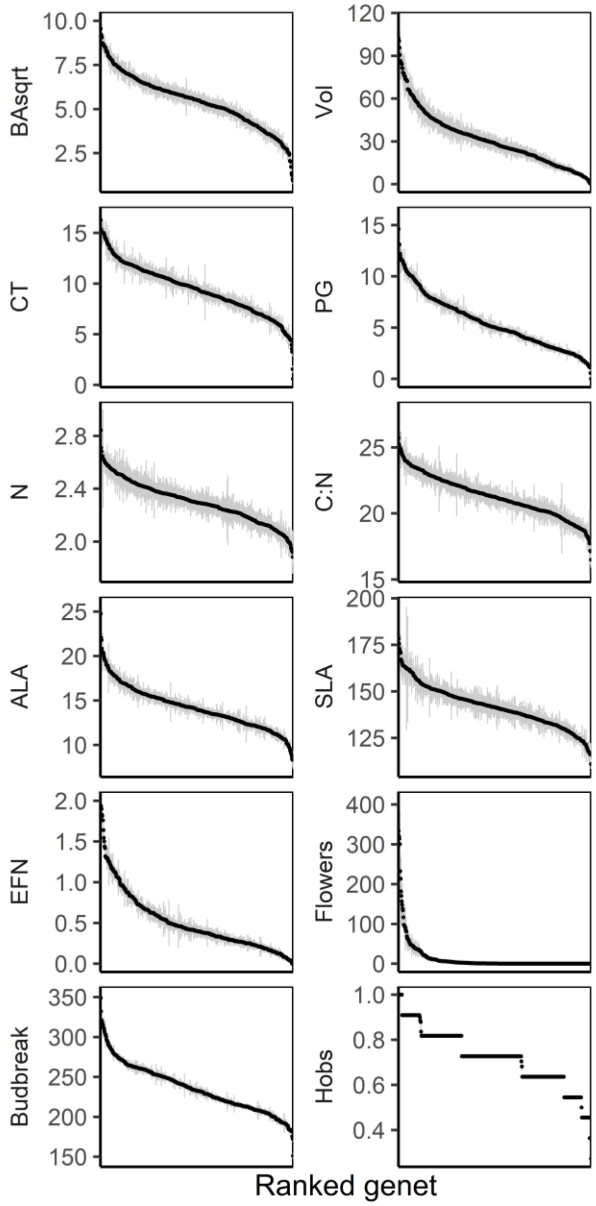
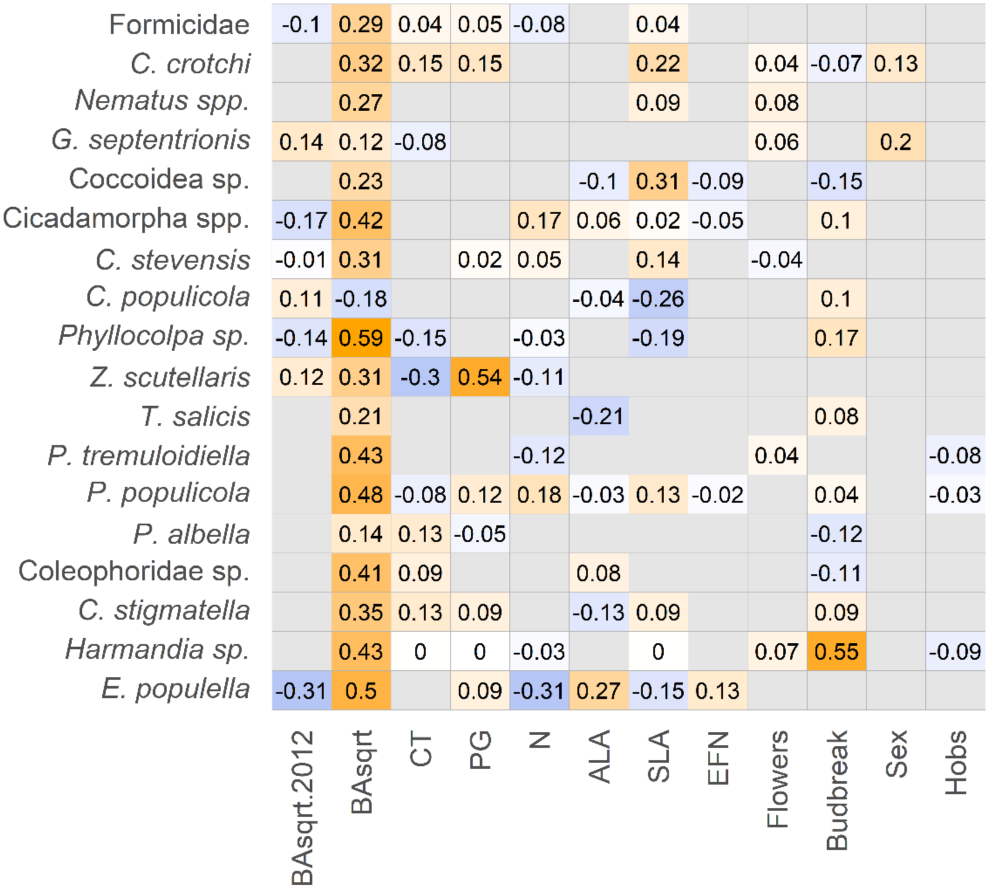


Figure 2: Variation in ecologically relevant aspen traits among aspen genotypes. Points represent the genotype average trait values and grey error bars represent ± 1 standard deviation. Panels correspond to the different aspen traits.



	BAsqrt.2012	BAsqrt	CT	PG	N	ALA	SLA	EFN	Flowers	Budbreak	Sex	Hobs
Formicidae	-0.1	0.29	0.04	0.05	-0.08		0.04					
C. crotchi		0.32	0.15	0.15			0.22		0.04	-0.07	0.13	
Nematus spp.		0.27					0.09		0.08			
G. septentrionis	0.14	0.12	-0.08						0.06		0.2	
Coccoidea sp.		0.23				-0.1	0.31	-0.09		-0.15		
Cicadamorpha spp.	-0.17	0.42			0.17	0.06	0.02	-0.05		0.1		
C. stevensis	-0.01	0.31		0.02	0.05		0.14		-0.04			
C. populicola	0.11	-0.18				-0.04	-0.26			0.1		
Phyllocolpa sp.	-0.14	0.59	-0.15		-0.03		-0.19			0.17		
Z. scutellaris	0.12	0.31	-0.3	0.54	-0.11							
T. salicis		0.21				-0.21				0.08		
P. tremuloidiella		0.43			-0.12				0.04			-0.08
P. populicola		0.48	-0.08	0.12	0.18	-0.03	0.13	-0.02		0.04		-0.03
P. albella		0.14	0.13	-0.05						-0.12		
Coleophoridae sp.		0.41	0.09			0.08				-0.11		
C. stigmatella		0.35	0.13	0.09		-0.13	0.09			0.09		
Harmandia sp.		0.43	0	0	-0.03		0		0.07	0.55		-0.09
E. populella	-0.31	0.5		0.09	-0.31	0.27	-0.15	0.13				

Figure 3: Effects of aspen traits on insect community composition. Rows correspond to mixed effects models of insect incidence, chosen via stepwise selection according to lowest AIC values. Cells represent the standardized effects of aspen traits (x-axis) on incidence probability of each common insect (y-axis). Blank cells in a row indicate that the trait in the corresponding column was not included in the selected model. Warm colors (orange) represent positive effects, cool colors (blue) represent negative effects, and the intensity of the color represents the magnitude of the effect. Cells containing zero represent effects with a magnitude smaller than 0.001.

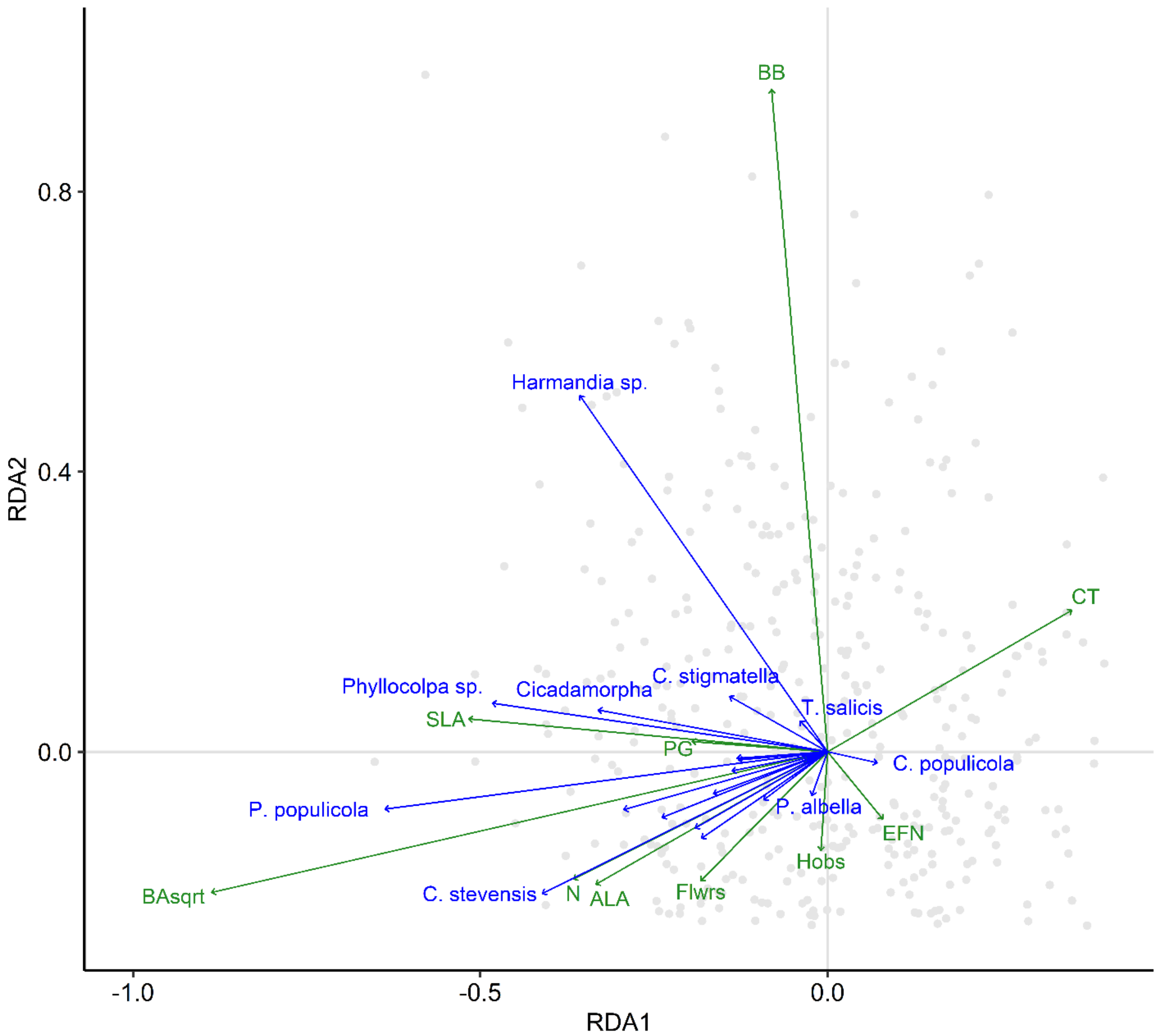


Figure 4: Redundancy analysis visualization for the effects of tree traits[4] (green vectors) on multivariate community structure. Blue vectors represent abundance of insect species. Angles between each vector are approximately proportional to the correlations among corresponding variables (90°: none, > 90°: negative, < 90°: positive). Gray points represent aspen genotype averages. Vectors can be considered as axes and the position of a point in the dimension of this axis, relative to other points, represents the

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[4] Trait abbreviations: *BB*, is budbreak timing, *Flwrs* is flower production, *BAsqrt* is the square-root of basal area, *PG* is concentration of phenolic glycosides, *N* is nitrogen concentration, *CT* is condensed tannin concentration, *EFN* is extrafloral nectary density, *SLA* is specific leaf area, *Hobs* is observed genetic heterozygosity

relative value of the corresponding variable The length of a vector indicates the degree of variation in the corresponding variable within the population. The two ordination axes that accounted for the most explained variation are shown: RDA1 accounts for 10.7% of the total variation and RDA2 accounts for 3.0%. See Table 2 for variance partitioning by trait.

Supplemental Figures

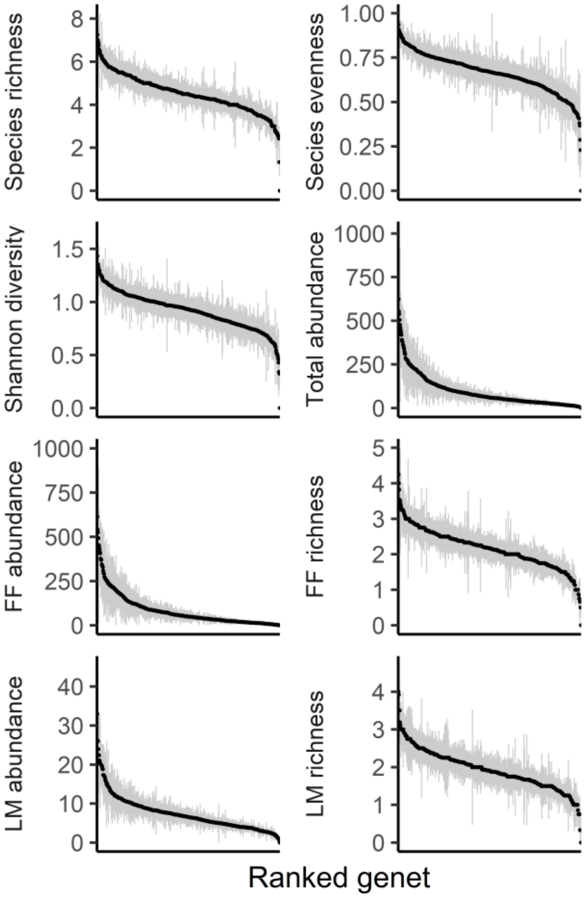


Figure S1: Variation in community metrics among aspen genotypes. The top four panels correspond to whole-community metrics and the lower four correspond to free-feeding (FF) and leaf-modifying (LM) functional groups. Points represent genotype trait averages and grey error bars represent ± 1 standard deviation. Genotypes are ordered by descending rank for each metric.

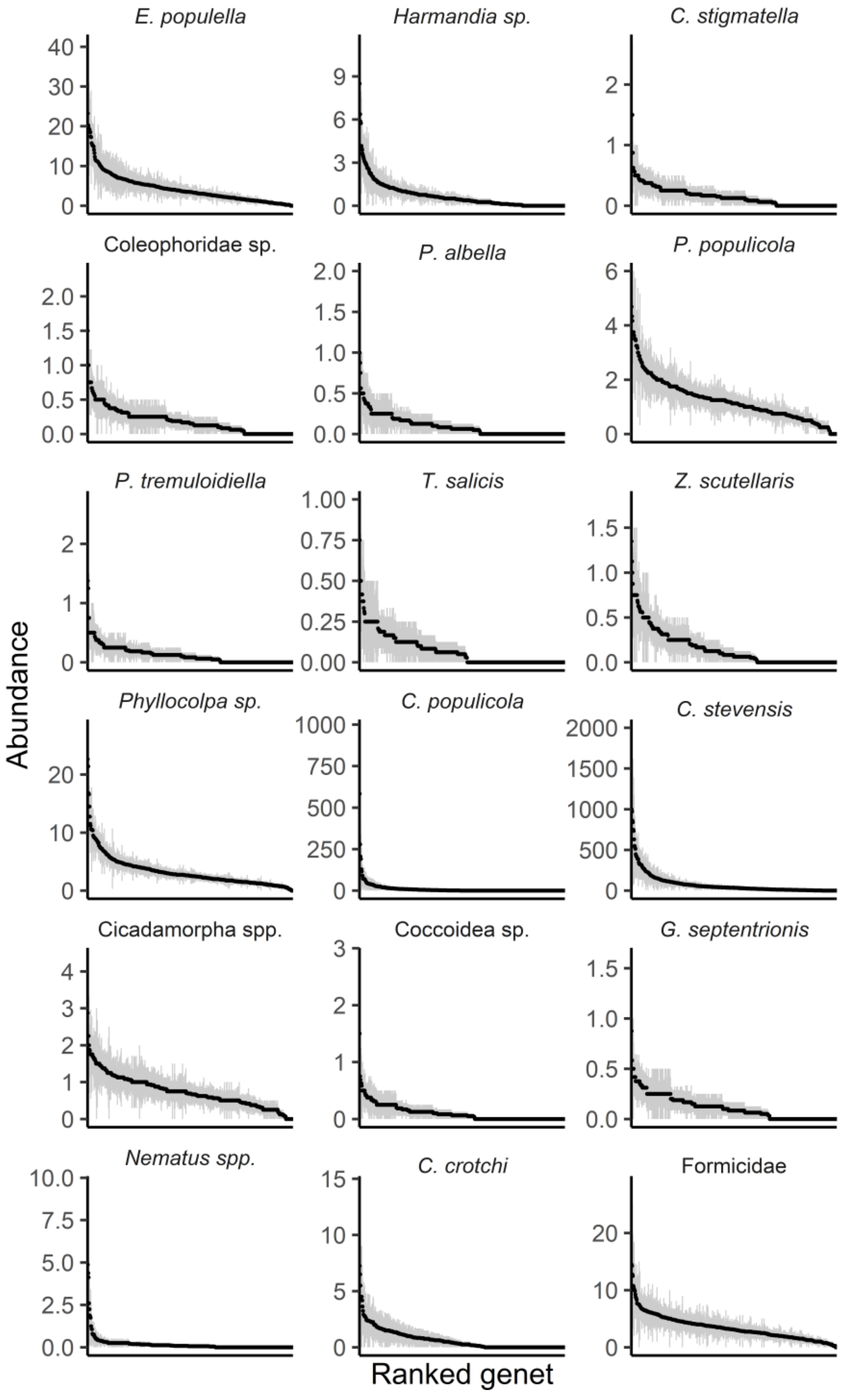


Figure S2: Variation in common insect abundance among aspen genotypes. Points represent the average insect abundance on a genotype and grey error bars represent ± 1 standard deviation. Genotypes are ordered by descending rank for each insect. Panels correspond to the different insect species.

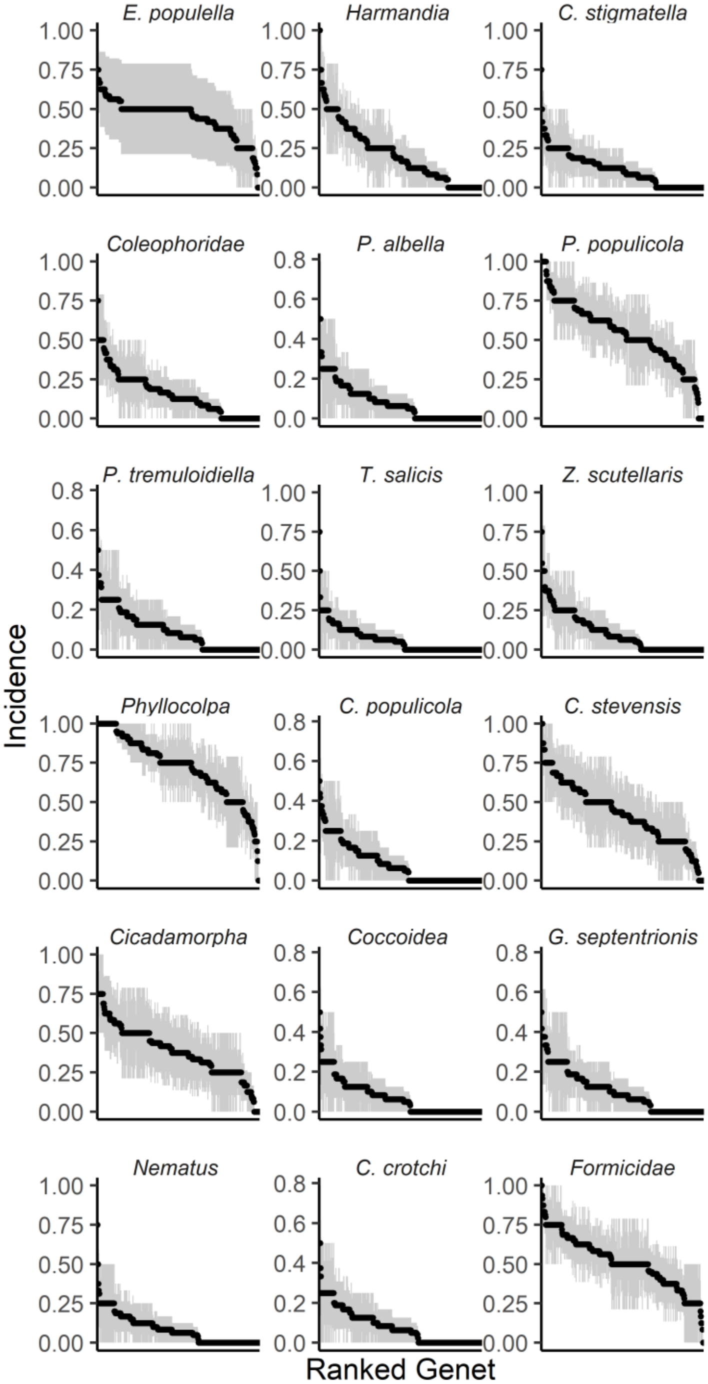
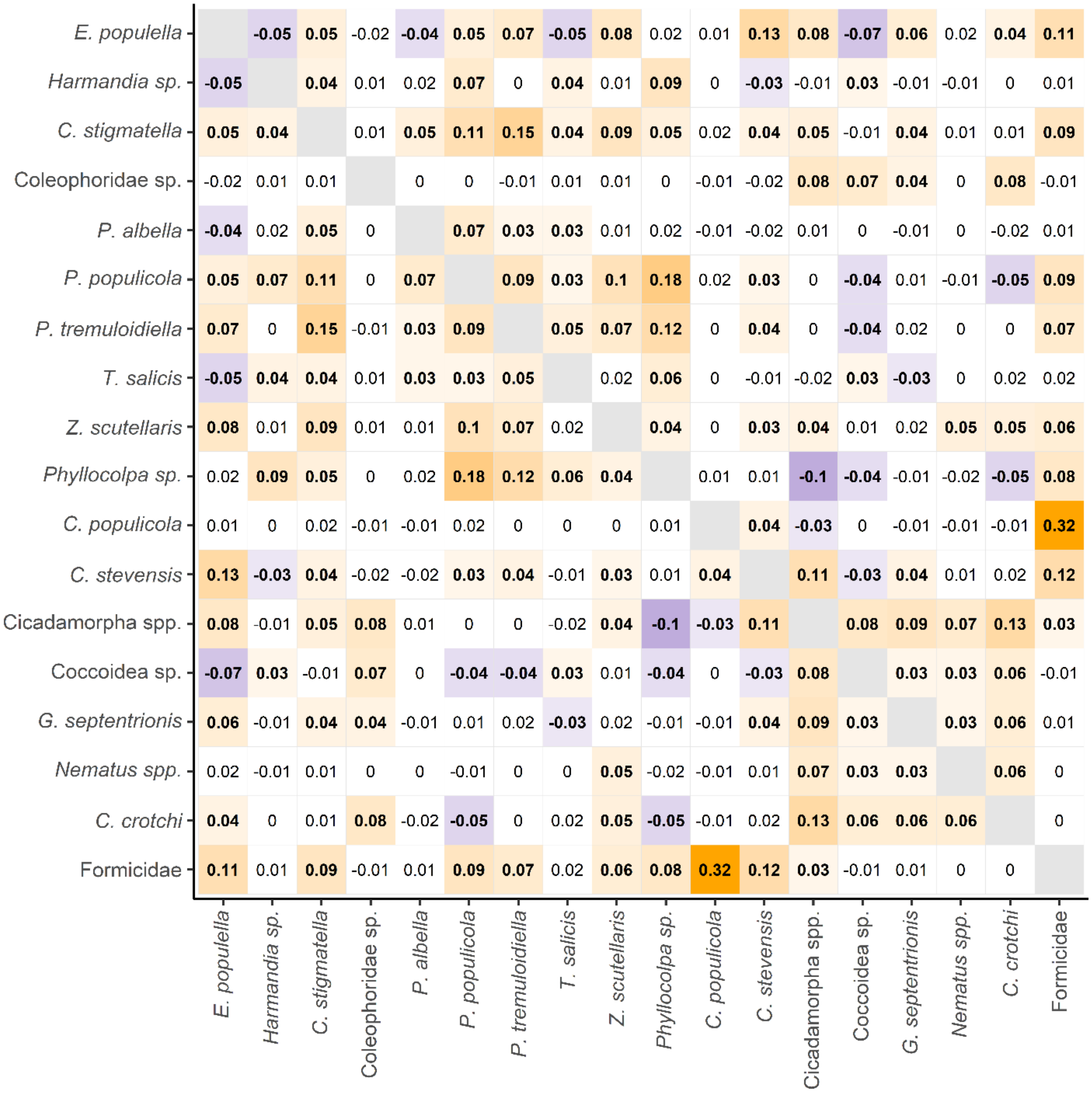


Figure S3: Variation in common insect incidence among aspen genotypes. Points represent the proportion of trees within a genet on which an insect occurred during a survey event. Grey bars represent ± 1 standard deviation across survey events. Panels correspond to the different insect species. Probabilities were derived from the logistic mixed effects models.



	E. populella	*Harmandia sp.*	*C. stigmatella*	Coleophoridae sp.	*P. albella*	*P. populicola*	*P. tremuloidiella*	*T. salicis*	*Z. scutellaris*	*Phyllocolpa sp.*	*C. populicola*	*C. stevensis*	Cicadamorpha spp.	Coccoidea sp.	*G. septentrionis*	*Nematus spp.*	*C. crotchi*	Formicidae
E. populella		**-0.05**	**0.05**	-0.02	**-0.04**	**0.05**	**0.07**	**-0.05**	**0.08**	0.02	0.01	**0.13**	**0.08**	**-0.07**	**0.06**	0.02	**0.04**	**0.11**
Harmandia sp.	**-0.05**		**0.04**	0.01	0.02	**0.07**	0	**0.04**	0.01	**0.09**	0	**-0.03**	-0.01	**0.03**	-0.01	-0.01	0	0.01
C. stigmatella	**0.05**	**0.04**		0.01	**0.05**	**0.11**	**0.15**	**0.04**	**0.09**	**0.05**	0.02	**0.04**	**0.05**	-0.01	**0.04**	0.01	0.01	**0.09**
Coleophoridae sp.	-0.02	0.01	0.01		0	0	-0.01	0.01	0.01	0	-0.01	-0.02	**0.08**	**0.07**	**0.04**	0	**0.08**	-0.01
P. albella	**-0.04**	0.02	**0.05**	0		**0.07**	**0.03**	**0.03**	0.01	0.02	-0.01	-0.02	0.01	0	-0.01	0	-0.02	0.01
P. populicola	**0.05**	**0.07**	**0.11**	0	**0.07**		**0.09**	**0.03**	**0.1**	**0.18**	0.02	**0.03**	0	**-0.04**	0.01	-0.01	**-0.05**	**0.09**
P. tremuloidiella	**0.07**	0	**0.15**	-0.01	**0.03**	**0.09**		**0.05**	**0.07**	**0.12**	0	**0.04**	0	**-0.04**	0.02	0	0	**0.07**
T. salicis	**-0.05**	**0.04**	**0.04**	0.01	**0.03**	**0.03**	**0.05**		0.02	**0.06**	0	-0.01	-0.02	**0.03**	**-0.03**	0	0.02	0.02
Z. scutellaris	**0.08**	0.01	**0.09**	0.01	0.01	**0.1**	**0.07**	0.02		**0.04**	0	**0.03**	**0.04**	0.01	0.02	**0.05**	**0.05**	**0.06**
Phyllocolpa sp.	0.02	**0.09**	**0.05**	0	0.02	**0.18**	**0.12**	**0.06**	**0.04**		0.01	0.01	**-0.1**	**-0.04**	-0.01	-0.02	**-0.05**	**0.08**
C. populicola	0.01	0	0.02	-0.01	-0.01	0.02	0	0	0	0.01		**0.04**	**-0.03**	0	-0.01	-0.01	-0.01	**0.32**
C. stevensis	**0.13**	**-0.03**	**0.04**	-0.02	-0.02	**0.03**	**0.04**	-0.01	**0.03**	0.01	**0.04**		**0.11**	**-0.03**	**0.04**	0.01	0.02	**0.12**
Cicadamorpha spp.	**0.08**	-0.01	**0.05**	**0.08**	0.01	0	0	-0.02	**0.04**	**-0.1**	**-0.03**	**0.11**		**0.08**	**0.09**	**0.07**	**0.13**	**0.03**
Coccoidea sp.	**-0.07**	**0.03**	-0.01	**0.07**	0	**-0.04**	**-0.04**	**0.03**	0.01	**-0.04**	0	**-0.03**	**0.08**		**0.03**	**0.03**	**0.06**	-0.01
G. septentrionis	**0.06**	-0.01	**0.04**	**0.04**	-0.01	0.01	0.02	**-0.03**	0.02	-0.01	-0.01	**0.04**	**0.09**	**0.03**		**0.03**	**0.06**	0.01
Nematus spp.	0.02	-0.01	0.01	0	0	-0.01	0	0	**0.05**	-0.02	-0.01	0.01	**0.07**	**0.03**	**0.03**		**0.06**	0
C. crotchi	**0.04**	0	0.01	**0.08**	-0.02	**-0.05**	0	0.02	**0.05**	**-0.05**	-0.01	0.02	**0.13**	**0.06**	**0.06**	**0.06**		0
Formicidae	**0.11**	0.01	**0.09**	-0.01	0.01	**0.09**	**0.07**	0.02	**0.06**	**0.08**	**0.32**	**0.12**	**0.03**	-0.01	0.01	0	0	

Figure S4: Correlations among insect species. This figure is a graphical representation of a correlation matrix of insect abundances. Warm colors correspond to positive correlations and cool colors to negative correlations and color intensity corresponds to magnitude of the correlation. Numbers represent Pearson’s correlation coefficient, and statistically significant ($p < 0.05$) correlations are bolded.

Supplemental Tables

Table S1: Genomic associations with aspen traits; Columns represent traits, associated SNP IDs, gene IDs, description of the known gene function, effect of the minor alleles on insect incidence, p-value, and Storey's q-value. Missing gene and annotation entries indicate that the gene in which the SNP is located remains unknown.

Trait	SNP	Gene	Annotation	Coefficient	p-value	q-value
EFN	Potra000613:36082	Potra000613g04664	probable polygalacturonase	0.2376	0.0000008	0.0897
Flowers	Potra003360:9560			20.2735	0.0000883	0.1413
Flowers	Potra002011:10034			22.9675	0.0000011	0.0176
Flowers	Potra001830:1116			20.8740	0.0000247	0.0847
Flowers	Potra179589:10982	Potra179589g28026	ABC transporter B family member 1;zinc finger protein 593	19.3534	0.0000349	0.0936
Flowers	Potra003095:11323			17.2710	0.0000052	0.0478
Flowers	Potra002370:11739			21.5176	0.0000194	0.0710
Flowers	Potra002370:11789			19.8863	0.0000283	0.0864
Flowers	Potra000831:14132	Potra000831g06665	protein ABHD11 isoform X1	22.0439	0.0000015	0.0176
Flowers	Potra003722:14151	Potra003722g22573	Homoserine O-acetyltransferase	14.6633	0.0000788	0.1331
Flowers	Potra001465:15308			16.7313	0.0000616	0.1215
Flowers	Potra001465:15381			17.5326	0.0000307	0.0864
Flowers	Potra001465:15399			17.1997	0.0000404	0.0965
Flowers	Potra002492:19040	Potra002492g18832	aluminum-activated malate transporter 12-like	19.7561	0.0000438	0.1002
Flowers	Potra000179:19529	Potra000179g00698	yae1 domain-containing protein 1-like isoform X1	20.6225	0.0000302	0.0864
Flowers	Potra000655:23796			22.2036	0.0001101	0.1460

Flowers	Potra002557:25018	Potra002557g19269	pentatricopeptide repeat-containing protein At1g08070, chloroplastic;tocopherol cyclase;tocopherol cyclase, chloroplastic	19.0534	0.0000960	0.1460
Flowers	Potra003994:25486	Potra003994g24046	UDP-glycosyltransferase 73C1-like	19.8085	0.0000404	0.0965
Flowers	Potra002243:28532	Potra002243g17245	phytoene dehydrogenase, chloroplastic/chromoplastic	33.8471	0.0000000	0.0008
Flowers	Potra001263:29158	Potra001263g10903	transcription factor bHLH137-like	23.0577	0.0000329	0.0902
Flowers	Potra001520:31078	Potra001520g12656	vam6/Vps39-like protein	23.8243	0.0000014	0.0176
Flowers	Potra002818:34295	Potra002818g20041	serine/arginine-rich splicing factor SR34A;IAA-amino acid hydrolase ILR1-like 5;IAA-amino acid hydrolase ILR1-like 3	19.2533	0.0001131	0.1460
Flowers	Potra002818:34337	Potra002818g20041	serine/arginine-rich splicing factor SR34A;IAA-amino acid hydrolase ILR1-like 5;IAA-amino acid hydrolase ILR1-like 3	19.2533	0.0001131	0.1460
Flowers	Potra000987:36334	Potra000987g08153	subtilisin-like protease SBT5.4	22.3181	0.0000177	0.0710
Flowers	Potra003428:37219	Potra003428g21635	hypothetical protein POPTR_0009s08770g;serine/threonine-protein kinase TOR	18.2227	0.0000622	0.1215
Flowers	Potra000454:37262	Potra000454g02582	ABC transporter G family member 14-like;histone H1	26.0026	0.0000109	0.0682
Flowers	Potra000759:38762	Potra000759g05981	protein SMG7L-like;B3 domain-containing transcription factor LEC2-like	21.7284	0.0000137	0.0690
Flowers	Potra003809:41142	Potra003809g22941	tubulin-folding cofactor A	16.7806	0.0001171	0.1478
Flowers	Potra002589:41363	Potra002589g19466	DEAD-box ATP-dependent RNA helicase 41	17.5329	0.0000068	0.0537
Flowers	Potra002560:41388	Potra002560g19293	F-box/LRR-repeat protein At3g26922-like	11.1633	0.0001030	0.1460
Flowers	Potra002461:43136	Potra002461g18651	alkane hydroxylase MAH1-like	21.1303	0.0001121	0.1460
Flowers	Potra000522:43553	Potra000522g03533	putative G3BP-like protein	19.7715	0.0000526	0.1112
Flowers	Potra002005:2215	Potra002005g15734	IAA-amino acid hydrolase ILR1-like 4	28.2367	0.0000000	0.0008
Flowers	Potra003941:49406	Potra003941g23670	bifunctional aspartokinase/homoserine dehydrogenase	16.0874	0.0001037	0.1460
Flowers	Potra003985:49461	Potra003985g23998	protein TRANSPARENT TESTA 16;protein TRANSPARENT TESTA 16-like	22.2990	0.0000174	0.0710
Flowers	Potra003985:49463	Potra003985g23998	protein TRANSPARENT TESTA 16;protein TRANSPARENT TESTA 16-like	22.2990	0.0000174	0.0710

Flowers	Potra003985:49501	Potra003985g23998	protein TRANSPARENT TESTA 16;protein TRANSPARENT TESTA 16-like	22.2990	0.0000174	0.0710
Flowers	Potra000571:50822	Potra000571g04226	nascent polypeptide-associated complex subunit alpha-like protein 2	10.6624	0.0000749	0.1331
Flowers	Potra000354:51695	Potra000354g01357	putative uridine kinase C227.14	15.0237	0.0001052	0.1460
Flowers	Potra003669:2337	Potra003669g22380	serine/threonine-protein kinase tricorner isoform X1	20.0184	0.0000453	0.1015
Flowers	Potra002524:52825	Potra002524g19049	protein SABRE isoform X1;GATA transcription factor 24-like isoform X1	21.9435	0.0000527	0.1112
Flowers	Potra003669:2441	Potra003669g22380	serine/threonine-protein kinase tricorner isoform X1	25.0984	0.0000018	0.0181
Flowers	Potra001330:57400	Potra001330g11428	probable pectinesterase/pectinesterase inhibitor 21;geranylgeranyl transferase type-2 subunit beta 1-like isoform X1	25.3412	0.0000300	0.0864
Flowers	Potra000489:59160	Potra000489g03058	CBL-interacting protein kinase 32;CBL-interacting protein kinase 32-like;CBL-interacting serine/threonine-protein kinase 3 isoform X2;probable peptide/nitrate transporter At3g43790 isoform X1	23.0257	0.0000786	0.1331
Flowers	Potra000489:59180	Potra000489g03058	CBL-interacting protein kinase 32;CBL-interacting protein kinase 32-like;CBL-interacting serine/threonine-protein kinase 3 isoform X2;probable peptide/nitrate transporter At3g43790 isoform X1	23.0257	0.0000786	0.1331
Flowers	Potra004010:61629	Potra004010g24171	BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1-like isoform X2;BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1;BRASSINOSTEROID INSENSITIVE 1-associated receptor kinase 1-like;nuclear transcription factor Y subunit B-1	22.2173	0.0000190	0.0710
Flowers	Potra000574:65122	Potra000574g04268	protein trichome birefringence-like 31	20.1236	0.0000184	0.0710
Flowers	Potra000574:65145	Potra000574g04268	protein trichome birefringence-like 31	-10.2868	0.0000747	0.1331
Flowers	Potra000487:67955	Potra000487g03013	6,7-dimethyl-8-ribityllumazine synthase;serine/threonine-protein phosphatase PP2A-2 catalytic subunit	26.7196	0.0000008	0.0176

Flowers	Potra000487:69884	Potra000487g03013	6,7-dimethyl-8-ribityllumazine synthase;serine/threonine-protein phosphatase PP2A-2 catalytic subunit;phytoene synthase 2, chloroplastic-like	22.7744	0.0000111	0.0682
Flowers	Potra001237:69981	Potra001237g10614	luc7-like protein 3;aldo-keto reductase family 4 member C9	23.2779	0.0000368	0.0939
Flowers	Potra001184:74346	Potra001184g10259	bidirectional sugar transporter SWEET15-like;leucine-rich repeat protein 1-like	23.4909	0.0000653	0.1236
Flowers	Potra002914:2765			14.5362	0.0000888	0.1413
Flowers	Potra003598:2767			27.1403	0.0000117	0.0682
Flowers	Potra000791:86315	Potra000791g06264	actin-related protein 8	26.4287	0.0000274	0.0864
Flowers	Potra001712:86971	Potra001712g13935	protein CASP	20.4560	0.0001016	0.1460
Flowers	Potra001042:91473	Potra001042g08802	2,4-dichlorophenol 6-monooxygenase isoform X1;2,4-dichlorophenol 6-monooxygenase;flocculation protein FLO11	20.7520	0.0001094	0.1460
Flowers	Potra000991:91852	Potra000991g08205	transcription factor MYB3R-3 isoform X1	20.7590	0.0000274	0.0864
Flowers	Potra000973:92429	Potra000973g08033	DNA-directed RNA polymerase III subunit RPC3;lipase class 3 family protein	17.9285	0.0001034	0.1460
Flowers	Potra001256:96915			25.0380	0.0000360	0.0939
Flowers	Potra001632:100665			22.3602	0.0001154	0.1474
Flowers	Potra000458:105260	Potra000458g02641	triacylglycerol lipase 2-like;triacylglycerol lipase 2;cytochrome P450 94B3	32.7805	0.0000000	0.0001
Flowers	Potra001115:107841	Potra001115g09792	—NA—;probable beta-1,3-galactosyltransferase 2 isoform X1;probable beta-1,3-galactosyltransferase 2	18.8279	0.0000753	0.1331
Flowers	Potra004004:111201	Potra004004g24122	glycoside hydrolase 9C1	17.4155	0.0000086	0.0629
Flowers	Potra002010:112137	Potra002010g15755	serine/threonine-protein kinase rio1-like	18.9635	0.0000550	0.1139
Flowers	Potra002010:112138	Potra002010g15755	serine/threonine-protein kinase rio1-like	17.7557	0.0000414	0.0967
Flowers	Potra001016:131314	Potra001016g08480	chaperone protein dnaJ 10	22.5543	0.0000144	0.0690
Flowers	Potra001016:131315	Potra001016g08480	chaperone protein dnaJ 10	22.5543	0.0000144	0.0690
Flowers	Potra001016:131319	Potra001016g08480	chaperone protein dnaJ 10	24.2872	0.0000302	0.0864
Flowers	Potra001655:132991	Potra001655g13592	beta-glucosidase 12-like	20.1965	0.0000016	0.0176

Flowers	Potra000406:159495	Potra000406g01981	CASP-like protein 1D1	28.7563	0.0000015	0.0176
Flowers	Potra000417:162754	Potra000417g02120	PREDICTED: uncharacterized protein LOC105116303 isoform X1;PREDICTED: uncharacterized protein LOC105116303 isoform X4;PREDICTED: uncharacterized protein LOC105116303 isoform X3	21.2563	0.0000786	0.1331
Flowers	Potra002021:3235	Potra002021g15846	cytochrome P450 724B1-like;subtilisin-like protease SBT5.3	20.9452	0.0000479	0.1052
Flowers	Potra000346:182411	Potra000346g01235	dnaJ homolog subfamily B member 6 isoform X2	22.6748	0.0000631	0.1215
Flowers	Potra000417:191626	Potra000417g02122	ankyrin repeat domain-containing protein EMB506, chloroplastic;NA;ATP-dependent Clp protease proteolytic subunit-related protein 1, chloroplastic	21.4143	0.0000585	0.1189
Flowers	Potra002046:3840			25.1108	0.0000068	0.0537
Flowers	Potra188252:4042	Potra188252g28584	auxin-responsive family protein;NA	23.6016	0.0000118	0.0682
Flowers	Potra195163:731			24.9127	0.0000853	0.1413
Flowers	Potra002021:752	Potra002021g15847	subtilisin-like protease SBT5.3	20.5117	0.0000211	0.0748
Flowers	Potra006505:5167	Potra006505g25700	probable galacturonosyltransferase 11;probable galacturonosyltransferase 11 isoform X1	14.2891	0.0000991	0.1460
Flowers	Potra000327:5996	Potra000327g01147	BTB/POZ and MATH domain-containing protein 2-like	22.3425	0.0000879	0.1413
Flowers	Potra002304:6073	Potra002304g17573	haloacid dehalogenase-like hydrolase domain-containing protein 3	15.6213	0.0000906	0.1421
Flowers	Potra001421:6293	Potra001421g12026	embryo-specific family protein;embryo-specific protein ATS3B-like	18.9137	0.0000986	0.1460
Flowers	Potra009102:6556	Potra009102g26288	putative H/ACA ribonucleoprotein complex subunit 1-like protein 1	14.7825	0.0000933	0.1443
Flowers	Potra006505:7038	Potra006505g25700	probable galacturonosyltransferase 11;probable galacturonosyltransferase 11 isoform X1	14.3837	0.0001098	0.1460
Flowers	Potra182098:7279	Potra182098g28206	flavin-containing monooxygenase FMO GS-OX-like 9	13.4844	0.0000129	0.0690

Flowers	Potra000817:8282	Potra000817g06506	hypothetical protein POPTR_0001s00840g	20.6756	0.0000376	0.0939
Flowers	Potra000817:8915	Potra000817g06506	hypothetical protein POPTR_0001s00840g	24.4507	0.0000002	0.0064
Budbreak	Potra182540:1252			-11.2187	0.0000066	0.0646
Budbreak	Potra001174:13069	Potra001174g10169	dr1-associated corepressor homolog;11-oxo-beta-amyrin 30-oxidase-like;cytochrome P450 4X1 isoform X1	20.2228	0.0000165	0.1016
Budbreak	Potra002201:22864	Potra002201g16952	histidine kinase 3	12.1206	0.0000049	0.0646
Budbreak	Potra002720:23256	Potra002720g19828	kinesin heavy chain isoform X2;kinesin-like protein KIN-6 isoform X1;hypothetical protein POPTR_0013s06510g	18.7558	0.0000235	0.1298
Budbreak	Potra003186:38359	Potra003186g20928	NDR1/HIN1-like protein 1;transmembrane protein 53;Transmembrane protein 53;transmembrane protein 53-like	12.4109	0.0000007	0.0469
Budbreak	Potra003186:38398	Potra003186g20928	NDR1/HIN1-like protein 1;transmembrane protein 53;Transmembrane protein 53;transmembrane protein 53-like	12.0553	0.0000017	0.0476
Budbreak	Potra003186:38401	Potra003186g20928	NDR1/HIN1-like protein 1;transmembrane protein 53;Transmembrane protein 53;transmembrane protein 53-like	12.1977	0.0000008	0.0469
Budbreak	Potra003186:38410	Potra003186g20928	NDR1/HIN1-like protein 1;transmembrane protein 53;Transmembrane protein 53;transmembrane protein 53-like	11.9429	0.0000015	0.0476
Budbreak	Potra003809:46937	Potra003809g22943	—NA—	-10.4263	0.0000076	0.0646
Budbreak	Potra002580:63210	Potra002580g19401	transcription repressor OFP17	15.0747	0.0000072	0.0646
Budbreak	Potra167680:2612	Potra167680g27295	uncharacterized GPI-anchored protein At4g28100	14.1312	0.0000034	0.0633
Budbreak	Potra167680:2613	Potra167680g27295	uncharacterized GPI-anchored protein At4g28100	14.1312	0.0000034	0.0633
Budbreak	Potra002153:69635	Potra002153g16652	mediator of RNA polymerase II transcription subunit 7a;mediator of RNA polymerase II transcription subunit 7a-like;lipid phosphate phosphatase delta-like	11.1288	0.0000107	0.0809
Budbreak	Potra000434:171992	Potra000434g02333	probable ubiquitin-like-specific protease 2B isoform X1;Phosphoglucose isomerase (PGI)	11.4500	0.0000274	0.1380

Budbreak	Potra004013:5135	Potra004013g24216	dicarboxylate transporter 2.1, chloroplastic-like;DUF946 domain-containing protein	-9.6255	0.0000117	0.0809
Budbreak	Potra001819:5495	Potra001819g14674	endonuclease III homolog 1, chloroplastic isoform X1	18.7605	0.0000047	0.0646
Budbreak	Potra189842:6934	Potra189842g28721	protein MEI2-like 2;NA	14.0280	0.0000257	0.1355
Budbreak	Potra000831:6977			-9.4821	0.0000062	0.0646
Budbreak	Potra000831:6986			-9.4821	0.0000062	0.0646
Budbreak	Potra000831:7047			-9.2276	0.0000154	0.1003
Budbreak	Potra000831:7054			-9.3455	0.0000114	0.0809
Budbreak	Potra000831:8489			-9.3367	0.0000184	0.1072

Chapter 3

Genomic models for detecting extended phenotype associations: a simulation study for detecting community genetics effects

Authors: Clay J. Morrow, Cécile Ané

Abstract

Identification of the genetic links to extended phenotypes that are predicted by community and ecosystem genetics requires accurate and reliable genomic association models. A reliable model should take the covariance structure of the system into consideration. For example, genetic, temporal, and spatial variation need to be accounted for in order for conclusions to be valid. A traditional approach extracts uses a best linear best unbiased predictor of the overall genetic effects (GBLUP) on the phenotype of interest and regresses this GBLUP against a genetic marker of interest. By simplifying the variation of the system to this single GBLUP variable, this two-step approach loses information about the correlative structure in the data. We use simulation studies to compare a suite of mixed effects models, without reducing this structure, to traditional two-step approach. We found that the full random effects models that correctly account for correlative structure outperform the GBLUP method, which exhibited extremely high type I error and was therefore unreliable for hypothesis testing. We show that an additive random effects model is appropriate for identifying genetic links with extended phenotypes. Our model exhibited controlled type I error and sufficient power to detect relatively small effects of a causal single nucleotide polymorphism (SNP) on an extended phenotype.

Introduction

Intraspecific variation can have important impacts on entire ecosystems and identifying the genetic mechanisms underlying these drivers is important for understanding ecological systems. Genes and the expression of phenotypes that those genes encode can shape communities and ecosystem processes in profound ways (Raffard et al.

2018). Plants fit extraordinarily well into this genes-to-ecosystems framework because of their potential for intraspecific variation, their importance to the communities in which they exist, and the effects that they have on their environment. In fact, intraspecific variation in plants accounts for a quarter of the total trait variation in plant communities on average (Siefert et al. 2015) and the impacts of that variation can be similar to among-species variation (Des Roches et al. 2018; Koricheva and Hayes 2018). Genotypic differences among individual plants can affect soil chemistry, microbial communities (Schweitzer et al. 2008; Horton et al. 2014; Gehring et al. 2017; Harrison et al. 2018; Veach et al. 2019), and arthropod communities (Horton et al. 2014; Barker et al. 2018; Koricheva and Hayes 2018; Nell et al. 2018), as a few well-documented examples. These ecosystem characteristics act as extended phenotypes of the plants, influenced by their genetic variation.

Identification of genomic mechanisms associated with extended phenotypes is important to fully understand the full scope of genes-to-ecosystems dynamics. Much research has shown that extended phenotypes can vary substantially among individual genotypes, but few candidate genes have been identified. This deficiency is largely due to the relatively few studies investigating genomic mechanisms underlying extended phenotype variation (Hersch-Green et al. 2011; Crutsinger 2016). The lack of methods tailored towards detecting extended phenotype associations is another likely contributor. The most common toolset used to search for potential genomic drivers are single-marker genomic association analyses (Hayes 2013), which have been adapted, largely unchanged, from their original use linking genes to disease in humans.

One major factor that needs to be considered when implementing a genomic association model is the correlative structure that exists within the data. Common sources of structure are genetic correlations among genotypes, spatial correlations among data collected from multiple sites, and temporal correlations among repeated measures in longitudinal studies. If no population structure (or other correlative structure) exists in a population, then a simple multiple regression $y = X\alpha + Z\beta + \varepsilon$ is appropriate to test for an association with a phenotype. In this formulation, y is the phenotype of interest, α is a vector of fixed effects for covariates X, β is the fixed effect of a genomic variant Z, and $\varepsilon \sim N(0, \sigma^2)$ are residual errors. In structured populations, correlations can be accounted for, with kinships or estimates thereof, using mixed-effect models (Hayes 2013). Temporal variation can similarly be accounted for by including correlations among individuals observed across multiple time points in these mixed models (Furlotte et al. 2012). Mixed models for genomic association analysis calculate the best-linear unbiased predictor (BLUP) of the random effects. This process requires estimating variance components for these effects and inverting a large covariance matrix. Because this step is computationally expensive, authors often calculate the BLUPs once for the phenotype of interest: “by assuming that each SNP only has a small to moderate effect on the phenotype, it is reasonable to assume that variance component estimates will be the same for each SNP. With this assumption it is only necessary to perform the variance component search once and thus feasible to perform the hypothesis test for each SNP within the genome” - Furlotte et al (2012, p. 464-465). To our knowledge, this assumption has not been adequately verified. Nor have these models been validated for detecting associations with extended phenotypes.

With this research, we aim to **evaluate and compare the efficacy of competing genomic association models for detecting genomic variants associated with extended phenotype variation** in simulated longitudinal datasets of plant-herbivore systems. To that end we: 1) simulated 180 settings, each with 2500 independent data sets. Each data set consisted of one population containing 200 clonal genotypes, each with three biological replicates for a total of 600 individuals. Populations were simulated with four intercorrelated traits, an extended phenotype, both clonal and temporal correlation structure, and variation in a causal single-nucleotide polymorphism (SNP). We then 2) fit mixed-effects models and a BLUP model to each simulated dataset and estimated the effect of SNP on extended phenotype. Finally, we 3) compared the different models in terms of accuracy and precision of the estimated SNP effects, Type I error control, and power to detect genomic associations. This research is a companion piece to a community genetics study which aimed to assess genomic drivers of herbivorous insect communities on *Populus tremuloides* (Ch. 2) and, as such, we designed and tested models with this system in mind and structured the simulated populations accordingly.

Materials and Methods

To assess the efficacy of mixed-effects genomic association models in a genes-to-ecosystems context, we fit six association models to simulated populations and compared their statistical properties. Our simulations include correlation between individuals of the same clone, temporal correlation, correlated traits and extended phenotypes affected by one genetic locus (SNP) of additive effect.

Simulations

To test and compare the accuracy and power of competing genomic association models, we simulated populations each with 600 individuals. We simulated four intercorrelated phenotypic traits, clonal population structure, temporal variation, genomic variation, and an extended phenotype. These plant populations were modelled after the tree species *Populus tremuloides* because of its substantial intraspecific variation and its ability to impact ecosystems through this variation (Stevens et al. 2014; Barker et al. 2016; Holeski et al. 2016; Falk et al. 2018). Traits were modelled after the ecologically relevant *Populus* traits: tree size, specific leaf area, condensed tannin concentration, and phenolic glycoside concentration (Ch. 2, Ch. 3). Simulated extended phenotypes were affected by clonal, phenotypic, and genomic variation of the plants as well as by random environmental variation. We modelled these extended phenotypes to match how insect herbivores are affected by the real *P. tremuloides* population, responding to host genotype and traits, and exhibiting temporal variation. Simulated populations contained 200 clones each with three replicate trees. Because the reference population of *P. tremuloides* does not have significant population structure (Barker et al. 2019b), clones were independent and identically distributed (i.i.d.) in these simulations. We simulated traits and extended phenotypes over four time periods, the same number of time periods as surveyed in the reference system (Ch. 2).

We introduced genetic variation, at a molecular level, by generating an ecologically relevant SNP within the population. For the purposes of this simulation study, the causal SNP was assumed to be independent from any other genetic effects encompassed by clonal variation. This corresponds to the underlying assumptions of the genomic association models tested. We encoded a SNP value for each clone as -1 for homozygous major variants (AA), 0 for heterozygous variants (Aa), or 1 for homozygous minor variants (aa). This encoding allowed us to test the additive effects of minor alleles. We assigned SNP variants to each clone by drawing randomly from the set {-1, 0, 1} with probabilities p_{AA}, p_{Aa}, and p_{aa}, respectively. As such, the SNP variable Z follows a multinomial distribution for each clone g: $Z_g \sim \text{Multinom}(p_{AA}, p_{Aa}, p_{aa}; n = 1)$. We assigned variant probabilities by specifying the minor allele frequency q of the population in each simulation and assuming Hardy-Weinberg equilibrium: $p_{AA} = (1 - q)^2$; $p_{Aa} = 2q(1 - q)$; and $p_{aa} = q^2$ (Weinberg 1908; Hardy 2010). The SNP was simulated with either low minor allele frequency $q = 0.1$ or high minor allele frequency $q = 0.4$. Both selected minor allele frequencies regularly occurred among SNPs in the reference *P. tremuloides* population (Lind-Riehl et al. *in review*) where the median minor allele frequency was 0.2.

We then simulated four genetically mediated and intercorrelated tree traits with the model given by equation 1. In this formulation, $X_i(t)$ is a vector containing values of trait *i* at time *t* across all 600 individuals. Z is a vector containing values of the causal SNP for each individual and the scalar ϕ_i is the additive fixed effect of the SNP on trait *i*. The systemic clonal effects on the traits are given by $G\gamma_{xi}$. The vector γ_{xi} contains the 200 random scalar effects for clones which are drawn independently, each from $N(0, \sigma_{xg}^2)$. The variance among clone effects is given by σ_{xg}^2, which does not differ among traits. For all traits *j* and *k*, γ_{xj} and γ_{xk} are independent. G is an incidence matrix with 600 rows and 200 columns where value G_{jk} is equal to 1 if the individual in row *j* belongs to the clone in column *k* and 0 otherwise. Trait *i* also grows at a constant rate during each time step, as determined by the scalar ρ_i. The vector of ones ($\mathbf{1}$ in equation 1) denotes that

ρ_i is the same for all individuals. Temporal autocorrelation is generated by $\delta_{xi}(t) = \delta_{xi}(t-1) + G\nu_{xi}(t)$, wherein $G\nu_{xi}(t)$ are temporally-specific clonal effects. Here, $\nu_{xi}(t)$ is a vector containing 200 clonal effects for trait *i* at time *t,* each of which is drawn from $N(0, \sigma_{xv}^2)$. The variance σ_{xv}^2 determines the magnitude of the effect. For all times *t* and *s*, $\nu_{xi}(t)$ and $\nu_{xi}(s)$ are independent and for all traits *j* and *k*, $\nu_{xj}(t)$ and $\nu_{xk}(t)$ are independent. G is the clonal incidence matrix described previously. $\delta_{xi}(t)$, then, is a vector of the accumulated effects of $\nu_{xi}(t)$ at each time step across all individuals. The residual variance for trait *i* at time *t*, $\varepsilon_{xi}(t)$, is independent across all individuals. Furthermore, $\varepsilon_{xi}(t)$ is independent of $\varepsilon_{xi}(s)$ for all times *t* and *s*. Residual variation is intercorrelated among the four traits according to the covariance matrix Σ_x whose values Σ_{xjk} for any traits *j* and *k* is equal to $cov\left(\varepsilon_{xj}(t), \varepsilon_{xk}(t)\right)$ across time and individuals. With this simulation model, phenotypic expression of intercorrelated traits is determined by fixed and random genetic effects, fixed temporal effects, temporally autocorrelated interactions of random clonal and temporal effects, and random residual effects.

$$X_i(t) = Z\phi_i + G\gamma_{xi} + (t-1)\rho_i\mathbf{1} + \delta_{xi}(t) + \varepsilon_{xi}(t) \tag{1}$$

To ensure simulation of realistic phenotypes, we chose parameter values derived from a real population of *Populus tremuloides* (Lind-Riehl et al. *in review*; Barker et al. 2018, 2019; Cole et al. 2021). For all simulations, we set the systemic clonal trait variance (σ_{xg}^2) equal to 0.5 and the time-specific variance (σ_{xv}^2) equal to 0.2, which match typical relative magnitudes of genetic and temporal variance of *P. tremuloides* traits, respectively. The trait growth coefficients were set to match annual trends in four ecologically important tree traits: tree size, specific leaf area, condensed tannin concentration, and phenolic glycoside concentration, respectively ($\rho = [0.87, 0.68, 0.12, 0.02]$). Covariance among the residuals of these traits (Σ_x) was also taken from estimates of the real population (Table 1). We simulated populations under three causal SNP conditions, either with no effect, with small effect, or with moderate effect on the first trait ($\phi = [0, 0, 0, 0]$, $\phi = [0.1, 0, 0, 0]$, or $\phi = [0.2, 0, 0, 0]$, respectively).

We also simulated an extended phenotype for each population, with varying degrees of dependence on population characteristics and environmental factors with the model given by equation 2. In this formulation, $Y(t)$ is a vector of extended phenotype values across all individuals at time t. $X(t)$ is a phenotype matrix containing trait values across individuals at time *t*. $X(t)$ has four columns corresponding to each of the four traits generated with equation 1. α is a column vector containing the additive effects of each trait. Z is the vector of causal SNP values for each individual, as in equation 1, and β is a fixed scalar of the direct SNP effect on the extended phenotype. Systemic clonal effects on the extended phenotype are given by $G\gamma_y$. The vector γ_y contains the 200 random scalar effects for clones, which are independently drawn from $N\left(0, \sigma_{yg}^2\right)$ with variance σ_{yg}^2. G is the clonal incidence matrix described previously. Random temporal effects are given by $\tau_y(t)$. For each of the four time points, the scalar $\tau_y(t)$ is drawn from $N\left(0, \sigma_{y\tau}^2\right)$, with variance $\sigma_{y\tau}^2$, and applied across all individuals. $\tau_y(t)$ and $\tau_y(s)$ are independent for all time points *t* and *s*. A random interaction between clone and time is given by $G\nu_y(t)$. The vector $\nu_y(t)$ contains 200 clonal effect values, each of which are drawn from $N\left(0, \sigma_{yg}^2\right)$. For all times *t* and *s*, $\nu_y(t)$ and $\nu_y(s)$ are independent. Residual variation for the extended phenotype is given by $\varepsilon_y(t) \sim N\left(0, \sigma_y^2\right)$ and are independent across all individuals and time points. With this model, expression of the extended phenotype is determined by fixed trait effects, fixed and random genetic effects, random effects of the interaction between genetic and temporal factors, and random residual variation.

$$Y(t) = X(t)\alpha + Z\beta + G\gamma_y + \tau_y(t)\mathbf{1} + G\nu_y(t) + \varepsilon_y(t) \qquad (2)$$

In each simulation, we set the effect of trait 1 (α_1) equal to 0.00, 0.125, or 0.250; and we set the effect of the other traits (α_2, α_3, α_4) to either 0.000 or 0.250 independently from each other and from α_1. With different combinations of α values, many possible effects of phenotype on extended phenotype were present in our simulations. We also varied the causal SNP effects across simulations by setting β to one of 0.00, 0.125, 0.250, or 0.500. For all simulations, we set the clonal variance for the extended phenotype (σ_{yg}^2) to 0.55 and the temporal variance ($\sigma_{y\tau}^2$) to 0.79. These values, and the residual variation $\sigma_y^2 = 0.64$, were typical among estimates of extended phenotype effects in a real population of *P. tremuloides*. The interaction effect was varied by setting $\sigma_{y\nu}^2$ equal to one of 0, 0.25, or 0.50. We simulated populations, SNPs, and extended phenotypes together, under each combination of parameters in the extended phenotype model, each value of ϕ_i from the trait model, and each minor allele frequency q considered. 3,000 simulations each were conducted under cases where $\alpha_2 = \alpha_3 = \alpha_4 =$

0 and 2,000 simulations were conducted for all other cases. For cases in which any of α_2, α_3, or α_4 were greater than 0.250, we simulated under limited conditions: $\phi_1$was restricted to either 0 or 0.2, σ_{yv}^2 was restricted to either 0 or 0.5, and q was restricted to 0.1 only. In total, we simulated 450,000 populations under one of 180 parameter combinations.

Association analyses

With the simulated data, we fit a series of competing models to assess their ability to detect genetic effects on an extended phenotype. We evaluated and compared ten separate genomic association models for each simulated data set. We first fit four types of mixed effects models, each with different random effects specification. Two versions of these four models were fit: one including traits as covariates and one not including trait covariates. An additional mixed effects model was also fit, but only the version without trait covariates was tested. The final model, against which the other models were compared, regressed the best linear unbiased predictor (BLUP) of genetic effects against the genomic marker.

In general, the fitted mixed models follow from equation 2, but with differences in how the effects of clone, time, and their interaction were specified. The first mixed model $\mathrm{MM}_{\mathrm{full}}$ (eq. 3) is the full model and exactly matches the extended phenotype simulation model (eq. 2), in which there are fixed SNP effects $Z\beta$, random clonal effects $G\gamma_y$, random temporal effects $\tau_y(t)\mathbf{1}$, random interactions between clone and time $G\nu_y(t)$, and optional fixed trait effects $X(t)\alpha$. The second mixed model $\mathrm{MM}_{\mathrm{add}}$ (eq. 4) assumes that the effects of clone and time are purely additive and independent, so no interaction is included. The next two models MM_{nestT} (eq. 5) and MM_{nestG} (eq. 6) are nested random effects models. MM_{nestT} assumes systemic random temporal effects and that clonal random effects are entirely time-specific. Conversely, MM_{nestG} assumes systemic random clone effects and that temporal random effects are entirely clone-specific. The final mixed model MM_{tfix} (eq. 7) assumes that the systemic temporal effects are fixed rather than random. Here, then, $\tau_{yf}(t)$is a fixed effect (as denoted by subscript "f" to distinguish from other $\tau_y(t)$ in other models) of time t to be estimated, rather than a random effect. Therefore, MM_{full} and MM_{tfix} differ only by treating temporal effects as random or fixed, respectively. The goal for all fitted mixed models is to estimate the effect of the causal SNP on extended phenotype ($\hat{\beta}$), independent of the other terms. The estimate of $\hat{\beta}$ is conditional upon the random effects: specifically, on the overall covariance structure constructed from covariance parameters θ. These covariance parameters are estimated via restricted maximum likelihood and then the fixed effects parameters (including $\hat{\beta}$) are estimated using maximum likelihood, conditional on the estimated $\hat{\theta}$. Finally, the random effects are predicted (as best linear unbiased predictors: BLUPs) from the covariance structure, fixed effects, and realized values of $Y(t)$. The term in the mixed model equation $[X(t)\alpha]$ indicates that a model was fit either with or without trait covariates. Because MM_{tfix} performed identically to MM_{full}, this model was not fit with trait covariates nor was it used beyond initial comparisons.

Fitted Mixed Effects Models

Name	**R formula**	**Equation**	**#**
MM_{full}	"Y ~ [X] + Z + (1|clone) + (1|time) + (1|time:clone)"	$Y(t) = [X(t)\alpha] + Z\beta + G\gamma_y + \tau_y(t)\mathbf{1} + G\nu_y(t) + \varepsilon_y(t)$	(3)
MM_{add}	"Y ~ [X] + Z + (1|clone) + (1|time)"	$Y(t) = [X(t)\alpha] + Z\beta + G\gamma_y + \tau_y(t)\mathbf{1} + \varepsilon_y(t)$	(4)
MM_{nestT}	"Y ~ [X] + Z + (1|time) + (1|time:clone)"	$Y(t) = [X(t)\alpha] + Z\beta + \tau_y(t)\mathbf{1} + G\nu_y(t) + \varepsilon_y(t)$	(5)
MM_{nestG}	"Y ~ [X] + Z + (1|clone) + (1|time:clone)"	$Y(t) = [X(t)\alpha] + Z\beta + G\gamma_y + G\nu_y(t) + \varepsilon_y(t)$	(6)
MM_{tfix}[5]	"Y ~ Z + factor(time) + (1|clone) + (1|time:clone)"	$Y(t) = Z\beta + \tau_{yf}(t)\mathbf{1} + G\gamma_y + G\nu_y(t) + \varepsilon_y(t)$	(7)

The final model, against which these mixed-effects models were compared, named G_{BLUP} (eq. 8), has been used by our group previously to detect genomic effects and identify candidate genes (Lind-Riehl et al. *in review*; Barker et al. 2019). This model regresses the BLUP of the clonal random effect on the SNP value of each clone Z_g and residual variation ε_g. Here, the clonal BLUP $\hat{\gamma}_y$ is first extracted from the mixed model $Y(t) = G\gamma_y + \tau_y(t)\mathbf{1} + \varepsilon(t)$ that does not include the causal SNP. In this way, $\hat{\gamma}_y$ represents the predicted overall genetic effect on the extended phenotype. Then, equation 8 correlates that effect with the causal SNP. An important assumption

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[5] In the equation for MM_{tfix}, the time effects $\tau_{yf}(t)$ are fixed coefficients to estimate rather than random effects. In this way, MM_{tfix} differs from MM_{full}.

underlying the G_{BLUP} model is that if the SNP is associated with the extended phenotype, then it should also be associated with the overall genetic effect (γ). This type of two-step approach was described by Stich et al. (2008) and is relatively common (e.g., Sikorska et al. 2013, 2015; Chhetri et al. 2019; Esmaeili-Fard et al. 2021). The two-step BLUP approach is used instead of full mixed effects models for its computational efficiency. In a system with many SNPs, a mixed model approach can be computationally expensive because of the need to estimate covariance parameters (θ) and invert the resulting covariance matrix (i.e., Σ_θ) for each SNP. To address this problem, the G_{BLUP} method fits a single covariance matrix for each response variable and recycles the resulting BLUP values, rather than fitting the covariance matrix for each SNP×response combination in real systems.

G_{BLUP} $$\hat{\gamma}_y = Z_g\beta + \varepsilon_g \qquad (8)$$

We evaluated the fit of all models, for all simulated populations, by comparing the estimated value of $\hat{\beta}$ to the true genetic effects on the extended phenotype and by the proportion of tests indicating that the null hypothesis ($H_0\colon \beta = 0$) was true (i.e., the rejection rate). We assessed the accuracy of each model under the various conditions (i.e., parameter space). All simulations and model fitting were conducted using the R statistical software library (R Core Team 2020). The G_{BLUP} model was fit using the “lm” function from the R package “stats” and mixed effects models were fit using the “lme4” package (Bates et al. 2015). Statistical tests of $\hat{\beta}$ for mixed models were conducted with the “lmerTest” package (Kuznetsova et al. 2017) , and we used Satterthwaite degrees of freedom (Fai and Cornelius 1996). We also calculated the 2.5% and 97.5% quantiles for estimates of $\hat{\beta}$, which show the values between which $\hat{\beta}$ was estimated for 95% of the simulations.

Direct, indirect, and total SNP effects

In these simulated systems, the extended phenotype is affected by the causal SNP in two ways: directly and indirectly through the traits. The direct effect of the SNP on $Y(t)$ is simply β. The indirect SNP effect is dependent upon both the SNP effect on traits (the column vector ϕ) and the effect of the traits on the extended phenotype (the column vector α). In fact, the indirect effect is the product $\phi'\alpha$. The total SNP effect on the extended phenotype is then equal to $\beta + \phi'\alpha$. This is proven algebraically by substituting the right-hand size of equation 1 in for $X(t)$ in equation 2 (i.e., eq. 9).

$$\begin{aligned} Y(t) &= X(t)\alpha + Z\beta + \cdots \\ &= (Z\phi' + \cdots)\alpha + Z\beta + \cdots \\ &= Z(\beta + \phi'\alpha) + \alpha(\ldots) + \cdots \end{aligned} \tag{9}$$

Results

All models not containing trait covariates accurately estimated the effect of the causal SNP on the extended phenotype and all mixed models were an improvement over the G_{BLUP} method. The G_{BLUP} model estimated SNP effects reasonably well but with a slight bias towards zero. The mixed effects models were more accurate on average than the G_{BLUP} method, but all models had comparable precision, as indicated by the empirical distribution of the estimated SNP effect (see 2.5% and 97.5% quantiles in Table 2).

Average estimates and empirical 2.5% and 97.5% quantiles for $\hat{\beta}$ were identical among the four mixed models lacking trait covariates across all simulations (Table 2).

While all models accurately estimated the SNP effect on the extended phenotype, they did not determine significance of these effects at comparable rates. Both the G_{BLUP} and MM_{nestT} models had extremely high Type I error rates (34.3% and 25.0%, respectively) that rendered them invalid for testing statistical hypotheses. The remaining mixed effects models MM_{full}, MM_{add}, MM_{tfix} and MM_{nestG} all had well-controlled Type I error rates (5.7%, 5.7%, 5.7%, and 5.5%, respectively) and power to detect even the smallest effects ($\beta = 0.125$) around 35% of the time on average (Table 3). Note that these models all assume a systemic clonal effect, indicating that this component is crucial. The rejection rates of MM_{full}, MM_{add}, and MM_{tfix} were identical across all levels of β. This, in addition to the identical estimates of $\hat{\beta}$ between these models, led us include only MM_{add} in further comparisons because it is the simplest model of the three.

Adding trait covariates to the genomic association mixed models resulted in similar patterns as without trait covariates. The models containing trait covariates were biased slightly toward zero in their estimation of SNP effects relative to models without covariates (Table 4). This is because these versions of the models, estimate the *direct* SNP effect, which is smaller than the *total* SNP effect estimated by the models without covariates. Both models are estimating the effects accurately but measured *different* effects (See Figure S1). The ability to detect significant associations was also slightly reduced when trait covariates were included (Table 5) for the same reason. Even with trait covariates, MM_{nestT} exhibited inappropriately high Type I error rates (23.3%; Table 5).

In addition to the expected impacts that the true value of β had on detection of significant associations (Figure 1), the parameters α, ϕ, and q, all substantially impacted the estimation of $\hat{\beta}$ and rejection of the null hypothesis (Table S2, S3). Increasing the effect of a SNP on trait 1 and the effect of trait 1 on the extended phenotype had the largest impacts. All else equal, increasing the indirect SNP effect $\phi'\alpha$ increased the ability of the models to detect significant effects (Figure 2). This is unsurprising, given that the total SNP effect is increased. The second largest driver of detection probability was the minor allele frequency q. All else equal, the power of our mixed models to detect SNP effects was greatly increased among SNPs with 40% minor allele frequencies when compared to SNPs with 10% minor allele frequency (Figure 3). In addition to the indirect genetic impact that trait 1 had on detecting association, the remaining trait effects also impacted detection rate. Increasing the effects of traits 2, 3, or 4 (α_2, α_3, or α_4) decreased the ability to detect significant SNPs (Figure 4) and traits that were more strongly correlated with trait 1 had larger impacts (Table S3, S4). Accounting for traits as covariates in the models eliminated these detrimental impacts (Table S5).

Discussion

This work demonstrated that mixed effects models for genomic association analyses can be effective tools for identifying genetic links between plants and extended phenotypes. We found that mixed models performed significantly better than a two-step GBLUP approach. We also determined that different specifications of hierarchical structure between genetic and temporal random effects substantially impacted viability of the mixed models. Including a main effect for clones was crucial to obtain acceptable type I error rates. These results suggest that a well-parameterized mixed effects model, that accounts for the correlation structure among data points, is a useful tool for detecting genetic drivers of extended phenotypes in real biological systems.

Detecting genomic associations with extended phenotypes

To obtain trustworthy results from a genomic association model, researchers must choose a model that correctly accounts for correlations in their data. Data collected from populations containing related individuals require accounting for this kinship when investigating genetic effects on phenotypes (Hayes 2013; Zhang et al. 2021). Similarly, observations taken from the same individual over time require accounting for temporal correlations (Furlotte et al. 2012). Failure to correct for either type of structure leads to a substantial loss of power for detecting the effects of a genetic variant (Furlotte et al. 2012; Hayes 2013), or worse, elevated Type I errors. Our results demonstrate, unsurprisingly, that this is also the case when applying these types of models to extended phenotypes. These results also suggest that estimating the random effects for each tested association provides more power than estimating a BLUP only once and assuming it is independent from the variant effects.

Because extended phenotypes are further removed from the genes that affect them, they are likely to exhibit more random variation than true phenotypes. For example, insect extended phenotypes experienced much larger temporal variation than tree traits in the model system for this study (Ch. 2). Spatial variation is also important to consider. One study estimated that spatial variation accounts for 11% of the variation in community composition on average (Soininen 2016) and community diversity is an important extended phenotype of plants (Schweitzer et al. 2008; Koricheva and Hayes 2018; Barker et al. 2019b; Veach et al. 2019). In addition to temporal effects, research into the genes-to-ecosystems paradigm should consider correcting for spatial variation among observations taken from different sites. To our knowledge, no studies to date have incorporated spatial structure into genomic association models.

As our results demonstrate, it is important to correctly account for hierarchical structure. We found that failing to account for systemic clonal effects drastically increased Type I error rates. Even though simulated extended phenotypes were affected by the interaction between clone and time, specifying a random interaction term did not result in any improvement over the model with additive mixed effects. It should be noted, however, that this depends upon the magnitude of the true interaction. We found that increasing the magnitude of the random interaction effect slightly reduces power in a mixed model that does not account for it (Figure 5). Researchers should be cautious to appropriately specify the hierarchical structure (or lack thereof) of their data in the mixed-effects models.

It is also important to consider what questions a model allows us to test or answer. In this work, inclusion of trait covariates in the fitted models led to different hypotheses being tested. Models that included trait covariates partitioned out the direct and indirect effects of the locus separately. In this case, the hypothesis tested is in reference to the *direct* effect (i.e., $H_0: \beta = 0$). By contrast, when traits were not included, all locus effects were pooled into the coefficient of interest. In this case, the tested hypothesis refers to the *total* effect (i.e., $H_0: \beta + \phi' \alpha$ = 0). Figure 6 shows the impact of including trait covariates in relation to the true effects, both direct and total, of the causal locus.

In practice, researchers will typically not know ahead of time which traits are associated with both the locus of interest and the extended phenotype, so it is important that they carefully consider the implications of including traits in a model. An ideal approach in such a system would be to use three models, as in path analysis: 1) one that tests the total effect of a locus (no trait covariates), 2) another that tests the direct effect of the locus (with trait covariates), and optionally 3) one that conducts a genomic association analysis on the traits through which the suspected indirect genetic effects are carried. Comparing (1) and (2) can reveal the degree to which the genetic effects are mediated by traits: if a locus effect is stronger in (1) than in (2), that indicates that the genetic link is mediated by traits to some degree; if (1) and (2) do not provide sufficiently different results, that indicates that there is little trait mediation; and if a larger effect is found in (2) than in (1), it indicates that the trait effects cancel out some or all of the independent locus effect. In this latter case, without accounting for traits, researchers may not be able to identify the causal locus with (1) alone. (3) can be used to estimate the magnitude of the indirect trait effects ϕ_i. In any case, traits that may be correlated with the extended phenotype of interest should be measured whenever possible and carefully evaluated for their contributions.

The ability to detect genomic associations is also dependent upon the distribution of alleles in the genetic marker. Reduced minor allele frequency significantly decreases power (Hayes 2013) and increases the number of false positives among association tests (Tabangin et al. 2009). Statistically, this is because lower minor allele frequency leads to greater asymmetry in sample sizes among the three allelic conditions (AA, Aa, aa). Take, for example, a SNP with minor allele frequency $q = 0.1$. In this case, the minor allele is expected to occur in only 38 genotypes from a population of 200 (i.e., $200(p_{Aa} + p_{aa}) = 200(.18 + .01) = 38$) and the major allele will occur in 198 genotypes. This relatively low sample size ratio results in lower power when compared with a $q = 0.4$ SNP, which will have 128 genotypes with minor alleles on average and 168 genotypes with major alleles. This second case is much more balanced and has many samples for each condition. Variants with low minor allele abundance, however, may be especially important for detecting associations. In humans, genomic analyses have revealed that minor alleles tend to be associated with disease (Park et al. 2011) and critical variants tend to have very low minor allele frequencies (Kido et al. 2018) because of the associated cost to evolutionary fitness. Whether these patterns hold true for plant systems and extended phenotypes remains unknown.

Application to biological systems

The most important finding from this work is that these mixed-effects genomic association models have good statistical properties and are appropriate for detecting genetic effects on extended phenotypes in real biological systems. In fact, these results allowed us to confidently apply such models to the real population of aspen upon which these simulations were built (Ch. 2). We were able to identify 73 genes associated with *P. tremuloides* traits and an additional 15 genes associated with insect herbivore extended phenotypes (Ch. 2) using these methods. Mixed effects models like the ones tested here can also easily be applied to populations which exhibit heritable variation in traits or extended phenotypes. Though, in our case, high-throughput computing resources were necessary to fit a mixed model for every SNP-response combination due to the size of our population (approximately 1500 individuals).

Our conclusion, that this study shows that methods tested here can be used with real populations, comes with a few caveats. First, we simulated SNPs with direct links to phenotypes and extended phenotypes. In this sense, the SNPs are also quantitative trait loci (QTL). In many real-world contexts, however, the markers used in the association analyses may not be the causal locus and methods to identify the true QTL may be needed (e.g., Zeng 1994). However, this is not yet possible in many plant systems, including *Populus*, where the full genetic architecture remains unknown. One limitation of this study is that we also simulated only one SNP per population instead of the many thousands tested by most genomic association studies. In most cases, researchers need to perform multiple-test corrections to account for the extremely large number of tests conducted. Common correction methods include false discovery control (Storey 2003) and permutation testing to determine genome-specific significance thresholds (Churchill and Doerge 1994). Another caveat of our results is that we conducted single-marker analyses, which assume that each marker is independent. This assumption is unlikely true in most systems because of linkage disequilibrium (Reich et al. 2001). If linkage disequilibrium is high, multi-marker methods may be more appropriate (Bot et al. 2005). Multi-marker methods can account for the correlations among each genetic marker, they out-perform mixed model approaches in the presence of strong genomic correlations, and they can detect markers of polygenic effect (Bot et al. 2005; Homer et al. 2008; Li et al. 2011; Klasen et al. 2016) in human genomic association analyses. The final caveat of these results involves the genetic covariance structure. We simulated genotypes without kinship among individuals beyond clonal identity, because no population structure existed in our real world *Populus* system (Lind-

Riehl et al. *in review*; Barker et al. 2019). In situations where genetic relationships among genotypes are strong or highly variable, genetic relatedness should be accounted for in the covariance structure of mixed models (Zhang et al. 2021).

Conclusions

We were able to validate mixed-effects models for genomic association analyses in their ability to accurately estimate and detect the effects of genetic variants on extended phenotypes. We demonstrate that appropriately accounting for covariance structure is critical to the validity of the mixed model. We also found that estimating the SNP-independent random effects, for each SNP, provided better Type I error control than estimating these random effects only once and assuming them constant across all tests. We conclude that mixed-effects genomic association models are appropriate for detecting genetic drivers of extended phenotypes in real populations.

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Tables

Table 1: Covariance among simulated traits, as in Σ_x. These covariances are derived from covariance structure among basal area (X_1), specific leaf area (X_2), phenolic glycoside concentration (X_3), and condensed tannin concentration (X_4) of a real aspen population.

	X_1	X_2	X_3	X_4
X_1	0.5100	0.1938	-0.0714	-0.1683
X_2	0.1938	0.5100	-0.0663	-0.1581
X_3	-0.0714	0.0663	0.5100	-0.1479
X_4	-0.1683	-0.1581	-0.1479	0.5100

Table 2: Mean estimates of SNP effects $\hat{\beta}$ for each true value of β for models without trait covariates. These results are averaged across all levels of α, ϕ, and q for a total of $N = 90000$ simulations per model. The 2.5% and 97.5% percentiles of the empirical distribution of $\hat{\beta}$ are given in parentheses.

	$\boldsymbol{\beta = 0}$	$\boldsymbol{\beta = 0.125}$	$\boldsymbol{\beta = 0.25}$	$\boldsymbol{\beta = 0.375}$	$\boldsymbol{\beta = 0.5}$
$\mathbf{G}_{\mathbf{BLUP}}$	0.009 (-0.142, 0.162)	0.107 (-0.045, 0.266)	0.203 (0.049, 0.37)	0.3 (0.139, 0.477)	0.395 (0.222, 0.581)
$\mathbf{MM}_{\mathbf{full}}$	0.011 (-0.16, 0.182)	0.12 (-0.05, 0.298)	0.227 (0.055, 0.412)	0.333 (0.157, 0.527)	0.436 (0.249, 0.637)
$\mathbf{MM}_{\mathbf{add}}$	0.011 (-0.16, 0.182)	0.12 (-0.05, 0.298)	0.227 (0.055, 0.412)	0.333 (0.157, 0.527)	0.436 (0.249, 0.637)
$\mathbf{MM}_{\mathbf{tfix}}$	0.011 (-0.16, 0.182)	0.12 (-0.05, 0.298)	0.227 (0.055, 0.412)	0.333 (0.157, 0.527)	0.436 (0.249, 0.637)
$\mathbf{MM}_{\mathbf{nestG}}$	0.011 (-0.16, 0.182)	0.12 (-0.05, 0.298)	0.227 (0.055, 0.412)	0.333 (0.157, 0.527)	0.436 (0.249, 0.637)
$\mathbf{MM}_{\mathbf{nestT}}$	0.011 (-0.16, 0.182)	0.12 (-0.05, 0.298)	0.227 (0.055, 0.412)	0.333 (0.157, 0.527)	0.436 (0.249, 0.637)

Table 3: Rejection rate corresponding to the null hypothesis $H_0: \beta = 0$ for models without trait covariates. The rejection rates are averaged across all levels of α, ϕ, and q for a total of $N = 90000$ simulations per model. Individual test p-values $\leq .05$ were considered significant. Red text indicates inappropriately high Type I error rates.

	Type I Error	**Power**			
	$\boldsymbol{\beta = 0}$	$\boldsymbol{\beta = 0.125}$	$\boldsymbol{\beta = 0.25}$	$\boldsymbol{\beta = 0.375}$	$\boldsymbol{\beta = 0.5}$
GBLUP	0.3431	0.7104	0.9477	0.9962	0.9999
MM$_{full}$	0.0572	0.3563	0.7764	0.9614	0.9970
MM$_{add}$	0.0572	0.3563	0.7764	0.9614	0.9970
MM$_{tfix}$	0.0572	0.3563	0.7764	0.9614	0.9970
MM$_{nestG}$	0.0546	0.3475	0.7692	0.9590	0.9966
MM$_{nestT}$	0.2507	0.6371	0.9243	0.9929	0.9997

Table 4: Mean estimates of SNP effects ($\hat{\beta}$) for each true value of β for mixed models with included trait covariates. These results are averaged across all levels of α, ϕ, and q for a total of $N = 90000$ simulations per model. The 2.5% and 97.5% percentiles of $\hat{\beta}$ are given in parentheses. The G_{BLUP} model was not included in this comparison due to the logistical challenges associated with adding covariates to this model.

	$\boldsymbol{\beta = 0}$	$\boldsymbol{\beta = 0.125}$	$\boldsymbol{\beta = 0.25}$	$\boldsymbol{\beta = 0.375}$	$\boldsymbol{\beta = 0.5}$
MM$_{add}$(X)	0 (-0.163, 0.162)	0.109 (-0.052, 0.278)	0.217 (0.053, 0.392)	0.323 (0.155, 0.508)	0.426 (0.246, 0.621)
MM$_{nestG}$(X)	0 (-0.165, 0.168)	0.11 (-0.055, 0.284)	0.217 (0.049, 0.398)	0.323 (0.15, 0.514)	0.426 (0.242, 0.628)
MM$_{nestT}$(X)	0 (-0.164, 0.162)	0.109 (-0.052, 0.278)	0.217 (0.053, 0.392)	0.323 (0.155, 0.508)	0.426 (0.246, 0.621)

Table 5: Rejection rate corresponding to the null hypothesis $H_0\!:\beta = 0$ for mixed models with included trait covariates. The rejection rates are averaged across all levels of α, ϕ, and q for a total of $N = 90000$ simulations per model. Individual test p-values $\leq .05$ were considered significant. The G_{BLUP} model was not included in this comparison. Red text indicates inappropriately high Type I error rates.

	Type I Error	**Power**			
	$\boldsymbol{\beta = 0}$	$\boldsymbol{\beta = 0.125}$	$\boldsymbol{\beta = 0.25}$	$\boldsymbol{\beta = 0.375}$	$\boldsymbol{\beta = 0.5}$
MM$_{\text{add}}$(X)	0.0502	0.3213	0.7744	0.9657	0.9980
MM$_{\text{nestG}}$(X)	0.0520	0.3110	0.7600	0.9603	0.9970
MM$_{\text{nestT}}$(X)	0.2334	0.6061	0.9212	0.9941	0.9998

Figures

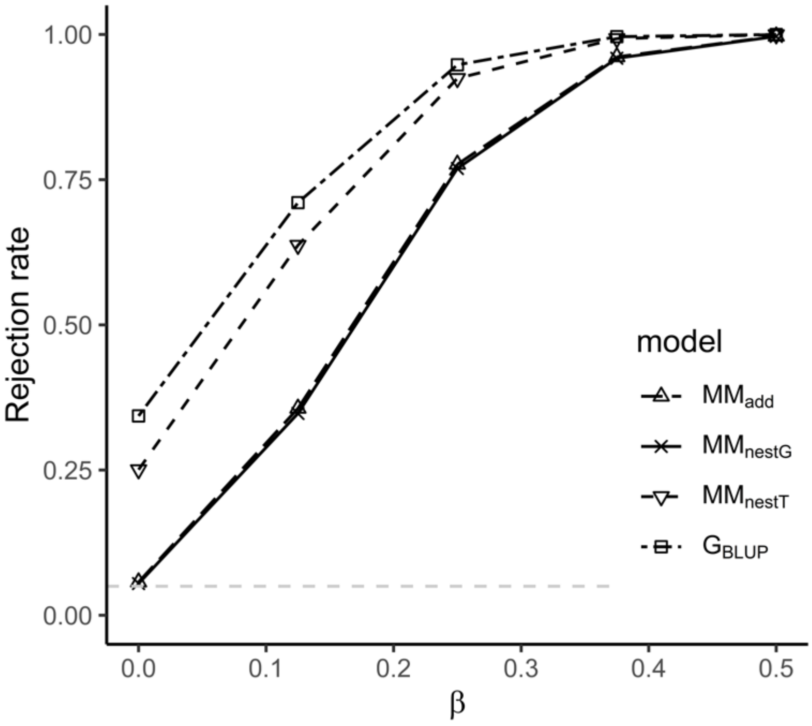

Figure 1: Power curves of competing genomic association models without trait covariates, over true levels of β. The models $\mathrm{MM}_{\mathrm{tfix}}$ and $\mathrm{MM}_{\mathrm{full}}$ are not shown because they perform identically to $\mathrm{MM}_{\mathrm{add}}$. Values are averaged over all levels of α, ϕ, and q for a total of $N = 90000$ simulations per model. Individual test p-values $\leq .05$ were considered significant.

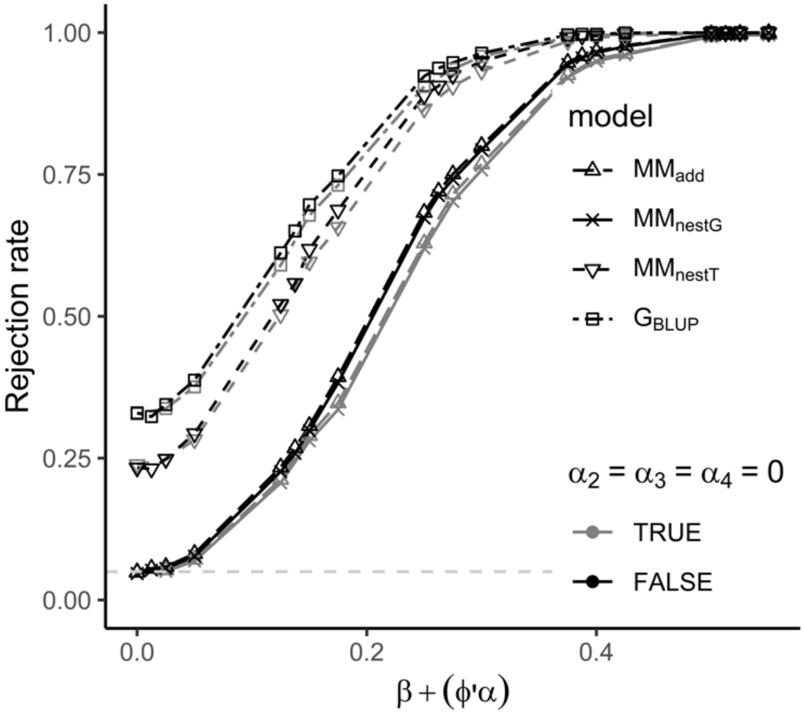

Figure 2: Power curves of competing genomic association models without trait covariates, over levels of the total SNP effects $\beta + (\phi'\alpha)$. The models MM_{tfix} and MM_{full} are not shown because they perform identically to MM_{add}. Grey lines and points represent cases in which none of traits 2, 3, or 4 had any effect on the extended phenotype and black lines and points represent cases in which at least one of these traits had effects greater than 0. Values are also averaged over the levels of q for a total of $N = 6000$ simulations per model. Individual test p-values $\leq .05$ were considered significant.

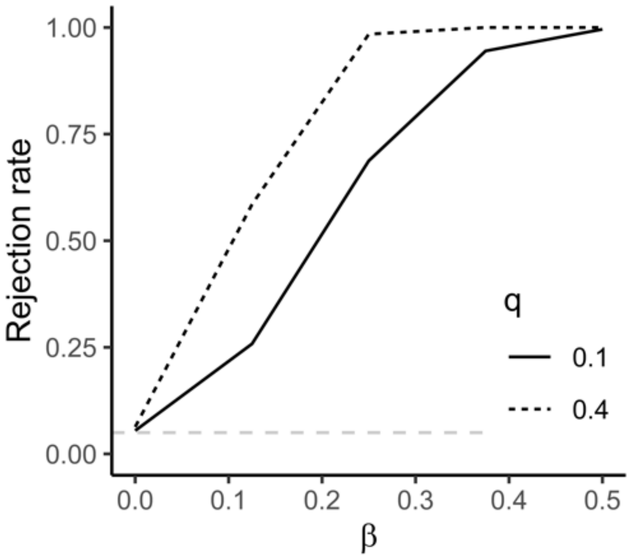

Figure 3: Effect of the minor allele frequency q on the power to detect genomic associations. The rejection rate of the MM$_{\text{add}}$ model without trait covariates, is shown as a function of the SNP effect β, averaged over all levels of ϕ and α, with a total $N = 90000$ simulations. All other mixed models responded similarly to changes in q but are not shown here for clarity.

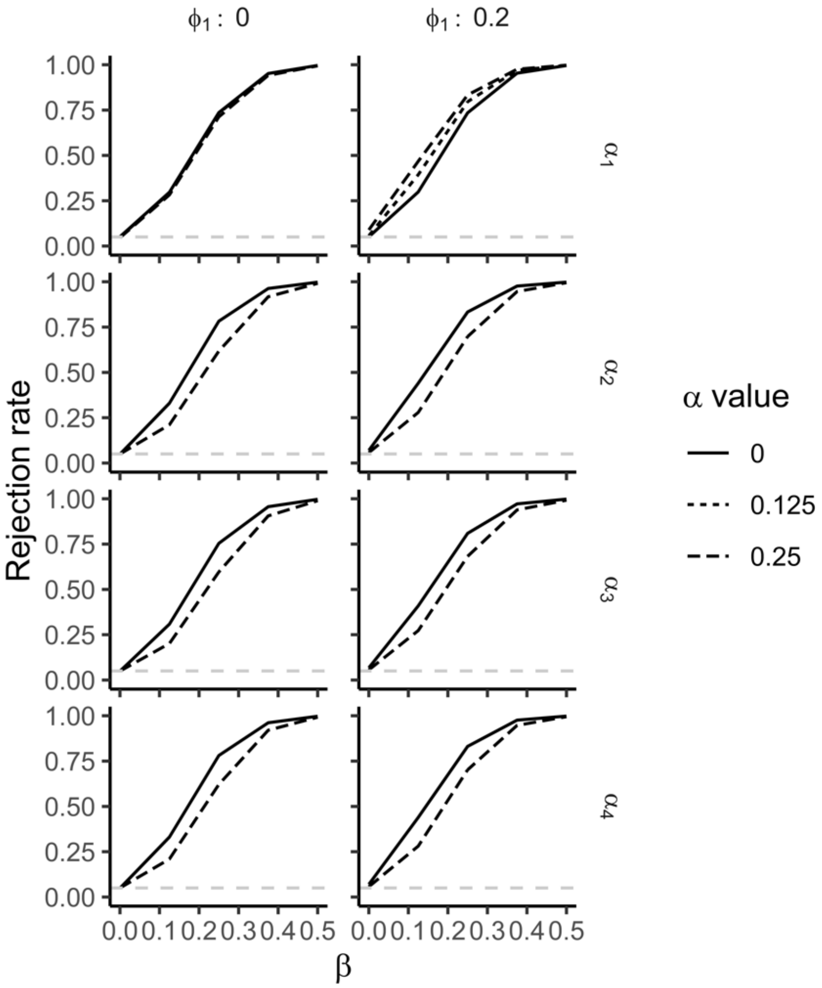

Figure 4: Impact of indirect genetic effects and phenotypic effects on detecting genomic associations, for models without trait covariates. The rejection rate of the $\mathrm{MM}_{\mathrm{add}}$ model is shown as a function of the SNP effect β for different values of α_i for each trait *i*, and ϕ_1, averaged across levels of minor allele frequency. Panels are divided into rows corresponding to the four different traits' effects and columns corresponding to the indirect genetic effect on Y through trait one. The different lines in a panel correspond to the tested levels of each trait effect α_i. Results are based on $N = 18000$ total simulations for each panel. All other mixed models responded similarly to changes in α and ϕ but are not shown here for clarity.

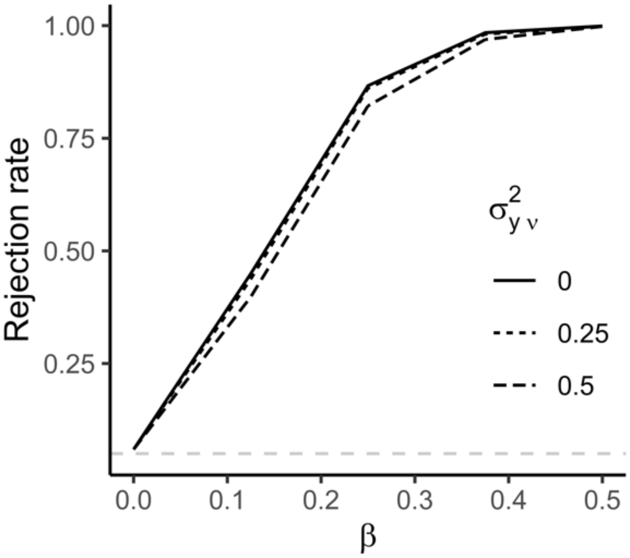

Figure 5: Impact of the magnitude of the random interaction between genetic and temporal factors ($\sigma_{y\nu}^2$) for the MM_{add} genomic association model without trait covariates. The line different values of $\sigma_{y\nu}^2$ are represented by the different line types. Results are averaged over all levels of α, ϕ, and q. Patterns in other mixed-effects models are similar but are excluded for visual clarity.

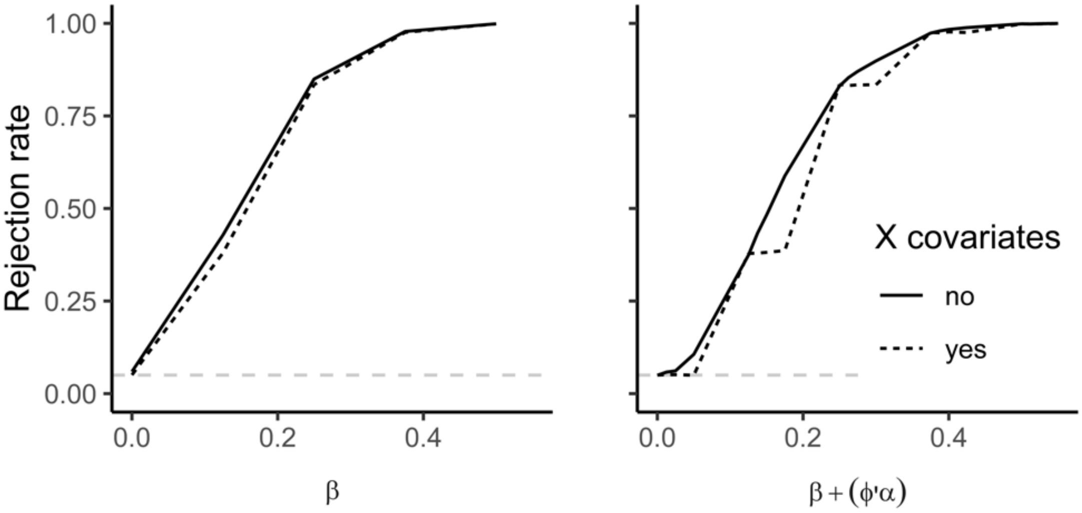

Figure 6: Impact of including X covariates in the MM$_{add}$ genomic association model. The left panel corresponds to the detection of parameter $\hat{\beta}$, given the true *indirect* effect β (x-axis), for models with and without covariates. The right panel corresponds to detection of $\hat{\beta}$, given the true *total* SNP effect $\beta + \phi'\alpha$. Solid lines represent the model fit without trait covariates and the dashed line represents the model including trait covariates. Results are averaged over all values of q. Patterns in other mixed-effects models are similar but are excluded for visual clarity.

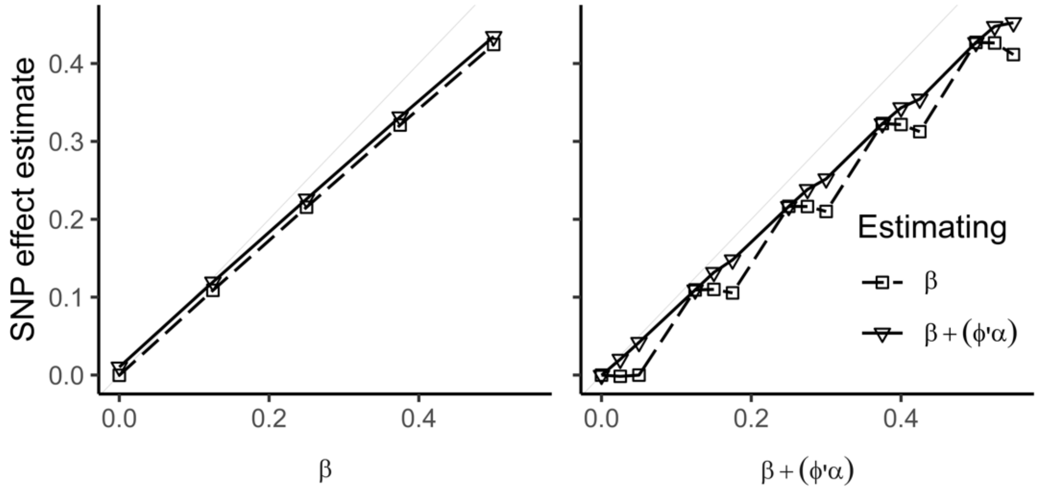

Figure S1: Estimated SNP effects of MM_{add} with and without trait covariates. Triangles and solid lines represent the version of MM_{add} without trait covariates and squares and solid lines represent the model that includes trait covariates. The y-axis represents the average effect estimated from the model while the x-axis represents the actual effect. The left panel shows the estimated effect vs. the true *direct* SNP effect and the right panel shows estimated effects vs. the true *total* SNP effects. The model with covariates estimates the *direct* effect, while the model without covariates estimates the total effect. Patterns in other mixed-effects models are similar but are excluded for visual clarity.

Chapter 4

remotePARTS: statistical analysis of very large spatial and spatiotemporal datasets

Authors: Clay J. Morrow, Anthony R. Ives

Abstract

1. Many spatiotemporal environmental datasets exhibit both temporal and spatial autocorrelation. Although statistical methods are available to account for temporal and spatial autocorrelation, these methods struggle to analyze the large remote-sensing datasets that consist of maps containing millions of pixels, with each pixel containing a time series of data.

2. PARTS (Partitioned Autoregressive Time Series) analysis can be used to conduct map-scale estimation and test hypotheses that are formulated as regressions. Here, we present remotePARTS, a software package for the R statistical programming language that contains the tools to conduct PARTS analyses. To demonstrate the applicability of PARTS to a variety of statistical and ecological problems, we conducted a set of simulation studies with the remotePARTS software.

3. We found that PARTS is a robust and accurate statistical approach for testing a variety of hypotheses. remotePARTS performed well in testing hypotheses about the effects of spatial variables, temporal variables, and spatiotemporal variables on spatial and spatiotemporal responses.

4. These results demonstrate that remotePARTS solves many of the challenges of using big spatiotemporal data to understand ecological, biogeographical, and environmental problems at global scales.

Introduction

Many environmental problems involve time and space. How does a species use different habitat types, and how does habitat use change over decades? Are fires becoming more prevalent or larger in some regions and not others? Are changes in plant phenology, driven by increasing global temperatures, more pronounced in some regions, and are these phenological changes increasing through time? These example questions all illustrate the importance of understanding spatiotemporal systems from a statistical perspective. Ecologists and environmental scientists are constantly addressing such questions and answering them requires accounting for both spatial and temporal autocorrelation. Tobler's first law of geography (Tobler 1970) states that nearby entities are more similar than distant ones. This is often true not only in space, but also in time: nearby locations are exposed to similar environmental conditions and those conditions tend to change slowly over time. Methods that fail to account for spatiotemporal autocorrelation can both falsely identify patterns that do not exist and overlook patterns that do (Cressie; Box et al. 2015).

Many of the questions that researchers ask using spatiotemporal datasets can be formulated as a regression problem with a response (e.g., habitat types, plant phenology) and multiple explanatory variables (e.g., time, latitude, land-cover classification). A simple and flexible regression model that contains spatiotemporal autocorrelation is

$$y_i(t) = \boldsymbol{X_i}(t)B_i + \varepsilon_i(t) \qquad \text{(Eq. 1)}$$

$$\varepsilon_i(t) = \rho_i \varepsilon_i(t-1) + \delta_i(t)$$

$$\delta_i(t) \sim N\big(0, \sigma^2 \Sigma(\boldsymbol{D})\big)$$

where $y_i(t)$ is the response variable for location i ($i = 1,\ldots,n$) at time t ($t = 1,\ldots,T$). We assume there are *k* explanatory variables contained in the 1 × k vector $\boldsymbol{X}_i(t)$. These explanatory variables may change through time; they may differ among locations but be temporally unchanging; they may consist of zeros and ones that differ among locations to give categorical variables corresponding to temporally invariant contrasts among locations; or they may equal one to give an intercept. The random error $\varepsilon_i(t)$ is a temporal autoregressive process of order 1 (i.e., AR(1)) in which the innovations $\delta_i(t)$ are spatially autocorrelated innovations given by the covariance matrix $\sigma^2\Sigma(D)$. The covariance matrix contains the covariance between $\delta_i(t)$ and $\delta_j(t)$ from locations i and j that depends on the distance d_{ij} between them contained in the matrix $\boldsymbol{D}$.

The model in equation (1) is linear regression in which the response and explanatory variables can vary in both space and time, and the random error $\varepsilon_i(t)$ contains spatiotemporal autocorrelation. Thus, it has the flexibility and generality of multiple linear models used broadly outside the realm of spatiotemporal dynamics. Furthermore, classical statistical methods such as Generalized Least Squares (GLS), Maximum Likelihood (ML), and Restricted Maximum Likelihood (REML) can be used for model fitting, giving rise to parameter estimates and hypothesis tests. Nonetheless, in application to big data which are increasingly common in ecology and evolutionary biology, classical methods are not computationally feasible. They are limited by the need to invert the covariance matrix of $\varepsilon_i(t)$, whose computational burden scales with the cube of the number of elements it contains, $(n \times T)^3$. For even a small remote-sensing study, for example, there may be 100,000 pixels containing data for 30 years.

Inverting the resulting dense 3,000,000 × 3,000,000 matrices might take a lifetime of CPU hours with existing computer resources.

remotePARTS

PARTS (Partitioned Autoregressive Time Series) is a two-step approach to statistical inference for spatiotemporal datasets that can account for spatiotemporal autocorrelation (Ives et al 2021a). The first step consists of a time-series regression analysis which effectively collapses the temporal dimension into a single parameter of interest per pixel (e.g., a trend coefficient). The second step uses GLS to regress these parameter estimates onto temporally invariant explanatory variables that differ among locations. In this way, both spatial and temporal variation are incorporated into the model but calculated separately. Although this reduces the full spatiotemporal model to a spatial model, for large datasets this is still numerically challenging. PARTS addresses this problem by subsetting the spatial dataset into random partitions, estimating parameters from each partition, and performing a single test on the collection of results. As a consequence of partitioning, the computational burden for PARTS scales linearly with N. The statistical result making this possible is computing the covariance between the test statistics calculated from each partition so that an overall test can be computed (Ives et al. 2021, 2022).

Our R package, remotePARTS (Morrow and Ives 2021), provides the tools for implementing PARTS with any spatial or spatiotemporal dataset (Table 1). Two functions are provided for time-series analyses for the first step of PARTS; `fitCLS` and `fitAR`, respectively, use conditional least squares (CLS) and regression with AR(1) autocorrelated errors fit using REML. The companion functions fitCLS_map and `fitAR_map` apply these time-series methods to all pixels in a map. Users can also implement their own time-series analyses in place of those provided in remotePARTS. For the second step of PARTS, `fitGLS` performs a single GLS for the full dataset, whereas `fitGLS_partition` analyzes partitions that can be created with the function `sample_partitions`. In most applications to spatial data, the spatial autocorrelation should be fit with a "nugget" to allow for local (spatially uncorrelated) variation, which is estimated during fitting with `fitGLS` and `fitGLS_partition` (making these methods technically Estimated Generalized Least Squares, although we have dropped the "Estimated" as is commonly done). Spatial autocorrelation can be given different functional forms: `covar_exp` calculates exponential covariance; `covar_exppow` calculates covariance with an exponential-power function, `covar_taper` uses a tapered covariance function, and users can also create their own distance-based covariance functions. Parameters for spatial autocorrelation can either be obtained from the residuals of the time-series analyses using `fitCor` or fit during the spatial GLS using `fitGLS_opt`; the latter is necessary when performing analyses on purely spatial data. These seven functions provide users with access to the entirety of the PARTS method. The package also contains additional tools for more options, fine-scale control over methods, and additional functionality (Morrow 2022).

Relationship to other methods

Methods that can be used to analyze large spatiotemporal datasets have arisen both from time-series analyses and from spatial analyses. Methods developed to analyze multiple time series (e.g., Harvey 1989; Ives et al. 2003; Holmes et al. 2012; Tsay 2014) can be extended to the case of multiple time series on a map by specifying spatial correlations between them. Nonetheless, these methods are designed for data in which the temporal dimension (T) is large relative to the spatial dimension (n). In contrast, spatiotemporal methods arising from spatial methods such as kriging are better suited for data with large spatial dimension, such as pixels on a map. Numerous approximations have been developed to make it possible to fit equation (1) simultaneously in both temporal and spatial dimensions (Kang et al. 2010; Finley et al. 2012; Wikle et al. 2019). With existing R packages INLA (Krainski et al. 2019) and FRK (Zammit-Mangion and Cressie 2018), it is possible to analyze quite large datasets. As an extreme, the EUSTACE project aims to estimate daily weather data since 1850 for the globe at a resolution of 0.25 degrees, which involves estimating roughly 10^{11} values, although numerous simplifications, and lots of computing power, are needed (Rayner et al. 2020).

remotePARTS differs from other approaches for analyzing spatiotemporal data in both its primary goal and simplicity. The spatiotemporal methods arising from spatial statistics focus primarily on smoothing, interpolation, and extrapolation to points in space and time for which data have not been collected. An archetypal example is estimating the global distribution of CO2 concentrations using data consisting of 100,000 to 300,000-point samples per day from the NASA OCO2 satellite (Zammit-Mangion and Cressie 2021); the statistical problem is to interpolate across space and time from samples taken during repeated passes along a polar orbit that covers the globe roughly every 16 days. In contrast, remotePARTS is designed for regression problems such as whether the rate of greening (NDVI) inferred from satellite images over the last 30 years has been greater in one land-cover class than another. This question can be posed as a regression in the form of equation (2) by letting $y_i(t)$ be the annual average NDVI for year t in pixel i:

$$y_i(t) = b_{0i} + \ b_1 x_i + (\theta_0 + \theta_1 x_i)t + \varepsilon_i(t) \qquad \text{(Eq. 2)}$$

$$\varepsilon_i(t) = \rho_i \varepsilon_i(t-1) + \delta_i(t)$$

$$\delta_i(t) \sim N\big(0, \sigma^2 \Sigma(\boldsymbol{D})\big)$$

Here, $b_{0i}$is the fixed intercept for pixel i, b_1 is the systemic fixed effect land class 1, $\theta_0$is the fixed time trend (slope) of class 0, and θ_1 is the fixed time trend of class 1, independent of class 0 (i.e., slope of class 1 minus slope of class 0).The statistical test for whether greening is occurring more rapidly in land-cover class *x* = 1 is based on the coefficient θ_1. Because remotePARTS focuses only on the regression coefficients, it does not give predictions beyond those inferred from the estimates of the regression coefficients (e.g., that the rate of greening depends on θ_1, x_i).

The goal of only estimating regression coefficients simplifies the analyses for remotePARTS. To fit the model given by equation (2), it is necessary to estimate all parameters simultaneously for the entire dataset, and this requires assumptions about parameters other than θ_1. For example, NDVI is affected by precipitation, which is lower around 30 degrees latitude than either closer to the Equator or poles and is affected by numerous other variables such as elevation that have strong autocorrelation. Therefore, the intercept b_{0i} should not be treated as constant among all pixels, because b_{0i} itself is spatially autocorrelated in a way that cannot be accounted for by the spatiotemporal autocorrelation $\varepsilon_i(t)$. Similarly, the temporal autocorrelation in $\varepsilon_i(t)$, given by ρ_i, might differ among pixels (see Ives et al. 2021), making it necessary to incorporate spatial autocorrelation in the strength of temporal autocorrelation. remotePARTS greatly simplifies this problem by fitting time series for each pixel separately, thereby reducing the model in equation (2) to

$$y_i(t) = c_{0i} + c_{1i}t + \varepsilon_i(t) \qquad \text{(Eq. 3)}$$

$$\hat{c}_{1i} = \theta_0 + \theta_1 x_i + \gamma_i$$

$$\gamma_i \sim N\left(0, \sigma_\gamma^2 \Sigma_\gamma(\boldsymbol{D})\right)$$

where the spatial model is a regression of the coefficients from the pixel-level time-series analyses, $\hat{c}_{1i}$, against x_i. The costs of this approach are that (i) analyzing each time series separately as if they were independent does not leverage information from surrounding pixels to give better (e.g., true maximum likelihood) estimates, and (ii) information about the spatiotemporal dynamics is "thrown away" because only one parameter from the time-series analyses, $\hat{c}_{1i}$, is retained. The advantages of this approach, however, come from not having to specify the full spatiotemporal model, which makes remotePARTS robust against misspecification of the full model and computationally easier.

Simulation study of remotePARTS

We performed six simulation studies to investigate the performance of remotePARTS (Tables 2, 3). Four studies (Table 2; i, iv, v, Table 3; vi) simulated data with the same model used to fit the data, thereby giving information about the accuracy of the parameter estimators. Two studies (ii, iii) simulated data with a model different from that used to fit the data in order to investigate the robustness of remotePARTS to model misspecification. Three studies (i-iii) addressed only spatial data, while three studies (iv-vi) addressed spatiotemporal data. Although remotePARTS was designed primarily for spatiotemporal datasets, the studies using only spatial data both demonstrate its ability to analyze spatial data and give useful illustrations of its performance characteristics. The sixth study (Table 3) compared the performance of remotePARTS against a "gold standard" statistical model identical to the simulation model and fit with REML. We present the simulation studies along with their results below, building from the simplest to most complex, and at each step we only describe changes from the previous study. All analyses of simulated data used partitions of 2000 pixels each during Step 3 of the PARTS analysis – except where explicitly noted otherwise.

i. Spatial data

To investigate the effects of spatial extent and spatial autocorrelation on the performance of remotePARTS (Table 2, case i), we simulated data on a square grid containing 104^2, 144^2, 200^2, or 280^2 locations (pixels) consisting of two classes ($x_i = 0$ or 1) in a 4×4 checker-board pattern (Fig. 1). Spatial variation given by the random error δ_i was Gaussian, with variance $\sigma^2 = 1$ and correlations among locations i and j given by $exp(-d_{ij}/r)$ (i.e., using `covar_exp`) where d_{ij} is the distance between i and j, and

r is the "range" parameter that scales the extent of spatial autocorrelation. Distances d_{ij} were scaled to make the maximum distance between locations equal to one. When varying grid size, we used $r = 0.05$ and $\theta_0 = \theta_1 = 0$, while for the grid with 104^2 locations, we performed simulations with $r = 0$, 0.05, or 0.25 and $\theta_1 = 0.2$. When fitting simulation data, used a fixed nugget of 0.1.

In the simulations, the estimates for the effects of the classes $x_i = 0$ and 1 on $y_i(\theta_0 = 0$ and $\theta_1 = 0.2)$ were unbiased (Table 2, case i). With increasing spatial extent and decreasing spatial autocorrelation, the estimates of the coefficients became more precise (lower standard deviations). Finally, for the case of the grid with 104^2 locations, we performed the simulations 500 times to make it possible to assess type I error rates: as hoped for, in roughly 5% of the simulations, the hypotheses that $\theta_0 = 0$ and $\theta_1 = 0.2$ were rejected at the significance level of alpha = 0.05.

ii. Spatial data with non-Gaussian errors

Case ii involved simulations similar to case i, except data were simulated in which the random errors were given by a *t*-distribution with 3 degrees of freedom. The t_3 distribution has fatter tails (positive kurtosis) than a normal distribution. Applying the same estimation model as in case i for a grid with 104^2 locations, there was no bias in the estimates, and the precision was similar to that when simulated with a Gaussian distribution (case i). Furthermore, type I error rates were not inflated, showing that type I error rates are robust to non-Gaussian random errors.

iii. Spatial data with latent spatial autocorrelation

A common challenge when analyzing large spatial datasets is the confounding effects of unmeasured variables. We simulated spatial data with a latent variable z_i as a 2-dimensional sine wave,

$$z_i = \sin\left(\left(\frac{2\pi}{N} + \frac{\pi}{4}\right)(k + l)\right) \qquad \text{(Eq. 4)}$$

where k and l are the vertical and horizontal positions of location i, and N is the number of cycles on the grid (Fig. 2). When variation in the latent variable z was either coarser (Fig. 2, $N = 1$) or finer (Fig. 2, $N = 9$) than the spatial variation in classes x, the model was able to estimate the coefficients θ_0 and θ_1 with little bias and precision similar to that found without the latent variable (Table 2, compare case iii with i and ii). However, when scale of variation in the latent variable z was similar to that for classes x (Fig. 2, $N = 4$), estimates of θ_0 and θ_1 were biased. This shows the unsurprising result that if the variable under analysis covaries with an unmeasured latent variable, the estimates for the effects of the measured variable will be confounded.

iv. Spatiotemporal data

To simulate spatiotemporal data, we assumed that classes x_i affect not only the mean value of $y_i(t)$ at location i, but also the change in $y_i(t)$ as a linear function of time. We set the goal of the analysis to estimate the time trends associated with classes $x = 0$ and 1, coefficients θ_0 and θ_1 (Table 2 case iv). We simulated data for $T = 30$ time points on a grid with 104^2 points, with the random error given by equation (1) in which there is both autocorrelation through time (ρ_i= 0.4) and in space ($\sigma^2\Sigma(\boldsymbol{D}, r)$). We estimated θ_0 and θ_1 using the full remotePARTS two-part procedure, estimating r from the residuals of the time-series analyses using `fitCor` and the nugget during the spatial analysis using `fitGLS_partition`.

Estimates of the time trends $\theta_0 = 0$ and $\theta_1 = \frac{1}{30}$ were unbiased (Table 2, case iv), and precision decreased with increasing range of spatial autocorrelation (r = 0, 0.05, and 0.25). Nonetheless, there was no apparent inflation of type I errors. Thus, even though remotePARTS reduced the temporal dimension of the spatiotemporal data for the spatial analysis, estimation was still unbiased and type I errors appropriate.

v. Spatiotemporal data with latent spatiotemporal autocorrelation

In case v we added an additional spatiotemporal driver $u_i(t)$ to the simulation model, with the goal of assessing the ability of remotePARTS to detect associations between spatiotemporal variables. We assumed that $u_i(t)$ was a spatiotemporal random variable having the same form as $\varepsilon_i(t)$ (Table 2, case v) but with different temporal (ρ_u = 0 or 0.4) and spatial autocorrelation (r_u = 0 or 0.25). Estimates of spatially autocorrelated effects of $u(t)$ on y through time $\theta_0 = 0$ and $\theta_1 = 1$ were unbiased across all combinations of ρ_u and r_u and type I error rates were not inflated. These results show that remotePARTS can test hypotheses about spatiotemporal drivers of trends.

vi. Comparison with full spatiotemporal GLMM model

The two-step strategy of remotePARTS, performing time-series analyses on separate time series and then analyzing coefficients from the time series with a spatial model, discards information. Therefore, remotePARTS might be expected to have low statistical power to detect associations with explanatory variables inferred from regression coefficients. Because we expected this loss of information to have the greatest effect on statistical power for small datasets, and to speed computations, we performed 1,000 simulations on an 8×8 grid for 30 time points using the model given by equation (2). We then fit the simulated datasets with remotePARTS using `fitGLS`, rather than `fitGLS_partition`, because the small dataset did not need to be partitioned. For comparison, we fit the same datasets with a GLMM having exactly the same form as the model used to simulate the datasets; for fitting, we modified the pglmm function in the R package *phyr* (Li et al. 2020) to include the spatiotemporal random error $\varepsilon_i(t)$ (Ives et al. 2010) and used REML fitting.

remotePARTS and the GLMM showed almost identical results, with both showing little bias except for large simulation values of θ_1 (Table 3). The type I error rates (when the true value of θ_1 = 0) were slightly low for both methods, implying that the approximated *P*-values given by the methods were slightly too high. Surprisingly, the power of remotePARTS (the ability to reject the null hypothesis that θ_1 = 0 when in fact it is false) was similar between methods, with both methods rejecting the null hypothesis in ≈92% of simulated datasets when $\theta_1 = 0.75$.

Discussion

remotePARTS provides a robust method for performing regression analyses using very large spatial and spatiotemporal datasets. The robustness, flexibility, and computational speed of the method comes from focusing on the regression problem. For regression, it is possible to perform spatiotemporal analyses by first separately fitting time series and analyzing the fitted time-series parameters in a spatial model. Furthermore, the spatial analyses can be partitioned, with test statistics computed separately from all partitions then being stitched together using information about their covariance. In comparison with a full spatiotemporal GLMM, remotePARTS has good statistical power to identify statistically significant coefficients, even for small datasets. Although remotePARTS is not designed to predict values of the response variable and therefore cannot be used for smoothing, interpolation, or extrapolation, it nonetheless makes it possible to investigate relationships among variables in very large spatiotemporal datasets.

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Tables

Table 2: Main functions contained within remotePARTS, separated into the two steps for analyzing spatiotemporal data.

	Analysis	remotePARTS function	Description
Step 1	Time-series analyses	`fitCLS, fitAR`	Fit time-series regression to a location and return estimate of time trend coefficient
	Multiple time-series analyses	`fitCLS_map,` `fitAR_map`	
	Estimate spatial parameters (from residuals)	`fitCor`	Find ML estimates of spatial parameters by comparing residual correlations with distances among points
Step 2	Spatial analyses (small datasets)	`fitGLS`	Fit GLS to data, given covariance parameters
	Spatial analyses using partitions (large datasets)	`fitGLS_partition`	Fit GLS to partitioned data, given covariance parameters
	Generate random partitions	`sample_partitions`	Produce a random $m \times p$ partition matrix containing indices to locations in an *n*-length dataset

	Spatial covariance	`covar_exp,`
		`covar_exppow,`
		`covar_taper`
			Produces a covariance matrix from a distance matrix under exponential, power-exponential, or tapered covariance functions

	Combined covariance estimation and GLS	`fitGLS_op`	Estimate spatial parameters from data rather than residuals, fit covariance matrix, and fit GLS. Primarily used as alternate method for spatial parameter estimation in certain contexts

Table 2: Simulation studies for five cases to illustrate the performance of remotePARTS. Both simulation and fitting model are given, with part of the fitting model denoted by " when it is the same as the simulation model. Parameter values which differed among simulations are given. Bias is given by the average difference between parameter estimates and the true value, and $P(\theta_0)$ and $P(\theta_1)$ give the rejection rates of the null hypotheses $\hat{\theta}_0 = \theta_0$ and $\hat{\theta}_1 = \theta_1$, respectively, under the significance level of alpha = 0.05.

case	simulation model	fitted model	parameters	No. sims	$\hat{\theta}_0 - \theta_0$	$\hat{\theta}_1 - \theta_1$	$P(\theta_0)$	$P(\theta_1)$
i	$y_i = \theta_0 + \theta_1 x + \delta_i$	"	n = 104^2	200	0.014	0.026	0.035	0.050
	$\delta_i \sim N\left(0, \sigma^2 \mathbf{\Sigma}(D, r)\right)$	"	144^2	200	0.035	0.023	0.070	0.045
			200^2	200	0.022	0.023	0.045	0.045
			280^2	200	0.020	0.015	0.040	0.030
			r = 0	500	0.000	-0.001	0.046	1.000
			0.05	500	0.000	0.002	0.048	1.000
			0.25	500	0.002	0.002	0.048	1.000
ii[6]	$y_i = \theta_0 + \theta_1 x_i + \delta_i$	"	r = 0	1000	0.000	0.001	0.029	1.000
	$\delta_i \sim T_3\left(0, \sigma^2 \mathbf{\Sigma}(D, r)\right)$	$\delta_i \sim N\left(0, \sigma^2 \mathbf{\Sigma}(\mathrm{D}, \mathrm{r})\right)$	0.05	500	-0.001	0.001	0.028	1.000
			0.25	500	0.000	0.000	0.028	1.000

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[6] In case *ii*, δ_i in the simulated data follows a student's t-distribution with 3 degrees of freedom.

iii	$y_i = \theta_0 + \theta_1 x_i + z_i + \delta_i$	$y_i = \theta_0 + \theta_1 x_i + \delta_i$	N = 1	200	-0.051	0.101	1.000	1.000
	$\delta_i \sim N\big(0, \sigma^2 \mathbf{\Sigma}(D, r)\big)$	"	4	200	0.239	-0.503	1.000	1.000
			9	200	0.009	-0.028	0.030	1.000
iv	$y_i(t) = b_0 + b_1 x_i + (\theta_0 + \theta_1 x_i)t + \varepsilon_i(t)$	"	r = 0	200	0.000	0.000	0.055	1.000
	$\varepsilon_i(t) = \rho\varepsilon_i(t-1) + \delta_i(t)$	"	0.05	200	0.000	0.000	0.060	1.000
	$\delta_i(t) \sim N\big(0, \sigma^2 \mathbf{\Sigma}(D, r)\big)$	"	0.25	200	0.000	0.000	0.070	1.000
v	$y_i(t) = b_0 + b_1 x_i + (c_0 + c_1 x_i)t + (\theta_0 + \theta_1)u_i(t) + \varepsilon(t)$	"	r_u = 0, ρ_u = 0	200	0.000	0.065	0.000	1.000
	$\varepsilon_i(t) = \rho\varepsilon_i(t-1) + \delta_i(t)$	"	0, 0.4	200	0.000	0.070	0.000	1.000
	$\delta_i(t) \sim N\big(0, \sigma^2 \mathbf{\Sigma}(D, r)\big)$	"	0.25, 0	200	0.000	0.065	0.000	1.000
	$u_i(t) = \rho_u u_i(t-1) + \alpha_i(t)$	"	0.25, 0.4	200	0.000	0.030	0.000	1.000
	$\alpha_i(t) \sim N\big(0, \sigma^2 \mathbf{\Sigma}(D, r_u)\big)$	"						

Table 3: Simulation *vi*, Comparison between remotePARTS and a GLMM model. Columns give the average estimates from 1000 simulations and P(θ_1), the proportion of simulations in which the null hypothesis $\theta_1 = 0$ was rejected at the significance level of alpha = 0.05.

simulated θ_1	remotePARTS estimate	GLMM estimate	remotePARTS P(θ_1)	GLMM P(θ_1)
0	-0.001	-0.002	0.042	0.033
0.25	0.239	0.242	0.172	0.157
0.5	0.492	0.494	0.612	0.612
0.75	0.736	0.736	0.916	0.919

Figures

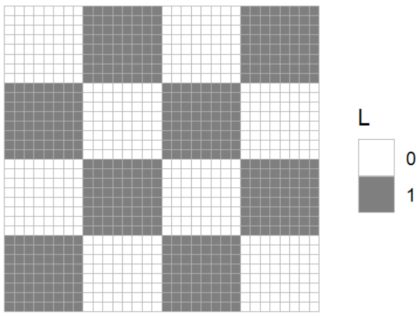

Figure 1: Distributional pattern of land-cover classes L.

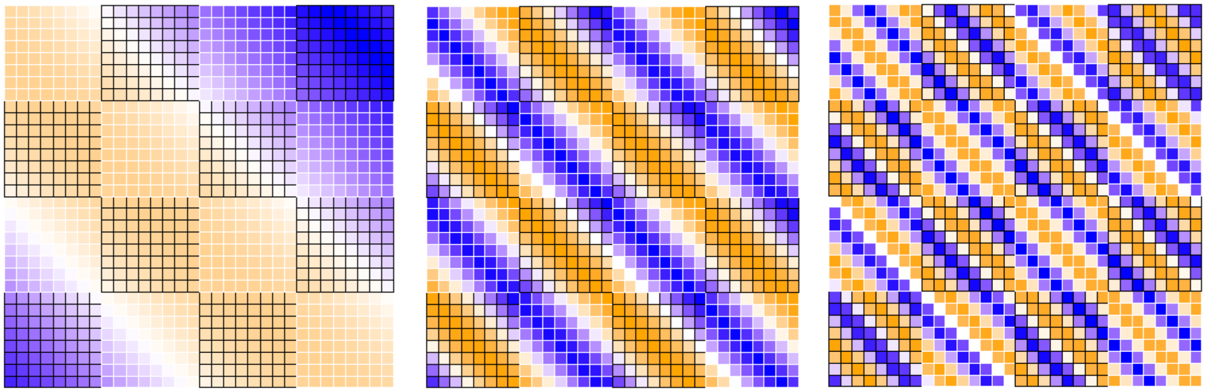

Figure 2: Fixed spatial variation given by 2D sin wave. The wave was generated with 1 (left), 4 (middle) or 9 (right) cycles per map.

Thesis conclusions

Understanding variation is key for studying ecological systems. Intraspecific variation, in plants especially, can shape the environment within which a species exists. Foundation plant species that are intimately linked with communities of associated insects can influence the structure and composition of those communities through genetic variation in key phenotypes. Intraspecific variation also exhibits patterns of intercorrelation that are predictable, with fast-growing individuals generally exhibiting lower defensive properties and higher rates of herbivory, particularly concerning generalist herbivores. Intraspecific variation, and ecological variation generally, is structured according to genetic and environmental similarity. Ecological and environmental variation is also structured through space and time, with points close together in time being more similar than those far apart. Similarly, nearby locations tend to be more similar than distant locations in space. Therefore, the tools that researchers use need to account for this structure. Ecologists should consider genetic, phenotypic, temporal, and spatial variation in the systems they study, whenever possible. The key findings of my research are as follows.

1. **Chapter 1: Intraspecific variation in plant economic traits predicts trembling aspen resistance to a generalist insect herbivore.** Intraspecific patterns of trait expression in aspen aligned well with both the global leaf economics spectrum paradigm and with growth-defense tradeoff theory. Fast-growing, resource-acquisitive aspen genotypes tended to have high concentrations of nitrogen, high SLA, and low concentrations of defensive compounds compared to slower-growing, resource conservative genotypes.

Resource-conservative genotypes also had better defense outcomes on average: *Lymantria dispar* larvae performed poorly on conservative genotypes relative to acquisitive genotypes and also chose to feed on conservative leaves at lower rates than acquisitive leaves.

2. **Chapter 2: Genomic variation in aspen underlies variation in insect communities.** Intraspecific aspen variation, driven by genetic variation, was significantly associated with insect communities in a number of ways. All measured aspen traits were highly genetically heritable and influenced the composition and structure of associated insect communities. Composition of insect communities was itself heritable, indicating that genotypic differences among aspen is a significant driver. Using the novel genomic association models tested in Chapter 3, fifteen unique genes were also identified as being associated with community composition. Further evidence suggests that even more genes are truly associated with community metrics but remain undetectable with the methods used, indicating that expression of community phenotype is likely highly polygenic in nature.
3. **Chapter 3: Genomic models for detecting extended phenotype associations: a simulation study for detecting community genetics effects.** Mixed-effects genomic association analyses performed much better than traditional methods for detecting associations with plant phenotypes. The commonly used two-part BLUP model, against which mixed models were compared, exhibited Type I error rates that render it invalid as a statistical tool. The mixed models, on the other hand, exhibited controlled Type I errors when

variance structure was properly specified. These models also performed well; they were able to detect relatively small effects of a causal SNP and estimated the effects accurately and precisely. The simulation studies revealed that a properly parameterized mixed effects model can be applied to real biological systems – to detect genomic associations with extended phenotypes – with confidence.

4. **Chapter 4: remotePARTS: a robust toolset for statistical analysis of spatial and spatiotemporal datasets.** The statistical package I developed, that implements the PARTS method for spatiotemporal trend analyses, performed well under simulations designed to test its limits. The method accurately tests map-level hypotheses in both spatial and spatiotemporal datasets under various map sizes, magnitudes of spatial autocorrelation, and temporal trends among different land-cover classes. The model also performs well when the normality assumption of linear regression is violated. The PARTS method only experienced inflated Type I error rates in the presence of confounding latent variables. The method performed as well as a gold-standard model of the simulated system. Collectively, these results indicate that remotePARTS is a robust tool for detecting spatial and spatiotemporal trends while appropriately accounting for correlation structure in the data.