

Running Title: Genotype-species networks

Title: Genotypic variation in foundation species generates network structure that may drive community dynamics and evolution

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47 **ABSTRACT**

48 Although genetics in a single species is known to impact whole communities,
49 little is known about how genetic variation influences species interaction networks in
50 complex ecosystems. Here, we use a network perspective to analyze interactions in a
51 community of arthropods living on replicated genotypes (clones) of a foundation tree
52 species, *Populus angustifolia* James (narrowleaf cottonwood), in a long-term, common
53 garden experiment. We also present a simulation experiment designed to investigate how
54 variation among individual tree genotypes affects network structure. Three findings
55 emerged. 1) The empirical “genotype-species network” exhibited non-random network
56 structure. 2) Even using a conservative null-model, significant co-occurrence patterns
57 were detected in association with individual tree genotypes. 3) Simulated “genotype-
58 species” networks displayed increased structure with increasing community-level
59 genotypic effect. These results demonstrate that genetic variation in a single species
60 contributes to the structure of ecological interaction networks, which could influence
61 ecological dynamics (e.g., assembly and stability) and evolution in a community context.

63 **INTRODUCTION**

64 The evolution of species interactions in complex communities is a central
65 question at the interface of ecology and evolutionary biology and in understanding
66 diverse theories of community structure ranging from random and neutral, to highly co-
67 evolved (Clements 1916; Gleason 1926; Hubbell 2006; Shuster *et al.* 2006; Ricklefs
68 2008). Indirect effects in interaction networks have been theoretically (MacArthur 1955;
69 May 1972; Allesina *et al.* 2011) and empirically (Bondavalli & Ulanowicz 1999; Bastolla
70 *et al.* 2009; Bascompte *et al.* 2010) shown to influence the structure and dynamics of

communities and ecosystems. For example, Bastolla *et al.* (2009) demonstrated decreased interspecific competition and increased co-existence of species in mutualistic networks. Network ecology has provided a means to approach the complexities of multi-species interactions, incorporating indirect effects, with some studies suggesting that evolutionary processes may lead to structural differences in mutualistic and trophic networks (Thébault & Fontaine 2011). In addition, phylogenetic analyses have revealed that shared evolutionary history contributes to ecological network structure (Rafferty and Ives 2013). Collectively, these studies point to the importance of evolutionary processes in determining network structure and the potential for network structure to impact ecological dynamics.

The field of community genetics studies the genetic basis for interactions in complex communities primarily focusing on foundation species (i.e. species that define much of the structure of a community by creating locally stable conditions; Ellison *et al.* 2005). Community genetics research has demonstrated how genetic variation in a single species can determine the structure of whole communities and ecosystem processes (Wimp *et al.* 2005; Whitham *et al.* 2006; Crutsinger *et al.* 2006; Rowntree *et al.* 2011; Gugerli *et al.* 2013). This approach of focusing on species that are “central” (*sensu* Borrett 2013) in ecosystems (i.e., interacting with a large proportion of the species in a community) has provided a framework to address genetically based evolutionary questions in complex ecosystems (Whitham *et al.* 2006).

In this study, we merge network ecology and community genetics to examine how genetic variation in a foundation species influences the structure of ecological networks in complex communities. Specifically, we examine the networks of foundation species

genotypes interacting with associated species, which we refer to as “genotype-species”
networks. This approach permits the evaluation of interaction network structure within an
evolutionary framework by including the intraspecific, heritable variation via the
foundation species’ genotypes. We hypothesize that genotypic variation in foundation
species produces patterns in the structure of interactions among species. More
specifically, we hypothesize that genotype-species bipartite networks will exhibit
structure similar to species-species networks. In addition, we propose that, since species
interactions tend to occur locally, this structure will determine co-occurrences among
species and alter interspecific interactions by modulating the frequency that species are in
close physical proximity. To test these hypotheses, we first examine the structure of an
empirical network of interactions between narrowleaf cottonwood (*P. angustifolia* James)
and its associated canopy arthropod community using data from a long-term (20 year),
common garden experiment with trees of known genetic identity. We use a conservative,
null model approach to test for significant structural patterns in this “real” genotype-
species network. Second, we conduct a simulation experiment using a community
genetics model where we vary the intensity of the genotypic effect of a foundation
species on its associated community to test for its effect on genotype-species interaction
network structure and the ensuing effects on the associated species interaction structure
that arise from shifting co-occurrence patterns. Our inclusion of heritable, intraspecific
variation in the study of network architecture provides the potential for understanding
species interactions comprising complex communities within an evolutionary context.

METHODS

Empirical network analysis

A network of interactions between canopy arthropod species and genotypes of *Populus angustifolia* James (narrowleaf cottonwood) were collected from a common garden following the methods of Keith *et al.* (2010). Narrowleaf cottonwood is a foundation species (Ellison *et al.* 2005) of western riparian forests supporting a rich community of associated species (Whitham *et al.* 2006). In 1991 replicate clones of genotypes from the Weber River Watershed (Utah, U.S.A.) were randomly planted in a common environment (Ogden Utah, U.S.A., latitude = 41.248146, longitude = -111.999830, elevation = 1302 m) to both minimize and randomize the effect of local environmental variation with respect to genotype (Martinsen *et al.* 2001). Surveys of four replicate trees for each of 10 genotypes (n = 40 trees) were conducted in August of 2008 using timed sampling of similarly sized branches. Previous analyses have demonstrated community compositional effects of tree genotype (Keith *et al.* 2010). We use a bipartite network model, which examines networks where interactions typically occur between two main groups in a network (e.g. plants and pollinators). Using bipartite networks provides a set of analytical tools and hypotheses developed by the studies of plant-mutualist (Bascompte 2010), plant-herbivore (Thébault & Fontaine 2010) and other species-species networks that we apply to a foundation tree, *Populus angustifolia*, and its arthropod community. As plant-herbivore bipartite networks are typically asymmetric (Thébault & Fontaine 2010), and because the genotypes were planted for the experiment, rather than through natural processes of establishment and selection by the local communities, we interpret these connections as directed effects of the genotype on the associated community. In addition, although these species comprise multiple trophic

levels from herbivores to predators, all of these species were observed in close contact with the tree, typically using it as a resource. Hereafter, we use network terminology to refer to genotypes of narrowleaf cottonwood, as well as species in the network, as “nodes” and their connections as “edges” (Wasserman & Faust 1994) comprising “genotype-species” networks.

We then analyzed the structure of this empirical genotype-species network. As no previous analyses have been conducted on genotype-species networks, we chose three network metrics (modularity, nestedness and centralization) and a measure of species co-occurrence (C-Score; Stone & Roberts 1990). These network metrics characterize the structure of the entire network across all nodes and edges, and each measures a different aspect of the network structure. Modularity is a measurement of the degree to which the network is comprised of groups of nodes that are relatively more connected to each other, and for our analyses we used the method developed by Newman (2006). Nestedness was calculated for the observed network using the nestedness temperature metric developed by Atmar and Patterson (1993, see also Santamaría & Rodríguez-Gironés 2006), which measures the degree to which species tend to interact with subsets of the community across “parts” of the network. We used Freeman’s (1979) centralization to compare how each network varied in tendency of one or a few nodes to dominate the edges in the network. We measured the co-occurrence patterns among the associated community using Stone and Robert’s (1990) C-score, which is the number of “checkerboard units” averaged across all pairs of species, which provides an average measure of species associations. The checkerboard unit is calculated as $(r_i - S_{ij})(r_j - S_{ij})$, where r is the total number of occurrences for a given species and S is the total number of times a species

pair occurs, and the C-score has been shown to have robust statistical properties (Gotelli 2001).

We tested for the significance of all network statistics and the C-score using a conservative null-model based randomization method. We chose this null model because previous work has demonstrated the importance of controlling for the total abundances of species in plant-mutualistic bipartite networks (Blüthgen 2010). More specific to our data, this null model constrains the matrices to maintain the marginal totals, meaning the total abundance of the community across all species for a given genotype or across all genotypes for a given species. After an initial series of 100 “burn-in” permutations of the original matrix, a set of 5000 randomizations was generated and used to test the significance of the all metrics. For each metric we calculated a non-directional p-value as the proportion of null model metrics that were equal to or more extreme than the original (i.e. “observed”) metric, and because this approach produces an empirical distribution it avoids the need to make assumptions of the distribution for our statistics of interest. We also calculated a standardized score as $z = (x - \mu)/\sigma$, where x is the observed metric and μ and σ are the mean and standard deviation for the null simulation metrics, respectively. Note that in the co-occurrence literature the standardized C-score is typically referred to as a standardized effect size (SES).

Simulating genotypic effects on network structure and co-occurrence patterns

As the structure of the empirical network could arise from factors other than phenotypic variation among foundation species genotypes, we conducted a simulation experiment testing the effect of genotype on genotype-species network structure. We used the community genetics simulation method previously developed in Shuster *et al.*

(2006). Briefly, this method uses a combination of both individual-based and mass-action modeling approaches. It starts by creating a population of individuals assigned a genotypic value (i.e. genotypes). Each genotype is comprised of multiple replicate individuals (e.g. clones randomly planted in a common garden), which are assigned phenotypes as a single numeric value for each individual sampled from a uniform distribution. This population represents the foundation species. Next, a set of species representing the associated community was assigned an average genotypic value that was then mapped to a numerical phenotypic value using an additive, bi-allelic genetic system. At each step of genotype-phenotype mapping, variance was introduced through random draws from a uniform distribution, simulating the introduction of phenotypic variance arising from non-genetically based “environmental” variation. Last, mass-action methods were used to determine the equilibrium population value for each associated species given the phenotypic values for each foundation species individual and the carrying capacity of each associated community member (Supplementary Materials).

We used this method to conduct simulations of communities with different levels of foundation species’ genotypic effect on the community. To do this, we adjusted the coefficient determining the foundation species’ genotypic effect for each species in the associated community, which modifies the fidelity of the mapping of a tree genotype to phenotype to an arthropod species by varying the power of the co-efficient per the method of Shuster *et al.* (2006; Supplementary Materials). In addition, to explore the impact of variation in associated species abundances, we produced two sets of simulations, one ($n = 80$) with a carrying capacity (K) of 100 individuals (i.e. even species abundances), and a second set ($n = 80$) with carrying capacities for the dependent

species selected from a Poisson distribution ($\lambda = 5$), ranging from $K = 100$ to $K = 5$ (i.e. un-even species abundances). This distribution was chosen for its similarity to the highly skewed, “un-even” distribution of species total abundances commonly observed in ecological communities (Blüthgen et al. 2008). As intended the diversities of the even communities (Shannon’s $H = 3.25 \pm 0.05$ SD) were greater than the un-even communities (Shannon’s $H = 2.25 \pm 0.15$ SD), which were very similar to the diversity of the empirical canopy arthropod community (Shannon’s $H = 2.15$). The simulated communities were generated using the same initial phenotypes for both the “foundation species” individuals ($n = 100$; 10 individuals for each of 10 genotypes) and the “associated species” (25 total). To test and compare the effect of genotype on the four metrics, we used correlation analysis employing Kendall’s τ as our correlation coefficient to capture non-linear monotonic relationships.

Simulation and analytical software

All simulations and analyses were conducted in R version 3.0.2 (R Core Team 2014). Simulations were conducted using the *ComGenR* package (<https://github.com/CommunityGeneticsAnalyses/ComGenR>), and simulation scripts are publically available (https://github.com/MKLaui/cg_simulations). Non-metric multidimensional scaling (NMDS) ordination and nestedness tests were conducted with *vegan*, and networks were plotted using *bipartite*.

RESULTS

Supporting our hypothesis that a genotype-species network would display non-random structure, in the field we found significant structure and co-occurrence patterns

among associated species in the empirical network. The cottonwood foundation species genotype and canopy arthropod network (Fig. 1) had levels of modularity (observed = 0.20, $z=3.82$, $P = 0.038$), nestedness (observed = 38.17, $z = -3.00$, $P = 0.003$), centralization (observed = 0.31, $z = 3.90$, $P = 0.003$) and C-Score (observed = 0.47, $z = 1.95$, $P = 0.025$) that all differed from the null model based expectation. Modularity, centralization and C-Score all showed greater structure than the null expectation (i.e. more modules, greater centralization and more checkerboard units); however, the observed nestedness was lower than the null model.

In line with previous simulations of community level genetic effects, our simulated communities displayed genetic impacts that were similar to the results of Shuster *et al.* (2006) for both the even and un-even simulations. The simulated trees differed in their individual phenotypic trait values (Fig. 2A). Consequently, the community level effects of this variation also led to differences in community composition among genotypes (Fig. 2B).

As with the empirical network patterns, we observed genotypic effects in our simulations that supported the hypothesis of a genetic basis to network structure. All four metrics of simulated network structure and co-occurrence patterns increased with increasing genotypic effect, but for some metrics the effect depended on the evenness of the associated community. Even community network structure (i.e. even species abundances) and co-occurrence patterns showed increasing structure with increasing genotypic effect with modularity (Fig. 3a; $\tau = 0.82$, $P < 0.001$), nestedness (Fig. 3b; $\tau = 0.83$, $P < 0.001$), centralization (Fig. 3c; $\tau = 0.89$, $P < 0.001$) and C-score (Fig. 3d; $\tau = 0.70$, $P < 0.001$) all showing significant, positive correlations with genotypic effect.

The evenness of the associated communities affected how network structure changed with increasing genotypic effect. Three of the four metrics for the un-even network structure (i.e. un-even species abundances, which is thought to best reflect natural communities) displayed significant correlations with genotypic effect: modularity (Fig. 3a; $\tau = 0.69$, $P < 0.001$), nestedness (Fig. 3b; $\tau = -0.28$, $P = 0.001$) and centralization (Fig. 3c; $\tau = -0.87$, $P < 0.001$). The C-score for the un-even community simulations across all levels of genotypic effect was not significant (Fig. 3d; $\tau = -0.01$, $P = 0.95$); however, as the relationship was clearly not monotonic, restricting the simulations to values over a threshold of genotypic effect corresponding to a broad-sense community heritability of 0.35 or greater increased the correlation between the C-score and genotypic effect (Fig. 3d) to $\tau = 0.23$ ($P = 0.06$).

DISCUSSION

Our results support the hypothesis that genotypic variation in a foundation species contributes to ecological network structure. In the field, we observed significant empirical network structure for all network metrics, including modularity, nestedness and centralization, which were also corroborated by significant co-occurrence patterns of species among trees. These findings emerged even though they were tested against a conservative null model that restricted tree genotype and associated species totals that greatly reduced the probability of detecting significant structure. Our controlled simulation experiment, which manipulated both genotypic effect and community evenness, displayed significant effects of genotypic variation with all metrics in the “even” community simulations, also supporting the empirical findings. The “un-even”

simulations displayed similar patterns with all three network metrics. Taken together, these two lines of evidence (empirical and simulation based) support the conclusion that genotypic differences among individuals of a foundation species can generate interaction network structure in ecological communities.

Genotypic variation contributes to network structure

Significant network and co-occurrence patterns in the empirical genotype-species network indicate a strong genetic basis to ecological interaction network structure. In terms of the network structure metrics, modularity in plant-herbivore networks is often attributed to the specialization of a few species on a set of host species (Fontaine *et al.* 2011), while centralization generally can arise through the presence of a few generalists interacting with a larger number of specialist species (Sazima *et al.* 2010). Applying this to the empirical network, modularity could be arising from the specialization of some highly interactive arthropods on particular genotypes (e.g. the gall aphid, *Pemphigus betae*; Keith *et al.* 2010). It is likely that the same mechanism is contributing to species co-occurrence patterns, as the C-Score was much less than the null expectation, indicating that species tended to aggregate (i.e. co-occur), as would be the expected pattern if groups of species track similar genotypes and co-occur more frequently on preferred genotypes. The contrasting pattern of relatively lower nestedness and higher modularity, which has been observed in other studies of network structure (Thébault & Fontaine 2010), lends further support and suggests the possibility that tree genotype modules break up the nested structure of the arthropod community, which could simultaneously reduce the impact of herbivores and increase the competition among species that reduce tree fitness.

The results of the simulation experiment revealed the underlying impacts of genotypic variation in structuring interaction networks, further supporting the generality of the empirical findings. We found that when species total abundances are even, all metrics of network structure and co-occurrence patterns increase with the influence of variation among foundation species genotype. A more complicated set of patterns was observed in the un-even network simulations. Modularity increased dramatically with increasing effect of genotype, as it did in the even simulations; however, centralization decreased and both nestedness and the C-Score decreased then increased as the genotypic effect went up. The complex patterns found for nestedness and C-Score are likely the result of the counterbalancing effects of genotype versus species on nestedness and co-occurrence patterns, where initially the species abundances are determining the value of the metric. Then, as the influence of genotype increases, the metric is dominated by the response of the community to the genotypic differences. Similarly, as genotypic effect increases centralization decreases as genotypic differences decrease the dominance of a few species, and thus, centralization in the even and un-even communities converge toward a similar level of centralization. Although this null model simulations such as this are an obvious oversimplification of real ecological dynamics (Gotelli 2001; Blüthgen et al. 2008), the behavior of these models is consistent with an underlying genetic mechanism that is supported by observations from an empirical data set in a common garden (Shuster et al. 2006).

Genetic variation and the evolution of ecological networks

Why should foundation species' genotypic variation have effects on ecological network structure? Multiple empirical approaches support our findings. First, the

multivariate plant resource/defense phenotype demonstrates extensive genetic variation in n-dimensional traits including chemical defenses, ontogeny, induction, phenology, sink-source relationships, productivity, leaf litter, and other genetics based traits (Larson & Whitham 1997; Schweitzer *et al.* 2008; Grady *et al.* 2011; Holeski *et al.* 2012 and others). In combination, these factors result in each tree genotype differing from other tree genotypes in important traits that affect communities of organisms ranging from microbes to vertebrates. Thus, the greater the variation in the multivariate plant resource/defense phenotype, the greater the variation in the associated communities a species will support. Second, genotypes that are more similar in their genetics and the traits they express support more similar communities than those that differ in their genetics and the traits they express (genetic similarity rule of Bangert *et al.* 2008; Barbour *et al.* 2009; Zytynska *et al.* 2011). Third, genetically based interactions between strongly interacting species can create greater habitat variation, which in turn supports different communities on different genotypes (e.g., Bailey *et al.* 2006; Shuster *et al.* 2006; Keith *et al.* 2010; Lamit *et al.* 2011, 2014; Busby *et al.* In Press). One example of this, Busby *et al.* (In Press), showed that the genetics-based interaction of the tree and a common pathogen played a major role in defining the arthropod community, which differed among genotypes based on the plant's resistance to the pathogen. Thus, species trait values could be averaging over ecologically relevant variation in traits of individuals within species. In combination, these findings provide a mechanistic explanation for why trait differences among individual tree genotypes should direct community network structure.

A genetic basis to network structure has implications for the consequences of selection and evolution in a community context. Directional, stabilizing and divergent selection on a foundation species (e.g. pathogens and climate change) will alter the structure of these interaction networks in ways that can affect the outcome of selection, which occurs in a community context (Shuster *et al.* 2006; Turcotte *et al.* 2012; Fortuna *et al.* 2013; Thompson 2013). For example, in line with the predictions of selection imposed by “super-generalist” species in co-evolutionary dynamics (Guimarães *et al.* 2011), if directional selection on a foundation species selects for a “generalist” genotype, i.e. a genotype that interacts with a large number of species, we would predict a reduction in modularity and an increase in species co-occurrences, which would likely increase the frequency of species interactions. This would also increase the centralization of the network, potentially making the community less resistant to disturbance if it were to impose a different selection pressure that selects against the generalist genotype.

Our finding of a genetic basis to ecological interaction network structure has two consequences for community dynamics. First, these network level effects are only manifested in a community context, and because the structure of the network has pervasive effects on important community members (e.g. herbivores, mutualists, pathogens), changes in the community network are likely to feed back to influence the fitness of individual trees (e.g., Schweitzer *et al.* 2012). This conclusion is further supported by the rich experimental documentation that different genotypes support different community and ecosystem phenotypes (review by Whitham *et al.* 2012), and that major species’ interactions are genotype specific (e.g. interacting foundation species hypothesis; Keith *et al.* 2010; Busby *et al.* 2014). Second, the primary theories of

community dynamics don't consider intraspecific variation at the community level and are thus missing a potentially important mechanism directing how communities and whole ecosystems change through time. Our results don not support the neutral theory and its hypothesized species equivalence (Hubbell 2006) and the individualistic theory of Gleason in which species associations are the result of “coincidence” and that every species is a “law unto itself” (1926). As our local scale analyses of common garden studies demonstrate extensive community structure, they also are in opposition to Ricklefs’ (2008) concept of the “disintegration” of local communities in which “local coexistence can be understood only in terms of the distributions of species within entire regions...”. The existence of a genetic basis to network structure does support with the community dynamic concepts of Clements (1916). However, the large amount of variation in interactions is not in line with the Clements’ concept of tightly bound communities, and are more “loosely” coupled, as one would expect in a dynamic system where species interactions can shift due to stochasticity and in response to a multiple dimensions of abiotic and biotic gradients.

Conclusion

Understanding and predicting the responses of ecosystems is critical given the current pace of change ecosystems are currently experiencing (Scheffer et al. 2012). Species interactions play an integral role in ecosystems (Agrawal *et al.* 2007; Winfree *et al.* 2011) and how species interactions lead to evolutionary changes in participant species has been a topic of biology since Darwin’s writings on orchid pollinators (Darwin 1862). Studies of co-evolution between pairs and small groups of species have expanded the theory and support for evolutionarily dynamic species interactions (Ehrlich & Raven

1964; Jones *et al.* 2009; Thompson 2013). Studies of plant-mutualist and plant-herbivore networks have more recently provided a broader perspective, addressing more complex relationships among the many species in a community (Bascompte *et al.* 2010; Thébaud & Fontaine 2010) and revealing the importance of the community context of both ecological and evolutionary dynamics (Thompson 2013). As a genetic basis of traits is a key requirement for evolution by natural selection, and given that multiple studies have demonstrated rapid evolution of species in response to climate change (reviewed in Parmesan 2006) as well as the importance of co-evolutionary dynamics in ecological networks (Guimarães *et al.* 2011; Moya-Laraño 2011), further exploration of the structure of genotype-species networks is key to understanding evolutionary dynamics in real ecosystems.

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Figure Legends

Figure 1. The structure of the empirical bipartite network of 10 individual plant genotypes (left nodes) and 44 arthropod species (right nodes) living in the canopies of narrowleaf cottonwood (*Populus angustifolia*) in a common garden. Nodes are scaled by the marginal totals for genotypes (i.e. total arthropod abundance) and species (i.e. species total abundance). The nodes are arranged in order of increasing interactions, which corresponds to increasing centralization bottom to top, and are colored by module membership. Lines show interactions between genotypes and species scaled by the average abundance of each arthropod species across all individuals of a given genotype. Plant genotype names follow the naming presented in Keith *et al.* (2010) and taxonomic identification of the arthropod community is provided in Supplementary Materials.

Figure 2. Genotypic effect in simulated communities produced differences in individual phenotypic traits that contributed to variation in the associated community. The density plot (A) shows the variation in the simulated foundation “tree” phenotypic values among individuals with each line showing the distribution for a different genotype, while the NMDS ordination (B) plots the community composition of each genotype shown as the multivariate centroid for each genotype (± 1 SD).

Figure 3. Bivariate plots showing how network and co-occurrence patterns of the simulated networks vary with increasing genotypic effect. When species’ total abundances were even (black), modularity (A), nestedness (B), centralization (C) and the

C-Score (D) increased as the effect of foundation species genotype increased. When species total abundances were un-even (grey), only modularity showed a similar pattern of increasing structure (A), both nestedness (B) and centralization (C) decreased, while the C-Score (D) increased structure at higher levels of genotypic effect. Dashed lines show the empirical network values.

Figure 1

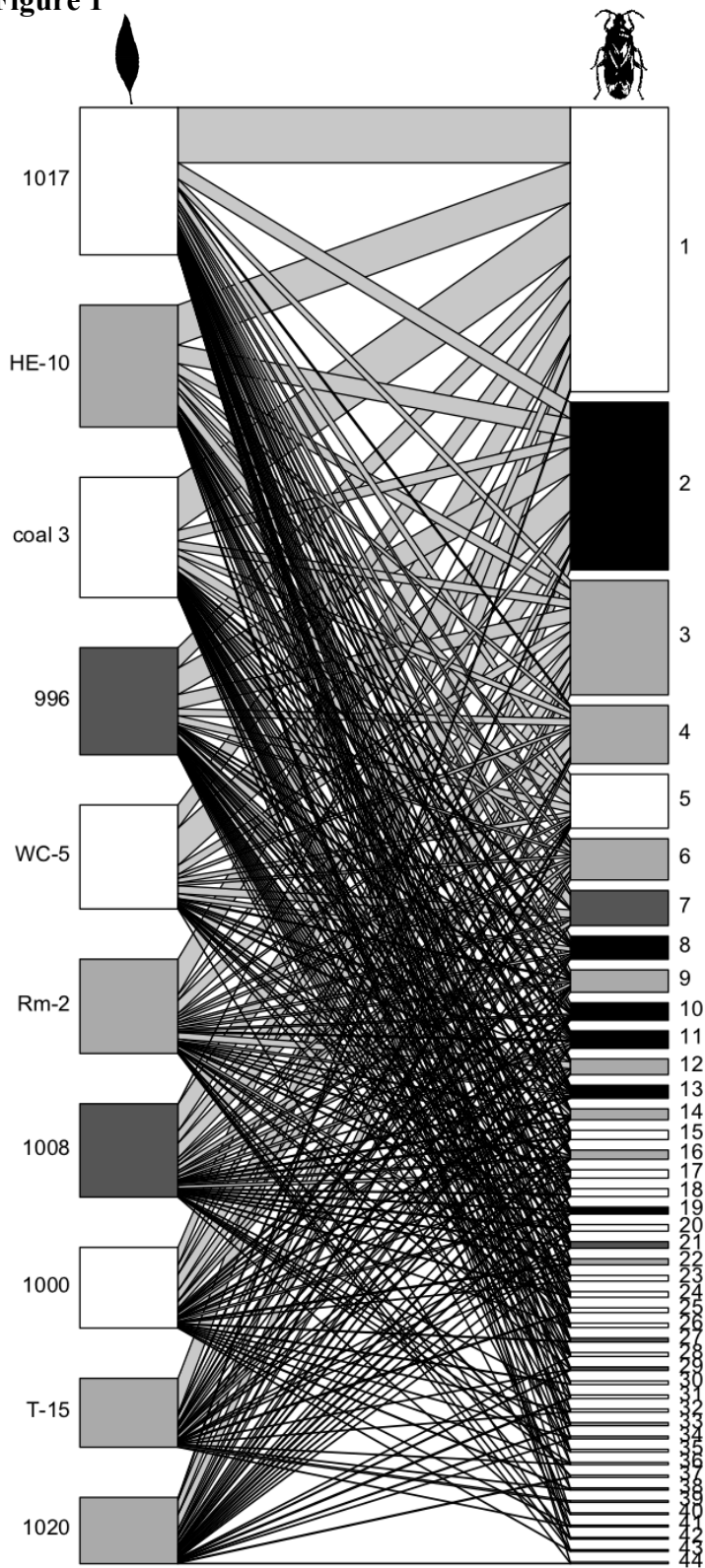
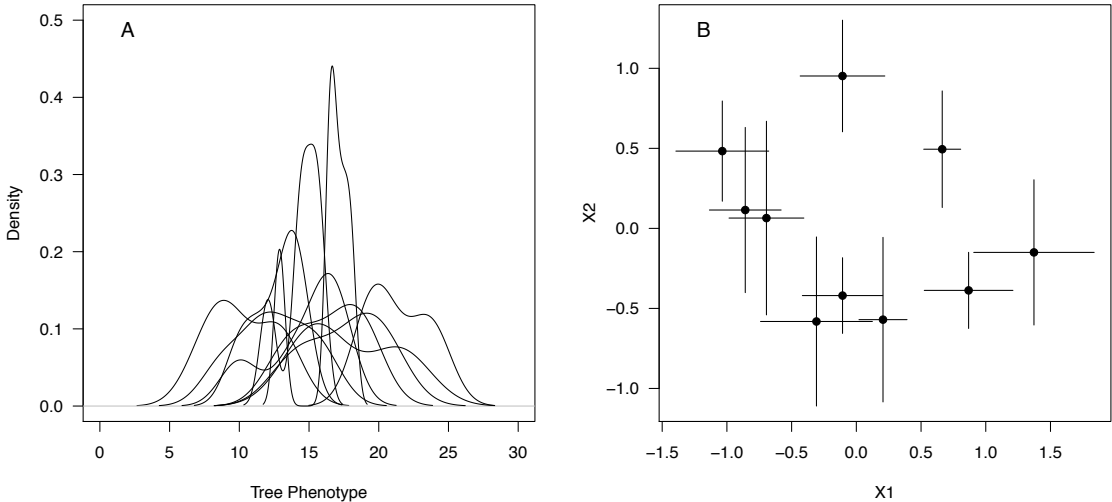
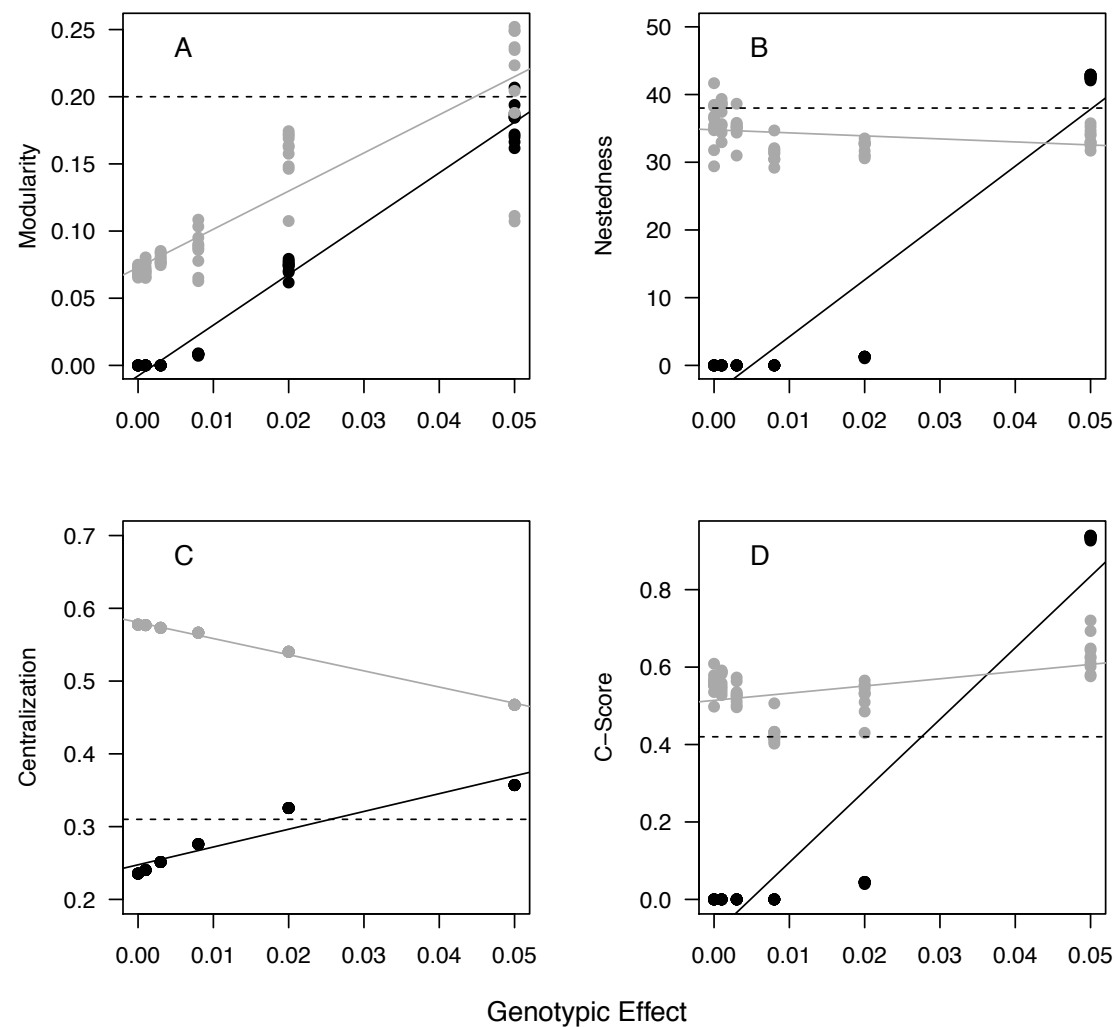


Figure 2



643 **Figure 3**



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