Consequences of Biodiversity in Tree Diversity Experiments

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Jeannine Cavender-Bares

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Only last week I went out among the thorns and said to the wild roses:
deny me not,
but suffer my devotion.

Mary Oliver (1998)

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Dedication

For Jared, with all my love

Abstract

This dissertation reports on four studies that explore the consequences of changes in tree biodiversity for three ecosystem processes (growth, leaf herbivory and disease, and leaf decomposition) in tree-dominated ecosystems in eastern Minnesota, USA.

In Chapter 1, I present the Forests and Biodiversity (FAB) experiment and assess the role of taxonomic, phylogenetic, and functional diversity in this experiment on stem growth of 12 species. Over the third to fifth years of the experiment, trees with more diverse neighborhoods produced more biomass than trees in less diverse neighborhoods. This complementary overyielding effect was associated with species richness (taxonomic diversity) and was better predicted by tree diversity at larger (12 m^2) rather than smaller (0.25 m^2) spatial scales.

I also measured three forms of invertebrate herbivore damage and two forms of disease damage on leaves of nine FAB species; results from this study are presented in Chapter 2. I assessed the consequences of diversity for damage across four spatial scales. Herbivory and disease responded to a variety of metrics of community diversity and these effects were species-specific. Damage, regardless of what kind, was better predicted by community structure and diversity at small spatial scales (1-4 m^2) than large scales (9-16 m^2).

Chapter 3 consists of the presentation of results from the Biodiversity in Willows and Poplars (BiWaP) experiment, in which both the genetic diversity and species diversity of three Salicaceous species was manipulated, and tree growth and herbivory were measured. Diversity did not have a consistent effect on productivity because one dominant species suppressed hetrospecific neighbors. In contrast, specialist gall formation was best predicted by genetic identity and genotypic diversity suppressed leaf mining.

Finally, through a separate litterbag decomposition experiment designed in parallel to FAB and presented in Chapter 4, I measured the consequences of leaf chemical diversity for decomposition over two years. When litter from multiple species were mixed, it did not lose mass, cellulose, or lignin differently than would be expected based on monoculture. But more labile carbon fractions (soluble contents and hemicellulose) decomposed more slowly in more functionally diverse litter mixes.

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Introduction[1]

Forests and tree plantations roughly a quarter of the terrestrial surface of the globe and provide humanity with critical resources and services, including wood, food, climate regulation, water purification, wildlife habitat, flood control, and cultural and spiritual meaning (Campos et al. 2005). These tree-dominated systems are also changing rapidly in extent and composition. Annual global deforestation rates of roughly 3% conceal net afforestation in temperate regions and losses of tree cover in the tropics (Keenan et al. 2015). Similarly, global patterns of biodiversity loss (Ceballos et al. 2015) mask drastic local compositional shifts (e.g. Frelich and Reich 2010), the long-term erosion of local diversity (Gonzalez et al. 2016), and the translocation of exotic species worldwide (Pimentel et al. 2001). These changes in the composition and diversity of tree-dominated ecosystems are likely to result from (Gonzalez et al. 2010) and both ameliorate and contribute to (Chapin III et al. 2000, Bonan 2008)climate change. As such, understanding the ecological consequences of changing forest diversity can allow for better prediction of, mitigation of, and adaptation to global change.

In this dissertation, I present four studies that explore the ecological consequences of changes in tree biodiversity. These studies, conducted across two tree diversity experiments and a companion litterbag experiment in eastern Minnesota, allow me to address the question of how more diverse forests differ from less diverse forests. In this introductory chapter, I

1) review the origins of the biodiversity-ecosystem functioning (BEF) discourse to which my dissertation research pertains;
2) sketch the expansion of first-generation BEF research to encompass multiple dimensions of biodiversity;
3) argue for the explicit consideration of spatial, temporal, and phylogenetic scale in BEF research; and
4) provide an overview of the foregoing empirical chapters.

The biodiversity-ecosystem functioning (BEF) discourse

The notion that diverse ecosystems might be more productive (Trenbath 1974, McNaughton 1977, Vandermeer 1981) or more resistant to disease or damage by herbivores (Elton 1958, McNaughton 1985) has been proposed periodically since Darwin (1859). Yet, the current era of biodiversity-ecosystem functioning (BEF) research dates conclusively to 1991, when discussion of the topic re-emerged at a conference in Bayreuth, Germany and in a subsequent collection of papers (Schulze and Mooney 1994).

[1] The first and second subsections of this chapter are adapted from material previously published in the Elsevier journal *Environmental and Experimental Botany* (Grossman et al. 2018) and are reprinted here with in accordance with the authors' retained rights.

Research from grasslands (Tilman and Dowling 1994, Tilman et al. 1996) and mesocosms (Naeem et al. 1994) soon provided the first evidence that biodiversity can enhance primary productivity beyond what would be expected based on monoculture yield (referred to as overyielding). This early BEF research mainly focused on primary productivity as a key ecosystem function that integrates the effect of biodiversity on other functions, such as resistance to pests and diseases (Cardinale et al. 2012). As such, productivity emerged as the most frequently studied metric of ecosystem functioning. Yet, additional studies of other ecosystem functions in grasslands quickly proliferated, consolidating the current consensus that biodiversity supports ecosystem functioning and multifunctionality (Hooper et al. 2005, Cardinale et al. 2006, Hector and Bagchi 2007, Tilman et al. 2012). Advances over the first 20 years of BEF research have also raised new questions about the generality of and mechanisms behind BEF relationships (Tilman et al. 2014, Weisser et al. 2017), the importance of different facets of biodiversity (e.g. species, functional and phylogenetic diversity) in shaping ecosystem functioning (Flynn et al. 2011), and the interacting effects of abiotic factors such as resource availability or drought (Craven et al. 2016).

In response to criticism (for instance Aarssen 1997, Huston 1997), BEF researchers have attempted to demonstrate that findings from controlled diversity experiments, especially the first generation of synthetic grassland and mesocosm studies, are relevant to real-world ecosystems and generalizable across ecosystem types. Over the last two decades, BEF research has expanded into a variety of ecosystems other than grasslands, including farm fields, forests, streams, lakes, and marine environments. Though BEF dynamics vary across systems, diversity repeatedly has affected ecosystem functionality (Cardinale et al. 2011, Lefcheck et al. 2015). As such, whether biodiversity positively affects ecosystem functioning is no longer widely debated, and research has largely shifted to understanding the mechanisms and context-dependency of BEF relationships. The work presented here attends to these concerns as well as to the role that multiple dimensions of biodiversity and scales of analysis can shape BEF dynamics in tree-dominated systems.

Distinct dimensions of biodiversity vary in their ecological consequences

Species richness remains the default metric of biodiversity in most BEF experiments, despite ecologists' growing awareness that other dimensions of biodiversity affect ecosystem functionality (Naeem et al. 2012). For some time, BEF investigators have explored the consequences for ecosystem functioning of diversity of functional traits (functional diversity; Tilman et al. 1997b, 1997a, Reich et al. 2001) and diversity in the evolutionary relationships among sympatric individuals, from the intraspecific (genetic diversity; Crutsinger et al. 2006) to the lineage (phylogenetic diversity; Maherali and Klironomos 2007) level. In some cases, data from experiments designed around gradients in richness have been re-analyzed, allowing for retrospective analysis of the contributions of, for instance, functional or phylogenetic diversity to productivity (Cadotte et al. 2009, some of the experiments in Flynn et al. 2011). More recent experiments have been designed to include a richness gradient, while also incorporating orthogonal

gradients in functional group, functional and/or phylogenetic diversity (e.g. Reich et al. 2004, Gravel et al. 2012, Perring et al. 2012, Cadotte 2013, Ebeling et al. 2014, Tobner et al. 2014, 2016, Grossman et al. 2017; Chapters 1, 2, and 4) or nesting a manipulation of genetic diversity within the richness gradient (e.g. Bruelheide et al. 2014, Moreira et al. 2014, Barsoum 2015; Chapter 3). Much less common are designs in which richness is held constant while another dimension, such as genetic (e.g. Barton et al. 2015, Fernandez-Conradi et al. 2017) or functional (Scherer-Lorenzen et al. 2007b, Hantsch et al. 2014, Tobner et al. 2014) diversity, is manipulated.

It is now quite common for BEF experiments – whether with herbaceous species or trees – to be designed to assess the consequences for ecosystem functioning of multiple dimensions of diversity, including trophic diversity (Parker et al. 2010, Cook-Patton et al. 2014, Verheyen et al. 2016). Because trees (and shrubs in the case of some experiments, including BEF-China) are often easier to monitor and manage at the level of the individual, such manipulations may, in some cases, be more tractable in tree diversity experiments. Experiments where genetic, phylogenetic, functional, and trophic diversity is manipulated rather than or in addition to species richness, will refine the developing consensus that biodiversity generally supports ecosystem functioning in many systems.

BEF relationships vary across spatial, temporal, and phylogenetic scales

Because the relationships between biodiversity and various ecosystem functions arise from material interactions among community members and their environments, it is reasonable to expect that BEF dynamics will vary across scales. The question of scale – generally thought of as the domain of space or time over which a given process occurs or is measured – has become central to ecology over the last fifty years (Levin 1992, Schneider 2001). A central goal for ecologists in many sub-disciplines is to determine and work within the scale(s) relevant to their pattern or process of interest and, if possible, to extrapolate to larger scales from local findings (Englund and Cooper 2003). Ideally, such informed cross-scale research could illuminate "domains of scale" characteristic for a given process (Wiens 1989). For instance, Germain and colleagues (2017) found that the composition of annual, serpentine grassland communities in California was structured by dispersal of seeds across two distinct spatial scales. Seed transfers between assemblages from one to five meters apart did not significantly alter community diversity, and the same was true for assemblages separated by five to 10 kilometers. Yet allowing dispersal from communities from five to 100 meters or from 100 meters to five kilometers did increase local diversity. In short, a "discontinuity" (Nash et al. 2014) in spatial scale occurred between five m and 5 kilometers in these grasslands – studies of community assembly carried out in one of these scales might not be generalizable to the other. Findings of such characteristic domains of scale for a given ecosystem process are uncommon in many research traditions in ecology, including the BEF discourse. In the research presented below, I incorporate an explicit focus on spatial, temporal, and phylogenetic scale.

Spatial scale has received some attention to date in the BEF literature. Some ecologists have questioned the meaningfulness of small-scale (<100 m^2) diversity experiments and the extrapolation of data collected in them to address pressing landscape-level or global concerns (Srivastava and Vellend 2005). It has generally been assumed that measurements taken in larger plots will correspond to meaningful scales for extrapolation to forests and tree plantations. Yet, as is often the case, many measurements of interest can only be collected on a per-plant or otherwise local basis (Schneider 2001). Such locally collected samples can inform larger-scale ecological research, but only given thorough planning and coordination. In this dissertation, I consider the relative strength of biodiversity-growth (Chapter 1) and biodiversity-herbivory/disease (Chapter 2) relationships across spatial scales, finding that tree diversity better predicts growth at intermediate spatial scales (12 m^2) but better predicts pest and pathogen damage at smaller (1-4 m^2) spatial scales.

The contemporary emphasis on long-term ecological research has fueled a greater understanding of the extent to which ecological dynamics vary over time and are thus temporally scale-dependent. Some ecological dynamics are recognized to be transient (e.g. plant acclimation to light over minutes or hours; Lambers et al. 2008), pertaining to only short time scales, whereas others are thought to characterize more stable long-term dynamics (e.g. atmospheric gas fluxes over years [carbon] or millennia [oxygen]; Chapin et al. 2011). Early findings from BEF experiments were often qualitatively distinct from later findings, and the positive biodiversity-productivity signal in two of the longest-running BEF grassland experiments has only grown stronger over time (Reich et al. 2012). This is a pattern that I also document from one year to the next of a two-year study period in a tree diversity experiment (Grossman et al. 2017; Chapter 1). Because decomposition is known to vary in time (Berg and McClaugherty 2014), biodiversity-decomposition relaitonships might also show characteristic domains of scale. My findings in Chapter 4 are suggestive of this: diversity only systematically affected decomposition of the fastest composing carbon compounds in forest litter.

Finally, in Chapter 3, I argue for consideration of phylogenetic scale, the grain and extent of evolutionary relatedness among community members (Cruz et al. 2005, Cavender-Bares et al. 2006), in BEF research (Chapter 3). It is recognized that particular processes are best predicted by dynamics at particular phylogenetic scales: Allee effects in invading, wind-pollinated grasses are by definition driven entirely by the population dynamics of relatives (Davis et al. 2004), while arbuscular mycorrhizal partnerships (Smith et al. 2009) represent interactions between species separated by over two billion years of evolution (Embley and Williams 2015). BEF research has largely focused on the ecological consequences of either genetic or species diversity, although a growing body of work has intentionally assessed dynamics across phylogenetic scales (Booth and Grime 2003, Fridley et al. 2007, Fridley and Grime 2010, Cook-Patton et

al. 2011, Crawford and Rudgers 2012, Moreira et al. 2014, Parachnowitsch et al. 2014, Abdala-Roberts et al. 2015b, c, Prieto et al. 2015, Schöb et al. 2015, 2017, Zeng et al. 2017, Hahn et al. 2017). Though this literature has yet to provide evidence of characteristic phylogenetic scales for BEF relationships, some studies have demonstrated some potential patterns of phylogenetic scaling in these dynamics.

Overview of the dissertation

The foregoing dissertation is split into four chapters, each of which presents one empirical BEF study.

Chapter 1 introduces the Forests and Biodiversity (FAB) experiment and documents the consequences for experimentally manipulated taxonomic, phylogenetic, and functional tree diversity for tree growth.

Chapter 2 presents a study in which I monitored invertebrate leaf herbivory and fungal disease in eight species in the FAB experiment and modeled their dependence on tree diversity across spatial scales.

Chapter 3 introduces the Biodiversity in Willows and Poplars (BiWaP) experiment, through which I assess the consequences of biodiversity across phylogenetic scales (genetic to species diversity) for tree growth and herbivory.

Chapter 4 describes a litterbag decomposition experiment based on the design of FAB. This experiment allows for analysis of the consequences of litter chemical and physical diversity for decomposition over two years.

Chapter 1

Species richness and traits predict overyielding in stem growth in an early-successional tree diversity experiment[2]

[2] This chapter was previously published in the journal *Ecology* (Grossman et al. 2017) and is reprinted here with permission of Wiley and Sons. This research was conducted in collaboration with Jeannine Cavender-Bares, Sarah E. Hobbie, Peter B. Reich, and Rebecca A. Montgomery.

Introduction

Despite documentation of the largely uninterrupted decline in the distinctness of the global biota, humans have failed to halt contemporary erosion of biodiversity (Butchart et al. 2010). As a result, ecosystems face consequential changes in biodiversity against a backdrop of general biodiversity loss.

Previous research in experimental ecosystems has established that more speciose ecosystems have higher productivity that is more stable in the face of environmental fluctuations (Tilman et al. 2006, Hooper et al. 2012, Srivastava et al. 2012). The positive biodiversity-productivity relationship was first demonstrated experimentally in mesocosms (Naeem et al. 1994) and grasslands (Tilman et al. 1996, Spehn et al. 2005), while recent research has shown that species richness sometimes supports productivity in forests (Paquette and Messier 2011, Zhang et al. 2012, Liang et al. 2016, Tobner et al. 2016) as well as other ecosystems (Engelhardt and Ritchie 2001, Worm et al. 2006, Bowker et al. 2010). In this prior work, species richness (SR) has been frequently treated as the de facto index of community diversity (Diaz and Cabido 2001)and SR has indeed proven to be an excellent predictor of productivity (Hooper et al. 2012). Species richness can also serve as an intentional surrogate for the evolutionary distance embodied in the divergence among lineages in a community (phylogenetic diversity; PD) or distance among community members in functional traits (functional diversity; FD) (Flynn et al. 2011, Winter et al. 2013). Populations and species are expected to become increasingly divergent in their traits with phylogenetic distance, although distantly related clades may ultimately converge in their traits as a result of selection (Lord et al. 1995, Webb et al. 2002, Cavender-Bares et al. 2004). For this reason, the apparent positive relationship between species richness and productivity may be explained in terms of correlated diversity along a phylogenetic (Cadotte et al. 2008, 2009) and/or functional (Bengtsson 1998, Cadotte et al. 2011) axis. Paquette and Messier (2011) employed this interpretation when, in their meta-analysis of forest and boreal forest plots, though PD and FD both predicted tree productivity, their effects were impossible to disentangle from the effect of SR.

Experimental research has demonstrated that increases in productivity with SR may stem from multiple species' partitioning of available resources or from the chance inclusion ("sampling effect"; Aarssen 1997) or disproportionate impact ("selection effect"; Loreau and Hector 2001) of particular species. In the former case, "complementary" interactions among species related to functional differences (Hector 1998, Reich et al. 2012, e.g., rooting depths, root:shoot partitioning, or nutrient concentrations) are such that community composition drives the biodiversity-productivity relationship. In the latter cases, the presence of highly productive species is responsible for higher productivity with greater diversity (Fargione et al. 2007). When complementarity rather than species selection dominates the relationship, it is reasonable to infer that non-additive species interactions, and not the influence of highly productive species, contribute to greater ecosystem productivity.

In most recent biodiversity research, plots have often been treated as experimental units, with fewer studies intentionally integrating an assessment of spatial scale into their work (see Kennedy et al. 2002, Castagneyrol et al. 2013 for examples). Yet biodiversity-productivity relationships are inherently scale-dependent, and their magnitude, direction, and structure may change with scale (Chase and Leibold 2002, Chalcraft et al. 2004 but see Roscher et al. 2005). Because trees are easier than herbs or smaller organisms to track and measure individually, tree diversity experiments provide a novel opportunity to investigate the relationship between biodiversity and productivity across scales. In natural systems, neighborhood-level analyses have suggested that traits (to a greater extent than phylogenetic distance) can alter tree performance (Uriarte et al. 2010), complementing work done at the plot scale (Paquette and Messier 2011). Controlled tree diversity experiments allow for experimental assessment of diversity-productivity patterns documented previously in natural and managed systems from the neighborhood scale of a focal tree and its neighbors (Uriarte et al. 2004, Canham et al. 2006) to the scale of a plot or stand (dozens of trees; Erskine et al. 2006).

We present findings after the third year of a tree diversity experiment in eastern Minnesota, USA. We measured aboveground stem biomass ("biomass," hereafter) of planted juvenile trees. We expected that growth in biomass would increase with SR, PD, and FD. We also expected that, in our comparison of the consequences of PD vs. FD across polycultures, PD would, by incorporating diversity in evolutionarily conserved but unmeasured functional traits (Srivastava et al. 2012, Winter et al. 2013), serve as an especially strong predictor of productivity (Cadotte et al. 2008, 2009). Finally, we expected that because trees were small and crown closure had not yet occurred, diversity in the local neighborhood of focal trees would contribute more to growth than would plot diversity.

Our contribution to the forest diversity-productivity literature (Erskine et al. 2006, Healy et al. 2008, Haase et al. 2015, Tobner et al. 2016) is unique in three ways. First, this diversity experiment intentionally contains many plots with two species, including a subset that varies orthogonally in both PD and FD, enabling analyses that hold species richness constant to assess the independent effects of PD and FD on stem biomass growth. Second, these plots are nested within a larger tree diversity experiment consisting of plots ranging from one to 12 species and varying widely in PD and FD, allowing us to contrast the effects of PD and FD with the effects of SR. Finally, we have addressed the role of spatial scale in structuring biodiversity-ecosystem productivity relationships by analyzing the effects of diversity at both the plotand focal tree-level.

Materials and Methods

Experimental design

In May 2013, we established the Forests and Biodiversity experiment (FAB) at the Cedar Creek Ecosystem Science Reserve (Cedar Creek), a 2300-ha reserve and National Science Foundation Long Term Ecological Research site in eastern Minnesota, USA (Fig. 1.1; 45°250 N, 93°100 W). FAB is a member of the IDENT network (Tobner et al. 2014). The site is situated on the Anoka Sand Plain, a flat outwash plain with infertile, excessively drained soils consisting of upwards of 90% sand. Warm summers and cold winters are typical of the site's humid continental climate. Cedar Creek is located at the historically fluid regional confluence of the Midwestern tallgrass prairies, Eastern deciduous forests, and Northern boreal forests (Baker et al. 2002, Goldblum and Rigg 2010) and contains plant assemblages typical of each. We established FAB in an abandoned old field dominated by herbaceous species and fenced to exclude large mammalian herbivores. The experimental site was burned, then mulched with wood chips (from non-native western red cedar [*Thuja plicata*]) to prevent regrowth of herbaceous species. The experiment was planted over one week in late May 2013 with regionally sourced bare root seedlings of unknown genetic relatedness that ranged from 1 to 2 yr in age. Prior to planting, seedling roots were coated with commercial ectomycorrhizal and endomycorrhizal inoculum including species known to associate with all genera included in the experiment (Bio Organics, New Hope, PA). We used sprinkler irrigation to water newly planted seedlings *ad libitum* through June and July 2013. We replanted seedlings as needed in May/June 2014–2015; mortality was roughly 7–10% following replanting.

The FAB experiment consists of 8,960 trees of 12 native species. Four of these species are gymnosperms: eastern red cedar (*Juniperus virginiana*) and white (*Pinus strobus*), red (*P. resinosa*), and jack (*P. banksiana*) pine. The eight angiosperm species include red (*Quercus rubra*), pin (*Q. ellipsoidalis*), white (*Q. alba*), and bur (*Q. macrocarpa*) oak; red maple (*Acer rubrum*) and box elder (*A. negundo*); paper birch (*Betula papyrifera*); and basswood (*Tilia americana*). In a trial experiment in 2011–2012 using 20 common tree species native to Cedar Creek, these 12 showed highest survival rates for these soils in the absence of amendments. They span the seed plant phylogeny and differ widely in the nine functional traits (related to leaf and wood economics, resource use, and environmental tolerance) considered in the design of the FAB experiment (Fig. 1.2). As climate change disrupts historically stable plant communities some of these species (*Quercus* spp., A. rubrum) are likely to remain widespread at Cedar Creek, whereas others are likely to become more (*J. virginiana*) or less (*Pinus banksiana*, *B. papyrifera*) abundant (Frelich and Reich 2010, Reich et al. 2015). Each of FAB's three blocks (spaced 4.5 m apart) consists of either 46 or 47 square plots, each 3.5 m on the edge; plots are planted with one, two, five, or 12 species, with two-species plots additionally designed to tease apart functional and phylogenetic diversity. Each plot contains 64 trees, planted at 0.5 m intervals. Within a block, all trees are planted on a contiguous grid, without extra space in between plots. Though this design allows trees from neighboring plots to interact, trees on the edges of plots have eight neighbors and only trees on the edges of blocks experience an unequal density of neighbors. This allows for analysis that treats all trees in the experiment as points on a continuous grid.

And because placement of plots within blocks is random with respect to plot composition, effects from neighboring plots do not bias assessments of treatment effects. Each block contains 12 monocultural plots and 28 bicultural (two-species) plots; each of these plot types (or compositions) is therefore replicated three times across the experiment. Each block also contains either three or four random-draw five-species polycultures, the compositions of which are not replicated in the experiment, giving replication of the five-species level of richness but not of each five-species polyculture's composition. Each block also contains three or four 12-species polycultures, such that this composition is replicated 10 times across the experiment. Half of the 28 bicultural plot compositions were chosen by random draw. The other remaining bicultures were chosen using a stratified random approach (Appendix S1) designed to provide plots both low and high in PD and FD.

The design of FAB allows us to consider it as two connected experiments. The 36 monoculture plots and 84 biculture plots form a 120-plot biculture vs. monoculture-only experiment that specifically allows us to disentangle the effects of PD and FD on growth at constant SR. A second, 98-plot random-draw experiment, including all fiveand 12-species polycultures but only randomly chosen bicultures allows for analysis of the consequences of (sometimes confounded) SR, PD, and FD for overyielding in productivity across a broader diversity gradient. Composition, species richness and phylogenetic and functional diversity for all FAB communities are given in Supplementary Table 1.1 and trait values are given in Supplementary Table 1.2.

Diversity metrics

In developing the experimental design of FAB and analyzing preliminary data, we calculated a variety of diversity indices at two spatial scales. We define "neighborhoods" as the eight neighbors within 1 m^2 of each focal tree – we expected that trees within a given neighborhood would interact most strongly during the establishment of the experiment. We also consider plots (up to 64 trees within 9.25 m^2), the original level of replication in the FAB experimental design. Because many indices are correlated, we only included a subset of them in our models; all indices calculated are presented and described more fully in Supplementary Table 1.3; indices included in the present work are described below.

Species richness (SR; number of species) was calculated for all communities and ranged from one to eight (for focal tree neighborhoods) or 12 (for plots). For each community, we also calculated the proportion of all trees of each of the 12 species in the experiment and treated these proportions as continuous predictors of stem growth; because we replanted dead trees, these remain constant from year to year. We calculated and report PD

as either Faith's (1992) Phylogenetic Diversity (FPD; strongly correlated with SR) or Phylogenetic Species Variability (PSV; Helmus et al. 2007, independent of SR) and FD as either Scheiner et al.' (2017)

functional trait dispersion (FTD; correlated with SR) or Laliberté and Legendre's (2010) functional dispersion (FDis; independent of SR). To calculate multidimensional FTD and FDis, we chose traits that represent axes of variation known to be critical for plants in terms of stress tolerance, nutrient acquisition, light capture, water use and microbial and faunal interactions belowground. These included: (1) wood density (g/cm^3), (2) leaf mass per area (LMA; g/cm^2), (3) leaf N concentration (%), (4) dominant mycorrhizal type (arbuscular-dominated – AM [0], ecotomycorrhizal-dominated – EM [1]), (5) leaf habit (deciduous [0], evergreen [1]), (6) leaf calcium concentration (ppm), (7) shade tolerance, (8) drought tolerance, and (9) waterlogging tolerance (all tolerances range from 1 to 4). Species mean traits values were obtained from previously collected data in the region (Reich et al. 1997, Wright et al. 2004, Holdsworth et al. 2008, Cavender-Bares and Reich 2012, J. J. Grossman, unpublished data) and, in the case of shade, drought and waterlogging tolerance, from Niinemets and Valladares (2006); they were collected mostly on mature trees. Classification based on mycorrhizal type is discussed further in Appendix S1. Though traits of individuals of a given species change over development (Cavender and Bazzaz 2000, Sendall et al. 2015), we assume that seedlings in the FAB experiment, by virtue of growing in open, high-light conditions, will have similar trait values to adult trees, and that rank-order of species for any given trait will remain constant over ontogeny. FDis for each of nine functional traits as well as multidimensional FDis and FTD were calculated. We present a full description of all diversity indices used, their selection, and their calculation in supplementary materials (Appendix S1, Supplementary Table 1.3).

Data collection

In September of 2013–2015, we measured basal diameter and height to leader of all living trees. We measured basal diameter at 5 cm above the soil surface and measured to the tallest leader, stretching the plant as needed. We used allometric equations, calculated from extra seedlings or drawn from literature estimates for plants of appropriate age and size (Peichl and Arain 2007, Falster et al. 2015, Supplementary Table 1.4) to estimate the incremental change in stem biomass from one year to the next.

Data analysis and modeling

All calculations and analyses were carried out in R (R Core Team 2014, ver. 3.1.0). Details regarding the calculation of incremental stem biomass, the net biodiversity effect (NBE), complementarity (CE) and selection (SE) effects are presented in Appendix S1.

We report stem biomass growth in two ways: on an individual plant basis and on a plot basis. In the case of individual plants, stem biomass growth is allometrically determined stem biomass in year t less stem biomass in year t–1. Plot-level average stem biomass growth is calculated similarly: the entire stem biomass of the plot in year t–1 is summed and then divided by the number of living trees in the plot in year t–1, yielding a per-plant estimate of biomass in year t–1 that can be subtracted from a similarly calculated

estimate of biomass in year t. This gives a density-independent, per-capita estimate of stem growth, rather than the whole-plot, density-dependent measures used in many earlier biodiversity experiments (i.e., Tilman et al. 1996). Though the per-capita approach has limitations, we compared it to a density-dependent approach and conclude that it better represents patterns in productivity given species-dependent mortality (Appendix S1). As such, we present plot-level stem biomass growth as per-tree averages based on performance of trees within a given plot. In calculating plot-level stem biomass, we also excluded all trees on the edge of plots; as such, plot-level estimates reflect the growth of trees whose closest neighbors are all within the focal plot.

To model the diversity-biomass relationship, we adopted a four-step approach of full model construction, variable selection, model comparison, and refitting with random effects and/or an appropriate variance structure. We began variable selection by elucidating five models of biomass for a given year (e.g., 2013–2014) and scale (neighborhood or plot-level) and, driven by our hypotheses, constructed several rival fixed-effects "full" multiple linear regression models including all reasonable predictors. For the random plots dataset, these models were:

A. NBE ~ Covariates + p_1 + ... + p_{12}

B. NBE ~ Covariates + SR + PSV + multidimensional FDis

C. NBE ~ Covariates + SR + FPD + multidimensional FTD

D. NBE ~ Covariates + SR + $FDis_1$ + ... + $FDis_9$

E. NBE ~ Covariates + SR + CWM_1 + ... + CWM_9

in which NBE (kg/year) is observed stem biomass less predicted stem biomass based on monoculture averages and is positive in the case of "overyielding" (biodiversity increases yield) and negative in the case of "underyielding" (biodiversity decreases yield); Covariates are average community plant height and diameter in year t and number of trees alive in the plot in year t, a surrogate of plot mortality; pi is the proportion of species i in the plot (having value 0 if the species is absent); PSV is Phylogenetic Species Variability; FPD is Faith's PD; FDis is multidimensional Functional Dispersion; FTD is multidimensional Functional Trait Dispersion; FDisj is the single-trait Functional Trait Dispersion of trait j; and CWMj is the Community-Weighted Mean of trait j. For the monocultures and bicultures only dataset, we followed the approach described earlier with two modifications. SR was removed as a predictor from the monocultures and bicultures only analysis since these models only compare plots with two species. We also did not include model family C in analysis of the monocultures and bicultures data either, since model families B and C are conceptually equivalent when SR is held constant.

Though we had a priori expectations about the consequences of individual predictors for NBE, we were also interested in determining systematically which variables would produce, in combination, a predictive model of NBE. We therefore used regression with empirical variable selection (REVS; Appendix S1; Goodenough et al. 2012). We compared the AIC scores of the five reduced models developed by applying REVS to our five original full models. We selected as our "best" model from each set the model with the lowest AIC score. When AIC scores of two or three models were close (DAIC ≤ 3), we treated them as equivalent and chose the more interpretable model.

We also repeated all plot-level modeling with CE and SE as response variables rather than NBE in order to assess whether different diversity indices were important predictors of these components of the net biodiversity effect. Based on results from multivariate regression models described previously, and in order to explore the extent to which individual diversity metrics could predict overyielding or underyielding in our dataset, we also fit simple linear regression models of NBE across random polycultures and monocultures and bicultures only. Predictors include all those used in multivariate models.

We present each plot-level model of stem growth as a mixed-effects model for a particular year including the fixed-effects variables selected through REVS and a random intercept term accounting for plot composition. We inspected all models for violations of regression assumptions and removed outliers in one case in which extreme values suggested measurement errors.

For neighborhood-level models, we incorporated the predictors from the REVS-selected model as fixed effects in a new mixed-effects maximum likelihood regression model with species included as a random effect and a correlation structure. We fit models with random intercepts corresponding to the species of the focal tree because focal tree species was always retained by REVS. To account for spatial autocorrelation in the location of focal trees, we also included a spherical correlation structure based on the easting and northing coordinates of each tree in the focal tree models (Legendre et al. 2002, Zuur et al. 2009).

Results

Species differences in stem biomass growth

Tree growth in monoculture varied among species by over four orders of magnitude (Supplementary Fig. 1.1). From 2014 to 2015, *P. banksiana* individuals grew significantly faster than all other species, accruing an average of 236 g/yr of stem biomass. *T. americana* (94.0 g/yr) and *P. strobus* (89.1 g/yr) grew at similar rates, while the remaining nine species accrued less than 25 g of biomass per tree (*B. papyrifera*, 22.0 g/yr; *A. rubrum*, 0.018 g/yr; other species intermediate) and were not significantly different in growth rate. Stem biomass varied widely, with trees ranging from 3.5 to 250 cm in height and 0.05 to 7.5 cm in diameter by 2015. Tree size also contributed to variation in stem growth: growth rates were highly correlated with stem

biomass (r = 0.98 for 2014–2015) such that the largest trees at the start of any given year were generally the fastest growing individuals in that year. Across both years of the study, species differed significantly in monocultural growth rate, even when initial biomass was included as a covariate (for 2014–2015: $F_{11, 1467} = 158.7$; $P < 0.001$). Stem biomass growth was highly correlated with growth in height and diameter (Supplementary Fig. 1.2).

Plot-level BEP modeling

During the first two full years of the experiment, the net biodiversity effect on plot-level stem biomass growth was positive – indicating overyielding – and consistently depended on two dimensions of biodiversity: species richness (SR) and the community-weighted means (CWMs) of specific functional traits (Table 1.1). We documented "transgressive overyielding" (yield beyond what would be expected in monoculture; (Trenbath 1974) in both years of the study period: the average net biodiversity effect was significantly ($P < 0.001$) non-zero and positive for plots with two (N=84), five (N=9), and 12 (N=9) species in both years of the study (Supplementary Fig. 1.3).

Random-draw polycultures vs. monocultures

The best predictors of positive NBE across the experimental diversity gradient were species richness (Fig. 1.3) and the community-weighted means of leaf nitrogen and calcium, mycorrhizal association, and waterlogging tolerance. Our best multivariate models of NBE for randomly selected plots were from model family "E" (trait means predict NBE) and included SR, CWMs of these four key traits, and, as a covariate, average initial plant diameter in the plot (Table 1.1 and Supplementary Table 1.5). Univariate regression – used to complement the multivariate approach – of NBE across random polycultures on a variety of diversity predictors echoed the importance of functional trait means and species richness (Supplementary Table 1.6).

The best univariate predictors of NBE from 2014 to 2015 were species richness and the PD and FD metrics that correlate strongly with it (FPD and FTD; $0.54 < r^2 < 0.61$; Supplementary Tables 1.5 and 1.6). However, diversity metrics uncorrelated with SR, including PSV and both multivariate and univariate FDis explained some variation in NBE ($0.10 < r^2 < 0.34$). And even though community-weighted means (CWMs) of single traits were included, alongside SR, in the best multivariate models of NBE, they performed relatively poorly as univariate predictors ($r^2 < 0.08$).

Bicultures vs. monocultures

When species richness was held constant at two, the best multivariate models of NBE were those from Family "E" (community weighted means predict NBE) and Family "A" (species proportions predict NBE; Supplementary Table 1.5). As such, the relative abundances and trait values of species in a given plot better

predicted growth relative to monocultural yields than did diversityrelated predictors. Univariate regression of NBE on diversity predictors across bicultures did indicate that a few metrics of diversity explained some variation in plant growth. For instance, the CWM of wood density was significantly and negatively associated with and explained almost half of the variation in NBE (Supplementary Table 1.6) from 2014 to 2015. Though other metrics were significantly associated with NBE, most explained little of its variation.

Neighborhood-scale BEP modeling

At the neighborhood scale, identity of an individual's eight closest neighbors mattered more than SR or any of the indices of PD or FD with which we attempted to model NBE. The best models for BEP at the neighborhood level, across years, were those from family "A," which included species abundances within the eight-tree neighborhood as well as covariates related to initial tree size. A given focal tree produced significantly more stem biomass when it was larger at the start of the growing season; when more of its neighbors were *Q. macrocarpa* (from 2014 to 2015 only) or *Q. alba*; and when fewer of its neighbors were *B. papyrifera* (from 2014 to 2015 only), *J. virginiana* (Fig. 1.3), or *P. banksiana* (Table 1.1, Supplementary Table 1.5).

Complementarity and selection effects

We found different patterns in the relationship between diversity and the two components of the NBE: complementarity and selection effects (Supplementary Fig. 1.4). Complementarity was generally positive ($t_{139(2)} = 5.73$, $P < 0.001$; all t-tests given here for 2014– 2015), whereas selection effects were idiosyncratic, smaller in absolute magnitude than complementarity ($t_{139(1)} = 2.83$, $P < 0.001$ for 2014–2015), and less obviously associated with diversity. In both years of our study, SE were no different than zero ($t_{139(2)} = 0.775$, $P < 0.440$).

Random-draw polycultures vs. monocultures

The best predictors of overyielding in polycultures across the diversity gradient shifted from the first to the second full year of the study (Table 1.2, Supplementary Table 1.5). From 2013 to 2014, a model including phylogenetic diversity (Family C) best predicted CE. The following year, the best model of CE came from Family A (species abundances predict CE), suggesting that CE was positive associated with *P. banksiana* abundance and negatively associated with *Q. rubra* abundance. The best models of selection effects across polycultures included plant size and shade tolerance as predictors in the first year of the study (Supplementary Table 1.5). In the following year, SR was a significant, positive predictor of selection effects, indicating that more diverse plots (e.g., 12-species polycultures) showed greater productivity from dominant species than did less diverse plots (e.g., bicultures).

Bicultures vs. monocultures

And as was the case for NBE, our consideration of complementarity effects across bicultures also produced best models that included as predictors the identity and proportion of constituent species (Family A), but not phylogenetic or functional diversity metrics (Supplementary Table 1.5). Selection effects in bicultures were best described by models from Family D, which include as predictors univariate FD metrics, and Family A, with few consistent effects across years of the study (Supplementary Table 1.5).

Discussion

We found that species richness and its surrogates were critical predictors of overyielding in stem biomass growth at the plot level, that the diversity and magnitude of key functional traits were critical predictors of this relationship, and that species identity of nearby trees weakly predicted biodiversity effects at the neighborhood scale. Our findings parallel past research demonstrating a positive relationship between diversity and biomass production in forests (Paquette and Messier 2011, Haase et al. 2015, Tobner et al. 2016). Because we report here on early stand development in a planted experiment, our results are most relevant to early-successional stands (Lasky et al. 2014) and should not be generalized to all forests.

For random-draw polycultures, species richness was an essential predictor of biodiversity effects

Whenever species richness was included in models of net biodiversity effects across polycultures in our system, it was a significant and positive predictor of stem growth beyond what was expected in monoculture (Fig. 1.3). By comparison, predictors that incorporate phylogenetic and functional information were subordinate predictors of or did not meaningfully predict overyielding, suggesting that richness plays a special role in the diversity-productivity relationship. This insight is critical, because it is often difficult to disentangle the various dimensions of biodiversity and understand which, if any, are stronger predictors of ecosystem productivity (Diaz et al. 2007, Cadotte et al. 2008, Venail et al. 2015). Here, we present two lines of evidence in support of the crucial role of SR.

Several correlated diversity metrics predicted overyielding in stem growth at the seedling stage when each metric was considered alone in univariate regression analysis. These included PD and multimensional FD (Supplementary Table 1.6); additionally, Faith's PD, which is correlated with richness, predicted complementarity in one year of the study (Supplementary Table 1.5). Yet both of these are highly correlated with each other and with SR (Supplementary Table 1.7), implying that there is some intrinsic quality that each metric shares. Metrics that are weakly correlated with SR – including PSV and FDis, which intentionally calculate PD and FD independently of species counts – are, on the other hand, less predictive of overyielding in univariate models. And community-weighted means, though they predicted overyielding when included in multivariate models with SR, were not strong univariate predictors when considered independently. As such, SR, or a dimension of diversity correlated with it, appears central to the diversity-productivity relationship.

We found that phylogenetic or functional metrics correlated with SR are primarily important in that they augment its explanatory power. Models that included SR and PSV or FDis (which are calculated independently from SR; Family B), generally outperformed models that included SR, FPD, and/or FTD (which are highly correlated with SR; Family C), in model comparison. And in variable selection, metrics of PD or FD were sometimes retained as significant predictors of NBE after SR, but the reverse was never the case.

Given all this, we conclude that a purely phylogenetic or purely functional approach may not be the best way to predict NBE on biomass, at least for this experiment at this stage. Species richness, phylogenetic diversity, and functional diversity are confounded in natural systems (Pavoine et al. 2013) and many biodiversity experiments (Flynn et al. 2011), making it computationally intensive or impossible to disentangle each dimension. We emphasize the importance of information captured by SR and its correlated phylogenetic and functional metrics for understanding the relationship between diversity and overyielding in productivity (Flynn et al. 2011, Venail et al. 2015, but see Pavoine et al. 2013).

In bicultures-only analysis, species identity and abundance predicted biodiversity effects

When we controlled for the effect of species richness on stem growth by modeling this relationship in bicultures only, we found that the species traits and relative abundance of individuals in a plot best predicted net biodiversity effects (Table 2.2, Supplementary Table 1.5). Univariate analysis did suggest that plots with lighter wood or coniferous trees overyielded most among bicultures (Supplementary Table 1.6). However, these CWMs are associated with species identity and this finding therefore contributes to our conclusion that species identity, rather than community diversity, best predicted overyielding at a single level of species richness. We had expected that phylogenetic diversity (PSV) across bicultures would serve as a similar or better proxy than functional diversity (FDis) for unmeasured functional variation among plots (Cadotte et al. 2008, Purschke et al. 2013) and that both would serve as strong predictors of NBE. Our findings did not support this expectation. Instead, these diversity metrics were not included in the best models of NBE for the bicultures-only analysis and did not substantially predict overyielding in univariate analysis.

At the neighborhood scale, species identity and abundance best predicted biodiversity effects

We found less evidence for a relationship between biodiversity and growth in stem biomass at the eight-tree neighborhood scale than at the 64-tree plot scale. Our best models of NBE at the plot level included as predictors species richness and single-trait metrics of functional trait magnitude, whereas composition of the local neighborhood (Uriarte et al. 2004, Canham et al. 2006) was more important in predicting growth of individual trees (Table 1.1, Supplementary Table 1.5). For instance, *Q. alba* grows slowly and is probably suppressed by fast-growing neighbors, reducing its contribution to plot-level biomass. At the

same time, *Q. alba* individuals may not shade or suppress other, larger neighbors, so they interfere with adjacent trees' growth at the neighborhood scale (Supplementary Figs. 1.5 and 1.6). Such findings are sensible in light of the fact that a given focal species may facilitate some neighbors and compete with others (Symstad et al. 1998, Kunstler et al. 2012), simultaneously compete with and facilitate neighbors (e.g., belowground vs. aboveground, Montgomery et al. 2010), inhibit close neighbors while facilitating them at a larger scale (van de Koppel et al. 2006), or interact asymmetrically with different-sized neighbors (Weiner 1990, Potvin and Dutilleul 2009).

We observed species-specific variation in the growth of FAB trees alongside heterospecific vs. conspecific neighbors. For instance, *A. rubrum* and *Q. rubra* generally showed elevated growth rates relative to monocultural growth regardless of their partner in bicultural plots (Fig. 1.4, Supplementary Fig. 1.7). These species are slow-growing, have higher stem wood density, and are of intermediate shade tolerance, so they may have experienced facilitation rather than competition from neighbors in the early years of the FAB experiment (as in Dickie et al. 2005). Shade-intolerant *P. resinosa* and *B. papyrifera* showed the opposite response, responding relatively little (DRY ~ 0) to heterospecific neighbors. Furthermore, we do not find obvious patterns of either phylogenetic attraction (improved performance with closely related species) or repulsion (improved performance with distantly related species (Webb 2000, Cavender-Bares and Wilczek 2003). Rather, performance of a given set of species appears to vary based on the particular identities of community members, and on their functional traits. Such species-specific interactions with neighbors (Callaway 1998, Coates et al. 2009) and, potentially, the capacity or inability to respond favorably to a diverse neighborhood (Kelty 2006, Lundholm 2009) in the early years of the FAB experiment may scale up from the neighborhood level to either reduce or augment plot-level productivity (Maestre et al. 2009, Wright et al. 2014).

Neighborhood-level models of overyielding not only included different predictors, but were also less explanatory than plot-level models (Table 1.1; Supplementary Table 1.5). This suggests that microenvironment (Beckage and Clark 2003), size of neighbors (Potvin and Dutilleul 2009), and other factors may influence the stem growth of tree seedlings more than does community diversity. Generally, our findings of different patterns in the biodiversity-productivity relationship at the focal treeand the plot-level highlight the importance of explicit consideration of scale in the design and execution of tree diversity experiments (Symstad et al. 2003).

Complementarity dominates biodiversity effects

Early critiques of biodiversity-ecosystem functioning research highlighted the potential that contributions from influential species, rather than interactions among species, can drive a positive relationship between biodiversity and productivity (Huston 1997, Wardle 1999). In such cases, it is not species interactions that

increase productivity, but the presence of species that can dominate in mixture. In our study, complementarity dominated overyielding across all polycultures, with selection playing a less pronounced, often negative role (Table 1.2; Supplementary Fig. 1.4), consistent with results from mature grassland biodiversity-productivity experiments (Spehn et al. 2005, Cardinale et al. 2007, Fargione et al. 2007, Reich et al. 2012). In contrast, recent work by Tobner et al. (2016), which assessed overyielding in productivity in a similar tree experiment, found that selection effects dominated the biodiversity-tree growth relationship. Our best models of selection effects in bicultures did include univariate functional trait diversity for several traits, suggesting that trait diversity did affect the degree to which influential species contributed to net biodiversity effects (Supplementary Table 1.5). And, in the second year of the study, richness was positively associated with selection effects, suggesting that dominant plants benefited from association with subordinate neighbors (Table 2.2).

Functional traits shape the diversity-stem growth relationship

Though we found that SR was a strong, primary predictor of overyielding in FAB (as in Liang et al. 2016), functional trait values and diversity complemented SR as important predictors in several of our models of stem growth (as in Reich et al. 2012). Other forest biodiversity studies have demonstrated a role for SR (Haase et al. 2015) and also PD and FD (Paquette and Messier 2011, Tobner et al. 2016) in explaining this relationship. In the present work, we contribute to the disentanglement of the consequences of these often-correlated dimensions of biodiversity for stem biomass growth because our bicultures vary PD and FD independent of SR. We observed that when SR was held constant, and abundance often best predicted NBE. Yet functional diversity and communityweighted means of single, influential traits were often predictors of overyielding and CE (Tables 1.1 and 1.2; Supplementary Table 1.5) – evidence of "trait-dependent complementarity," in which particular species' traits contribute to growth in polycultures in ways that do not occur in monoculture (Fox 2005). This observation supports our conclusion that functional trait magnitude and diversity, along with SR, contributed to tree growth in our experiment. Specifically, weighted values of key traits – including mycorrhizal association, leaf nitrogen and calcium, and waterlogging tolerance – served as consistent predictors of overyielding across polycultures, whereas univariate trait diversity was more important as a predictor of CE and SE. Integration of these results suggests some mechanistic explanations of the relationship between diversity and NBE on stem growth in our study.

Plant-mycorrhizal associations are ubiquitous and ecologically significant elements of temperate forests, both affected by plant diversity and substantially contributing to ecosystem productivity (van der Heijden et al. 2008). Yet trees partner with mycorrhizae to acquire nutrients in diverse ways (Lambers et al. 2009), and the composition of the mycorrhizal community in a given forest's soils has distinct ecological consequences for host trees and for the ecosystem. Most notably, arbuscular mycorrhizaeand

ectomycorrhizae-dominated ecosystems cycle nutrients in fundamentally different ways, giving rise to distinct nutrient economies in forests dominated by each fungal type (Phillips et al. 2013). Our findings from the first two full years of the FAB experiment affirm the importance of dominant mycorrhizal association as a key functional trait of temperate trees. Plots consisting primarily of tree species associated with ectomycorrhizal fungi (*Quercus* spp., *Pinus* spp., *T. americana*, and *B. papyrifera*) overyielded more than those consisting of primarily arbuscular species (*Acer* spp. and *J. virginiana*) or a mix of both strategies. This finding may stem in part from the fact that, in our experiment, all of the fastest growing tree species were ectomycorrhizal associates, and thus may be more phosphorus-efficient and nitrogen-"hungry" (Comas et al. 2002). Yet a consistent signal across years and subsets of experimental plots suggests that mycorrhizal type matters to the effect of biodiversity on tree stem biomass (Table 1.1, Supplementary Table 1.5), perhaps reflecting the benefit of ectomycorrhizae in these extremely N-poor soils.

Communities consisting of plants with traits from various positions in the leaf economic spectrum (Wright et al. 2004) tended to overyield the most in stem biomass. In assessing NBE (Table 1.1) across polycultures, we documented patterns of greater growth in communities dominated by trees with nitrogen-poor but calcium-rich leaves. At first blush, these observations seem incompatible. Our finding that high leaf calcium (*T. americana*) predicts overyielding suggests that plots with more angiosperm species are more productive. On the other hand, the pattern of low leaf nitrogen predicting overyielding suggests that gymnosperms (*Pinus* spp. and *J. virginiana*) promote stem growth as well. Given these findings, we conclude that communities with diverse leaf traits overyield more than more functionally similar communities (as in Flynn et al. 2011).

Our observation that functional trait values and diversity structure the diversity-productivity relationship emphasizes the ecosystem-level consequences of plant traits (Tilman et al. 1997b, Diaz and Cabido 2001, Lavorel and Garnier 2002, Díaz et al. 2004). The positive relationship between trait diversity and overyielding across random polycultures is consistent with the diversity hypothesis of Tilman et al. (1997) and with experimental evidence over 13 yr (Reich et al. 2012) supporting the idea that increased diversity in functional traits should enhance ecosystem function through the coincidental dominance of influential species (the selection effect) or through niche partitioning (complementarity). Yet the importance of specific CWMs in the prediction of overyielding also lends support to Grime's (1998) mass-ratio hypothesis, which proposes that the traits of especially dominant or abundant species contribute disproportionately to ecosystem processes (Mokany et al. 2008, Roscher et al. 2012, 2013). In such a scenario, some especially influential species (such as *T. americana*, which raises the CWM and FDis of leaf calcium of plots in which it is planted) contribute disproportionately to NBE on stem biomass growth.

Table 1.1 – Best models of net biodiversity effects (NBE) on stem biomass growth for random polyculture plots (A) and neighborhoods (B) in 2014-2015.

	Predictor			
	Std. Coefficient	*t*-Statistic	df	Significance
(A) All Polycultures – NBE				
Species richness	0.867	4.801	19	***
Mycorrhizal association CWM	0.900	4.233	19	**
Tree height	0.250	1.433	19	
Tree diameter	−0.087	−0.465	19	
Waterlogging tolerance CWM	0.963	2.849	19	*
Leaf nitrogen CWM	−1.252	−3.659	19	**
Leaf calcium CWM	0.873	3.218	19	**
(B) Neighborhoods – NBE				
Q. alba abundance	0.068	3.781	5970	***
Tree diameter	0.187	5.155	5970	***
J. virginiana abundance	−0.198	−8.909	5970	***
P. banksiana abundance	−0.222	−8.976	5970	***
Q. macrocarpa abundance	0.071	3.910	5970	***
B. papyrifera abundance	−0.087	−3.356	5970	***
A. rubrum abundance	0.005	−0.248	5970	
Tree height	0.087	2.048	5970	*

Notes: CWM, Community-Weighted Mean. For polyculture plots, mixed-effects model with random intercept based on plot composition, which consists of 25 levels and yielded a residual of 0.077. For neighborhoods, mixed-effects model with random intercepts based on species (with 12 levels and a residual estimate of 0.797) and a spherical correlation structure based on easting and northing location in the experiment. Conditional r^2 of polyculture plots = 0.925; neighborhood plots = 0.0964. Significance of predictors is given as non-significant ($P > 0.10$; blank), sig. ($0.5 > 0 > 0.01$; *), highly sig. ($0.01 > 0 > 0.001$; **), or very highly sig. ($P < 0.001$; ***). Regression coefficients are standardized. Denominator degrees of freedom are given for all terms. Numerator degrees of freedom are 1 in all cases as predictors are continuous.

Table 1.2 – Best models of Complementarity (A) and Selection (B) effects on stem biomass growth for random polyculture plots in 2014-2015.

	Predictor			
	Std. Coefficient	*t*-Statistic	df	Significance
(A) All polycultures – complementarity				
Q. rubra abundance	−0.351	−2.957	34	**
P. resinosa abundance	−0.161	−1.404	34	
P. banksiana abundance	0.223	1.874	34	|
(B) All polycultures - selection				
Species richness	0.284	2.299	23	*

Notes: For c*omplementarity* polycultures, mixed-effects model with random intercept based on plot composition, which consists of 25 levels and yielded a residual of 0.312. For selection polycultures, mixed-effects Model with random intercept based on plot composition which consists of 25 levels and yielded a residual of 0.322. Conditional r^2 of complementarity polyculture plots = 0.235; selection polycultures = 0.080. Significance of predictors is given as non-significant ($P > 0.10$; blank), marginally significant ($0.1 > P > 0.5$; |), significant ($0.5 > 0 > 0.01$; *), highly significant ($0.01 > 0 > 0.001$; **), or very highly significant ($P < 0.001$; ***). Regression coefficients are standardized. Numerator degrees of freedom are 1 in all cases as predictors are continuous.

Figure 1.1 – The Forests and Biodiversity (FAB) experiment (a) is located in Minnesota, USA. (b) The experiment consists of three 600 m2 blocks, each consisting of 49 plots, each 9.25 m2. Plots have a species richness of one (white), two (light gray), five (dark gray), or 12 (black). (c) Each plot consists of 64 trees, planted in a grid at 0.5 m. Photos show (d) several bicultural and monocul- tural plots and (e) an overhead view of a Quercus alba-Pinus strobus plot in 2015.

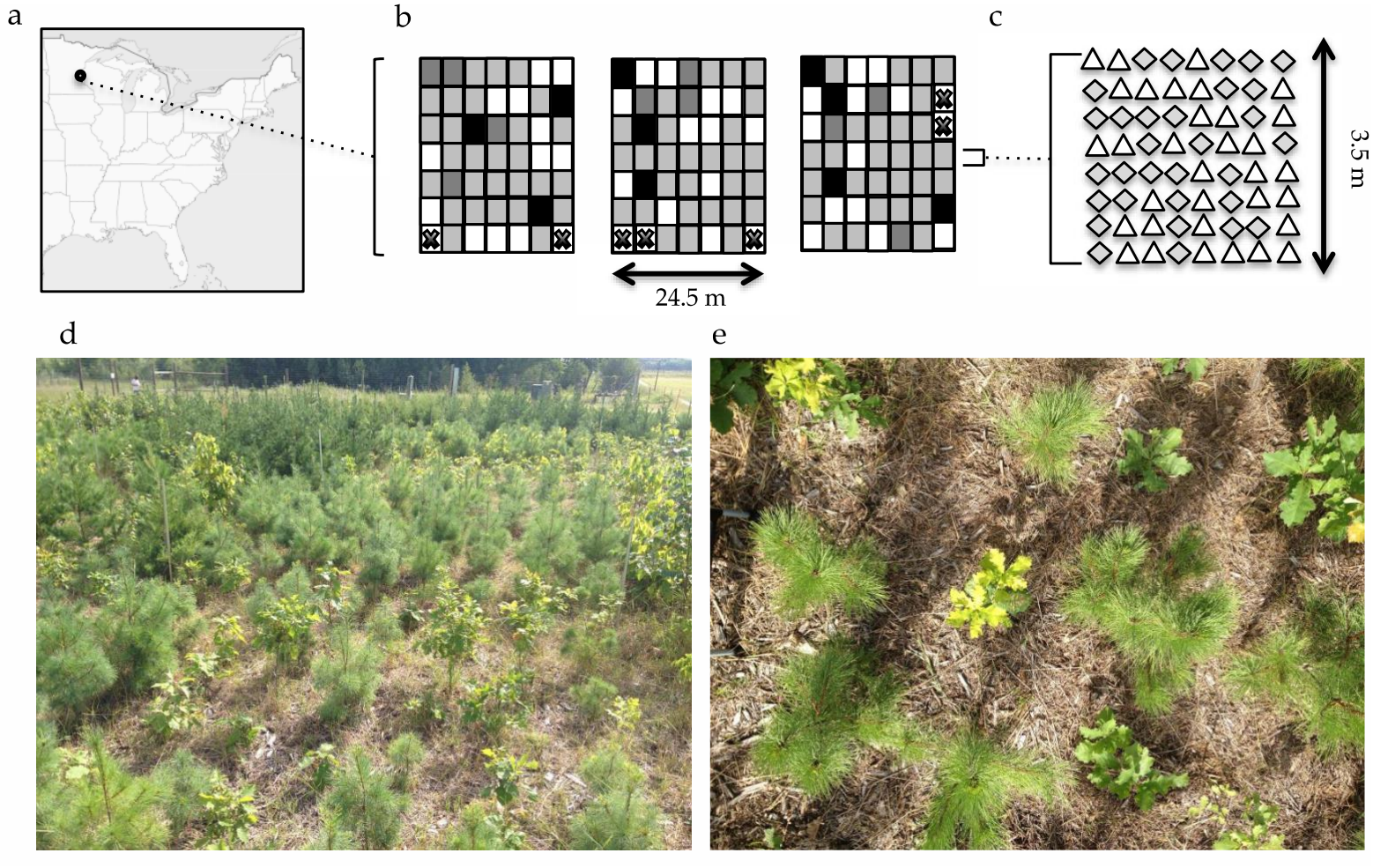

a
b
c
24.5 m
3.5 m
d
e

Figure 1.2 – Phylogenetic relationships and functional traits of all species in the FAB experiment. Continuous trait values vary between light gray (low) and dark gray (high). Leaf Habit is either broadleaf (light gray) or conifer (dark gray). Mycorrhizal associ- ation is primarily arbuscular (AMF; light gray) or ectomycorrhizal (EMF; dark gray). All trait values are given in Supplementary Table 1.2.

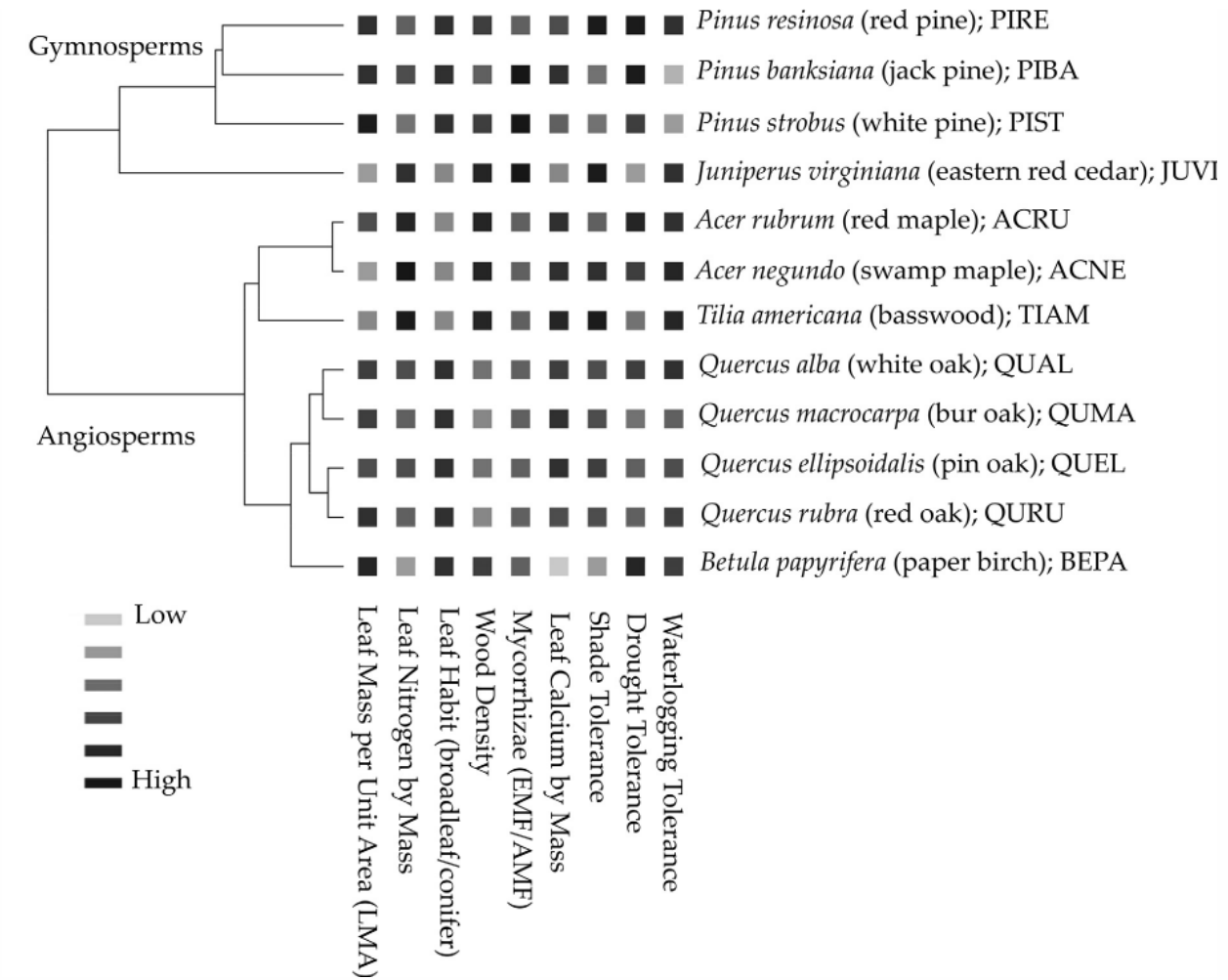

Gymnosperms
Angiosperms
Pinus resinosa (red pine); PIRE
Pinus banksiana (jack pine); PIBA
Pinus strobus (white pine); PIST
Juniperus virginiana (eastern red cedar); JUVI
Acer rubrum (red maple); ACRU
Acer negundo (swamp maple); ACNE
Tilia americana (basswood); TIAM
Quercus alba (white oak); QUAL
Quercus macrocarpa (bur oak); QUMA
Quercus ellipsoidalis (pin oak); QUEL
Quercus rubra (red oak); QURU
Betula papyrifera (paper birch); BEPA
Low
High
Leaf Mass per Unit Area (LMA)
Leaf Nitrogen by Mass
Leaf Habit (broadleaf/conifer)
Wood Density
Mycorrhizae (EMF/AMF)
Leaf Calcium by Mass
Shade Tolerance
Drought Tolerance
Waterlogging Tolerance

Figure 1.3 – Predicted response of Net Biodiversity Effects (NBE) on biomass (kg/yr; square root-transformed with sign retained) to (a) species richness and to (b) the proportion of a focal tree's eight closest neighbors that were J. virginiana (eastern red cedar; JUVI). Species Richness was a highly significant, positive predictor of average per-tree NBE at the plot level from 2013 to 2015 while proportion of JUVI neighbors was a highly significant, negative predictor of per-tree NBE at the neighborhood level in both years. In Panel a, Curves shown are 90% predictions from multiple linear regression models A (2013–2014; light green) and D (2014–2015; dark green) in Table 1.1 and Supplementary Table 1.5. In Panel b, curves shown are predictions from fixed-effects only model variants of models C (2013–2014; light green) and F (2014–2015 dark green) in Table 1.1 and Supplementary Table 1.5, with points jittered (factor = 0.5) to reduce overlap.

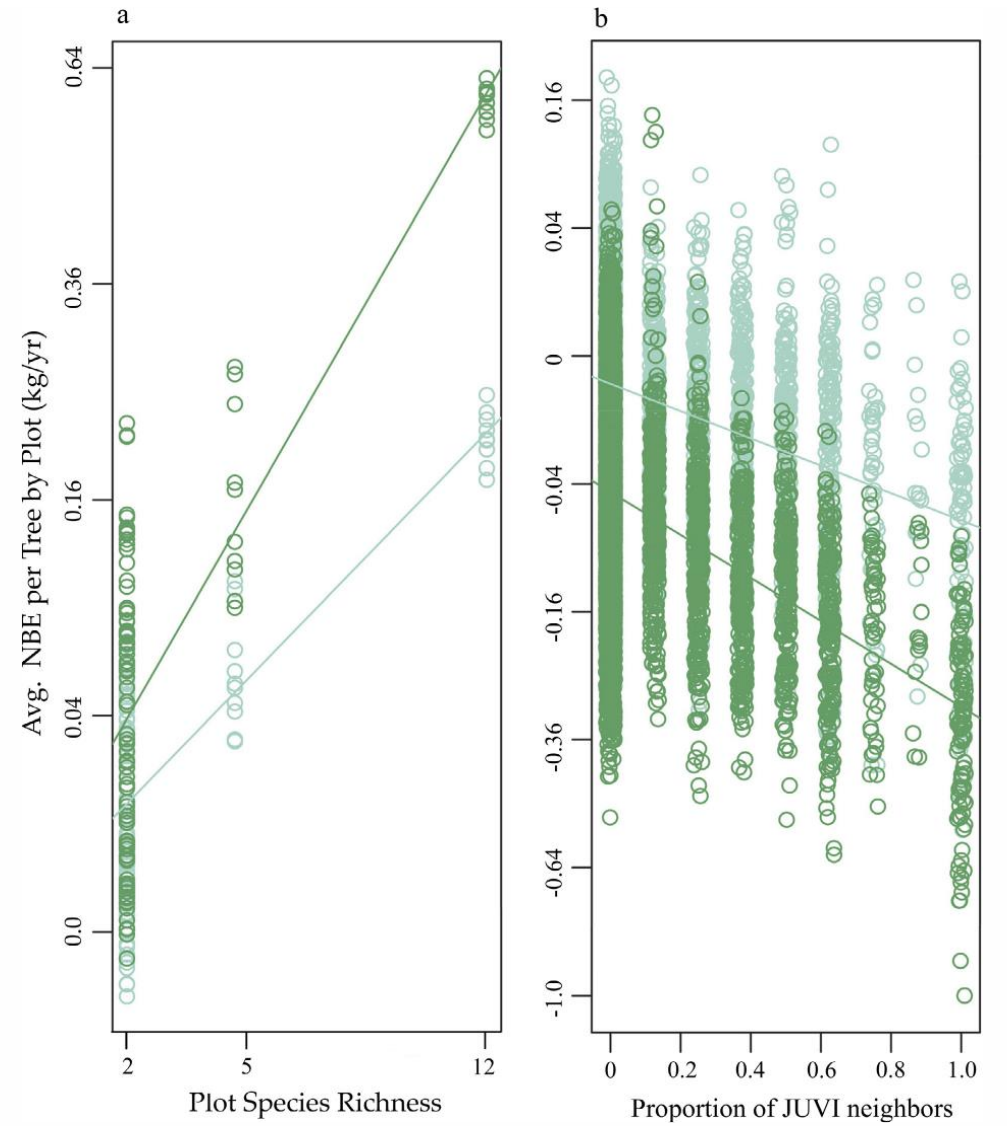
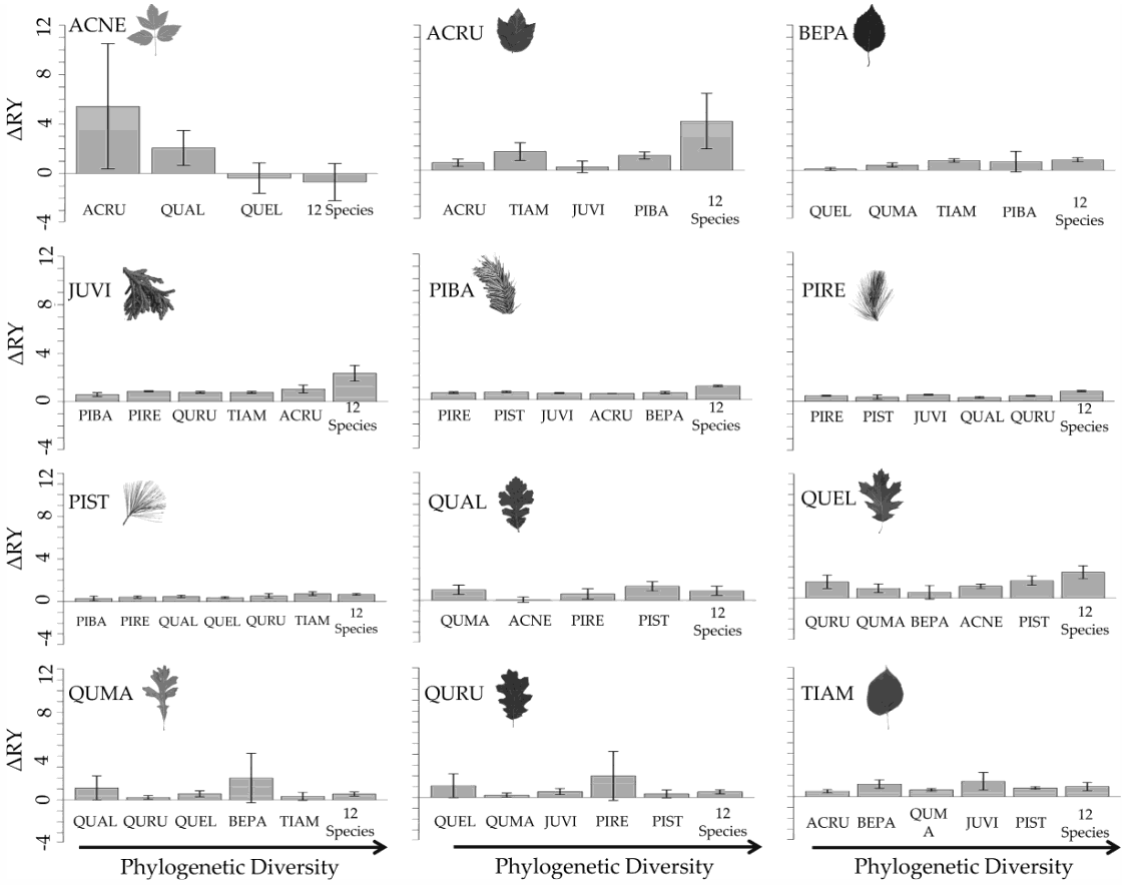


Figure 1.4 – Average difference between observed and expected yield (DRY; Loreau and Hector 2001) on a per-species basis for the 2014–2015 growing season in all biculture and twelve-species plots. Five-species plots were not compositionally replicated, and so are not included. Each column displays DRY for a focal species (upper left of panel) when grown with the species whose name is given at the base of the column. Error bars give one standard error, with plots serving as replicates. Zero indicates productivity as expected in monoculture. Positive values indicate overyielding and negative values indicate underyielding. Columns are ordered by Faith's Phylogenetic Diversity (FPD) with the least diverse community on the left of the panel and the most diverse community on the right. Because Faith's PD measures branch length across a community's phylogeny, twelve-species communities are always trea- ted as more phylogenetically diverse than bicultures.



Chapter 2

Consequences of community structure and diversity for herbivory and disease vary across spatial scales in a tree diversity experiment [3]

[3] This chapter has been accepted pending revision at the *Journal of Ecology* (April 2018). The research presented here was conducted in collaboration with Jeannine Cavender-Bares, Sarah E. Hobbie, Peter B. Reich, and Rebecca A. Montgomery.

Introduction

Herbivory is the process by which animals consume living plant tissue; pathogenic microbes, whether fungi or bacteria, also damage plants, causing disease. In forests, herbivores and pathogens can cause either stand-wide or species-specific dieback. This enemy-induced mortality leads to losses in both the timber and food supply (provisioning services) and aesthetic and recreational value (cultural services) of forests. As such, even though moderate damage does contribute to the healthy function of forests and the broader landscape (supporting and regulating services; Schowalter 2012), control of forest herbivores and pathogens remains a central objective of the silvicultural management of natural stands and plantations (Wainhouse 2005).

The capacity of biodiversity to protect forest trees from natural enemies has been demonstrated empirically (Qiong et al. 1996, Jactel et al. 2005, Jactel and Brockerhoff 2007, Haas et al. 2011, Lind et al. 2015). Yet this relationship appears far from general, with many experiments reporting no effect or a positive effect of diversity (Vehvilainen et al. 2007) on damage. Despite some preliminary work (Castagneyrol et al. 2013b, Schuldt et al. 2014, Kozlov et al. 2015), it is not clear which dimensions of biodiversity (Naeem et al. 2012) most strongly affect a tree's vulnerability to herbivores and pathogens.

Several mechanistic hypotheses have been developed to explain the empirically demonstrated relationship between biodiversity and natural enemy damage. The Resource Concentration Hypothesis (RCH; Root 1973) posits that the local density of acceptable hosts contributes to the damage that a particular individual experiences from herbivores or pathogens. Yet the expectations arising from the RCH depend on the host specificity of a given natural enemy (Castagneyrol et al. 2013b). A low density of hosts should decrease damage by a specialist (monophagous) or semi-specialist (oligophagous) herbivores by disrupting insect feeding, movement, or oviposition (Andow 1991), or by decreasing the local pathogen load (Mitchell et al. 2002), leading to "associational resistance" (Tahvanainen and Root 1972), in which association with diverse neighbors protects a particular plant. For generalist (polyphagous) enemies, the expectations from the RCH are less clear. Potentially, greater host diversity can increase damage by generalists through dietary mixing (Bernays et al. 1994) or spillover onto less-preferred but palatable hosts (Power and Mitchell 2004), leading to more damage with diverse neighbors – "associational susceptibility" (White and Whitham 2000, Schuldt et al. 2010). Alternatively, plant apparency theory (Feeny 1976, Endara and Coley 2011) predicts that a plant's vulnerability to a natural enemy will depend on how likely that plant is to be found by its predator or pathogen. Specialist enemies might be expected to find hosts more easily if hosts stand out from their neighbors in a structurally diverse environment (Castagneyrol et al. 2013a) or with more difficulty if diversity conceals suitable hosts (Pfister and Hay 1988, Zhu et al. 2000, Damien et al. 2016). In the case of pathogens, disease propagules transmitted by wind, for instance, might simply be

more likely to "encounter" a large plant or patch of suitable host plants at high density (Laine and Hanski 2006).

Though the consequences of diversity for ecosystem function have been shown to vary with spatial scale (Chase and Leibold 2002, Symstad et al. 2003), we lack a clear understanding of how scale affects the diversity-damage relationship (Thies et al. 2003, Hambäck et al. 2009, Loranger et al. 2013). It has been suggested that ecological processes should demonstrate and therefore be studied within characteristic domains of spatial scale (Wiens 1989). To date, research has suggested that such domains exist, at least for particular clades or geographic regions. For instance, community assembly is shaped by dispersal limitation locally (1 m to 10 km) for California's serpentine grasslands (Germain, Strauss, & Gilbert, 2017) but continentally (300 km to 3300 km) for European aquatic plant and cladoceran communities (Viana et al. 2016). Past work suggests that vegetation diversity is likely to shape herbivory and pathogen damage at small spatial scales by altering the movement and abundance of herbivores and pathogen propagules (Hambäck et al. 2009, Genung et al. 2012, Tack et al. 2014, Muiruri et al. 2016, Ekholm et al. 2017).

The objective of this study was to disentangle the consequences of different dimensions of host community diversity (species richness, phylogenetic and functional diversity, and host density) and structure (plant size and neighbor size) for damage by generalist and specialist herbivores and specialist pathogens across spatial scales. To this end, we measured putatively generalist leaf removal (in eight host species) and specialist galling (four host species) and leaf mining (five host species) herbivory and specialist anthracnose infection and rust infection (in one host species each) in a forest diversity experiment over three years. We expected that:

1) Increasing the neighborhood diversity of a given host tree should make it more vulnerable to leaf removal if leaf removers are generalists. Alternately, if leaf removers are (semi-)specialists, diversity should reduce leaf removal herbivory (Wein et al. 2016, Brezzi et al. 2017, Zhang et al. 2017).
2) Increasing host plant apparency and/or neighborhood density of conspecifics would make trees more vulnerable to specialist or semi-specialist leaf mining, galling, and pathogen damage (Castagneyrol et al. 2013a).
3) The consequences of biodiversity for natural enemy damage should demonstrate a characteristic domain of scale (Wiens 1989, Germain et al. 2017), with neighborhood structure and diversity having a stronger effect at small (1 m^2) spatial scales.

Methods

Experimental Platform

We measured herbivory and disease damage in the Forests and Biodiversity (FAB); this experiment is described in this dissertation (Chapter 2) and formally elsewhere (Grossman et al. 2017).

We modeled herbivory using characteristics of focal trees (selection procedures for these trees are described in Appendix S2), the physical structure of their community, and the diversity of their community; each of these is reviewed below and in Appendix S2. Focal tree height was included in all models as a covariate. To assess the degree to which damage varied with spatial scale, we define a focal tree's community at four scales spanning planted plot boundaries: a focal tree's eight (within 1 m^2), 24 (4 m^2), 48 (9 m^2), and 80 (16 m^2) nearest neighbors. All analyses were carried out in R (R Core Team, ver. 3.4.3).

Tree Size and Community Structure

We characterized focal tree characteristics including tree height and height apparency (one particular metric of plant apparency). Height to tallest leader (cm) for a given year was measured to the nearest 0.5 cm in September of the year prior to the one in which herbivory measurements were taken. Height apparency (ΔH) measures the extent to which a focal tree is more apparent to herbivores because its height is different than its neighbors' heights (Castagneyrol et al. 2013; Appendix S2). The metric becomes larger than 0 if a tree is taller than surrounding trees. To quantify community structure, we also used annual measurements of plant height in FAB to calculate the average diameter and height of a focal plant's community.

Community Diversity Characteristics

We calculated both neighborhood and plot diversity for each focal tree measured in this study using a number of metrics related to community composition and richness, phylogenetic diversity, functional trait means, and functional diversity. Compositional predictors include the proportions of each constituent species as well as the proportions of oaks, maples, and angiosperms in a focal tree's neighborhood. Likewise, we included species richness ranging from one to eight (for 8-tree neighborhoods) or 12 (for all others). To represent community phylogenetic diversity, we calculated Webb and colleagues' (2002) phylogenetic mean pairwise distance (PD), which increases from zero with increasing diversity. We used Zanne and colleagues' (2014) phylogeny and the "picante" package in R (Kembel et al. 2010) for calculation of PD.

For each neighborhood, we calculated multidimensional functional mean pairwise distance (FD; calculated as PD above) for six leaf traits we deemed potentially important for herbivory: specific leaf area (SLA) and leaf water content, and concentrations of lignin, nitrogen, phosphorus, and condensed tannins. We also calculated FD individually for each of these traits. Finally, we calculated the community-weighted mean

(CWM; Mokany et al. 2008) for each trait. We measured all traits on a species basis using leaves collected from experimental plants or nearby conspecifics (methods are detailed in Appendix S2; trait values are given in Supplementary Fig. 2.1).

Herbivory and Anthracnose Measurements

We measured leaf-level herbivory in late August and early September 2014-16, the second through fourth year of the FAB experiment (N = 1,225 tree-year measurement combinations). These surveys were conducted on the eight angiosperm species in FAB: box elder (*Acer negundo* L.), red maple (*A. rubrum* L.), paper birch (*Betula papyrifera* Marshall), white oak (*Quercus alba* L.; 2015-16 only), pin oak (*Q. ellipsoidalis* E.J. Hill), bur oak (*Q. macrocarpa* Michx.; 2015-16 only), red oak (*Q. rubra* L.), and basswood (*Tilia Americana* L.). In a given year, we measured herbivory in three individuals of each of these species in each plot in which they occurred, selecting only individuals in the interior of plots and with eight living neighbors. We measured the five youngest, fully expanded leaves on the leader stem of each plant measured. Each year, all measurements took place over two to three weeks and were conducted by the same investigator (further sampling details in Appendix S2). To quantify chewing herbivory (Fig. 2.1E; 2014-16) we measured each sampled leaf using a translucent grid divided in one cm^2 and recorded leaf size and estimated leaf area removed by herbivores to the nearest estimated 0.5 cm^2. We also surveyed galling on oak leaves and leaf mining on both oak and paper birch leaves in the 2015 and 2016 growing seasons. (We never observed birch galling.) We counted the total number of galls or mines per leaf on the leaves for which we measured removal herbivory. Finally, in 2015 and 2016, we also graded the five newest, fully expanded leaves on all measured red maple plants for anthracnose infection using a 0-5 categorical scale ranging from no infection to coverage of the entire leaf. Further natural history information about leaf galling, leaf mining, and anthracnose infection is given in Appendix S2.

Eastern Red Cedar Gall Rust Measurements

Following observations of infection in 2015, we monitored the abundance of galls formed by the basiodiomycete cedar apple gall rust (*Gymnosporangium juniperae-virginiae* Schwein.) infection in eastern red cedars (*J. virginiana* L.) in spring 2016 (Fig. 2.1F; Appendix S2). Once new galls had become prominent in the spring, we conducted a one-day survey of gall rust infection on all eastern red cedar individuals in the experiment (N = 719 trees). The same investigator surveyed each individual, spending roughly one minute per tree, and recorded the total number of fresh galls on the tree's branches. As trees were still shorter than 2 m in height, visual inspection of whole trees was feasible. We present these data as total number of cedar galls observed per plant.

Data Analysis

To assess the effect of diversity and plant size on leaf removal we treated the maximum proportion of a single leaf removed from a given plant in a given year as our response variable (Appendix S2). Whereas low-level removal – such as that of only 2% of a leaf's total area – does harm a host plant, we focus on removals of larger quantities of tissue with, we assert, greater fitness consequences. We emphasize in our interpretation that models of maximum leaf removal emphasize the effects of diversity on extreme leaf removal events. We modeled the effects of diversity for leaf removal across all species and all four spatial scales and for each angiosperm species, using mixed-effects linear models with random intercepts for tree, nested within plot, nested within block, and for study year ("lme4" R Package; Bates et al. 2015). The all-species model also included a random intercept for species. Fixed effects were selected from candidate predictors described above and including all focal tree, structural, compositional, and diversity metrics using the *glmulti* package (Calcagno and de Mazancourt 2010). All models included plant height as a covariate. Marginal r^2, which approximates variation explained by all fixed predictors in a mixed-effects model, and conditional r^2, which accounts for variation explained by all fixed and random predictors, were calculated using the *MuMIn* package (Burnham and Anderson 2002). Further details of variable selection and model fitting are given in Appendix S2.

We summed counts of galls and leaf miners on a per-plant basis and modeled these forms of herbivory across all four spatial scales using zero-inflated negative binomial Poisson regression (*zeroinfl* function in the "pscl" package; Jackman et al. 2015). These models consist of two parts. The first is a logistic regression component that gives the likelihood of finding any galls or miners at all on a plant; coefficients give the *vulnerability* of a particular plant to herbivory. The second model component is a typical Gaussian regression. Predictors from this model component describe the *intensity* of galling or leaf mining. Model selection and fitting are further described in Appendix S2.

We modeled anthracnose score as total score on a per-plant basis, ranging from zero for unaffected plants to 25 for plants with all leaf area covered on all five leaves using hurdle models (glmmADMB R package; Martin *et al.* 2005; Skaug *et al.* 2016). Hurdle modeling, like the integrated models used for galling and leaf mining, represents infection vulnerability and intensity as distinct processes.

Total counts of *G. juniperae-virginiae* galls were zero-inflated and Poisson-distributed. As such, we selected variables and built models for this response as described above for galling and leaf mining herbivory.

Results

We measured leaf removal, galling, and mining herbivory over three years, *A. rubrum* anthracnose leaf infection over two years, and whole-plant *J. virginiana* gall rust infection in a single year (Table 2.1). Leaf

removal and galling differed significantly across species and study year with a significant interaction between these factors. Leaf mining varied significantly only by species; neither it nor anthracnose infection varied by year. Leaf removal and anthracnose infection also varied significantly with leaf position, but galling and leaf mining did not (Supplementary Figure 2.2). Given this, tree species, study year, and leaf order are included in models described below as appropriate.

Leaf Removal

Surveyed leaves ranged from totally undamaged to completely consumed with only a petiole remaining, and herbivory rates depended significantly on study species, leaf order, and study year (Table 2.1). Notably, red oaks suffered significantly more leaf removal (17% of total area) than any other species; paper birch (7.3%) and box elder (6.6%) were significantly less vulnerable. The effect of leaf order on leaf removal varied with species (Supplementary Figure 2.2), but not consistently (Table 2.1). Finally, average leaf removal varied among study years (from 4.4% in 2014 to 7.3% in 2015; Table 2.1).

Compared to block and plot location and study year, fixed predictors of leaf removal, including plant size and community composition and diversity, explained little variation in leaf removal across all species ($r^2_{marginal} < 0.004$ and $0.03 < r^2_{conditional} < 0.46$ across spatial scales; Table 2.2). For particular species, height apparency, neighborhood composition, neighborhood diversity, and neighborhood functional trait means and diversity all had idiosyncratic effects on leaf removal. Selection of these variables and the magnitude and direction of their effects on leaf removal varied with species and spatial scale (Table 2.2; Supplementary Table 2.1).

Because height apparency was consistently included in the best models of leaf removal across species, we created a second set of models in which leaf removal at all spatial scales and for all species was predicted by only tree height and height apparency (and all random effects as described above; Supplementary Table 2.2). When height apparency contributed meaningfully to leaf removal ($R^2_{marginal} > 0.01$), species-specific patterns in its effects become evident. In box elder and paper birch, more apparent individuals incurred more herbivory. In contrast, across oak species and basswood, more apparent trees generally experienced less. In red maple, the effects of apparency switched between positive (at larger spatial scales) and negative (at the smallest one).

Models of leaf removal herbivory at smaller spatial scales (1-4 m^2) consistently outperformed those at larger scales (9-16 m^2). In model comparison, AIC scores were, with few exceptions, lower for models of leaf removal in 8and 24-tree neighborhoods than for 48or 80-tree neighborhoods (Fig. 2.2). This was the case both for models created through variable selection and for those in which height and height apparency were the only fixed predictors (Table 2.2, Supplementary Table 2.2 and 2.3)

Across models of leaf removal, fixed-effects predictors predicted very little of the observed variability in herbivory ($0.0001 < R^2_{conditional} < 0.164$); most of each model's predictive power was associated with random effects ($0.031 < R^2_{marginal} < 0.458$). Several plant traits emerged as predictors of maximum leaf removal at the species level. Leaf removal was negatively associated with leaf water content and phosphorus and, for some species, was positively associated with diameter (Appendix S2).

Oak Leaf Galling

Oak galls were very rare, so we pooled records of gall formation across all four oak species in order to model the relationship between gall formation and diversity. Model comparison indicated that the best model of oak gall vulnerability and intensity was one including focal plant species, height, and height apparency at the 24-tree spatial scale (4 m^2; Table 2.3), and proportion of oak neighbors at the 80-tree (16 m^2) scale. Though height apparency did not have a significant effect on oak galling, oaks with more congeneric neighbors were more likely to have galls (Fig. 2.3). White oaks (*Quercus* Section *Quercus*; white oak and bur oak) in the experiment were also more likely to suffer from gall formation than the red oaks (Sect. *Lobatae*; pin oak and red oak). Oaks in Sect. *Quercus* with more *Lobatae* neighbors were more vulnerable to galling herbivory (Supplementary Fig. 2.3), although the effect was not reciprocal.

Oak and Birch Leaf Mining

The best model of oak leaf miner vulnerability and intensity included focal plant height, height apparency, and proportion of oak neighbors at the 8-tree scale (1 m^2 neighborhoods). Height apparency did not significantly affect oak leaf miner vulnerability or intensity although taller trees were generally more likely to have leaf miners. Oaks with more congeneric neighbors within 1 m also experienced a higher intensity of leaf mining (Fig. 2.3). As was the case for galling, proximity to *Lobatae* neighbors made oaks in Sect. *Quercus* more vulnerable to leaf mining herbivory, although the reverse was not the case (Supplementary Fig. 2.3; Appendix S2).

The best model of paper birch leaf miner vulnerability and intensity included focal plant height, height apparency, and proportion of paper birch neighbors at the 8-tree scale (1 m^2 neighborhoods). Trees with more conspecific neighbors were marginally less likely to have leaf miners (Fig. 2.3). Among birches that were attacked by leaf miners, trees that were taller than their neighbors had significantly fewer mines (Table 2.3).

Red Maple Anthracnose Infection

Models of red maple anthracnose vulnerability and intensity generally performed similarly (< 2 ΔAIC). Results from the better-performing models indicate that maples with more phylogenetically diverse neighbors at the 24-tree (4 m^2) scale experienced a lower intensity of infection (Fig. 2.3, Table 2.3).

Eastern Red Cedar Gall Rust Infection

The best models of eastern red cedar gall rust infection included focal plant height, height apparency, and proportion of eastern red cedar at the 8-tree scale. The only significant predictor of gall rust infection was proportion of conspecific neighbors; trees with more conspecific neighbors at the 8-tree (1 m^2) scale had fewer galls (Fig. 2.3, Table 2.3).

We also observed both speciesand leaf-level relationships among vulnerability to leaf removal, vulnerability to galling, and vulnerability to mining; these are detailed in Appendix S2.

Discussion

The present work expands on recent biodiversity-ecosystem functioning (BEF) research addressing which aspects or dimensions of biodiversity drive the effect of diversity on ecosystem processes such as herbivory (Castagneyrol et al. 2013b, Loranger et al. 2013, Schuldt et al. 2014), and at what spatial scales (Thies et al. 2003, Hambäck et al. 2009). We found that the consequences of community structure (plant size and neighbor size) and diversity (species richness, phylogenetic and functional diversity, and host density) for herbivory and disease differed across clades of host and their herbivores and pathogen, and that they were best predicted at small (< 4 m^2) spatial scales (Hambäck et al. 2009). Plant height apparency, which often had host speciesand herbivore-specific effects, was frequently an important diversity-related predictor of herbivory (Castagneyrol et al. 2013a).

In our study, the consequences of community structure and diversity for one form of putatively generalist herbivory, leaf removal, depended on host species; we did not find evidence of the hypothesized general relationship between this form of herbivory and any one measure of diversity (Vehvilainen et al. 2007, Jactel and Brockerhoff 2007). Instead a variety of species-specific indices of community diversity emerged as predictors of herbivory. These included the species richness, trait diversity, and community-weighted trait means of the neighborhood surrounding a focal tree (Table 2.2). No single metric of community diversity or structure consistently predicted leaf removal across species, although height apparency was frequently recommended for inclusion in models through variable selection. This finding of the species-specificity of leaf removal damage suggests that this form of damage may be caused by multiple, more specialized herbivores preying on preferred hosts, rather than by generalists. The leaf removal we observed may have been caused by mechanisms including dietary mixing (Bernays et al. 1994, Unsicker et al. 2008,

Brezzi et al. 2017) and spillover effects (Power and Mitchell 2004, Vehviläinen and Koricheva 2006), but we cannot conclude this in the absence of information about herbivore identity and diet breadth. As such, future investigators should collect this information when possible along with measurements of herbivore damage (Vehvilainen et al. 2007, Lau et al. 2008, Castagneyrol et al. 2013a).

Like generalist herbivores, particular specialist herbivores and pathogens showed distinct responses, including both associational susceptibility and resistance, to changing community structure and diversity (Fig. 2.3). We documented associational susceptibility of birches to leaf miners and of eastern red cedars to gall rust in diverse plots, potentially due to either a reduction in the local intensity of herbivores or spores (the "host dilution effect"; Otway et al., 2005; Plath et al., 2012) or, in the case of birches, to "spillover" of oligophagous species that prefer other hosts but oviposit on birches in diverse environments (White and Whitham 2000, Plath et al. 2012). On the other hand, our finding that oak vulnerability to galling and intensity of leaf mining was more severe in the presence of nearby oaks conforms to expectations of associational resistance to specialist feeders (Tahvanainen and Root 1972) such as monophagous gall formers (Abrahamson et al., 1998; Hough, 1951) and oligophagous leaf miners (Auerbach and Simberloff, 1988; Faeth et al., 1981), which can feed on only one or a few related species (Jactel and Brockerhoff 2007, Lau et al. 2008, Orians and Björkman 2009, Himanen et al. 2010, Castagneyrol et al. 2013a). Similarly, we found that red maples experienced a lower intensity of anthracnose infection in more phylogenetically diverse environments (Gilbert 2002, Pautasso et al. 2005, Peay and Bruns 2014). This may be due to the fact that trees with many conspecific neighbors were likely to be physically proximal to large stores of anthracnose spores coming from the previous year's undegraded leaves, increasing their exposure (as in Fitzell & Peak 1984; Hantsch *et al.* 2013). Taken together, these findings of both associational susceptibility (in birches and eastern red cedar) and resistance (in oaks and red maples) to specialist herbivores and pathogens suggests that diversity does not uniformly affect specialist natural enemies, paralleling previous work in forest (Vehvilainen et al. 2007, Jactel and Brockerhoff 2007) and grassland (Meyer et al. 2017) ecosystems. Ultimately, further assessments of the degree to which biodiversity protects plants from specialist herbivores and pathogens can consolidate our understanding of the generality and mechanistic basis of these relationships (e.g. Damien et al., 2016; Dillen et al., 2017; Muiruri, Milligan, Morath, & Koricheva, 2015).

Across herbivore, pathogen, and host identity, we found that the effects of community structure and diversity on natural enemy damage to trees were strongest at small (< 4 m^2) spatial scales (Fig. 2.2; Supplementary Table 2.3). For chewing damage to six of eight species measured, oak and paper birch leaf mining, red maple anthracnose infection, and cedar apple gall rust infection, the best models of vulnerability to and intensity of damage were those that included community structure or diversity at the 8or 24-tree neighborhood scale (1 and 4 m^2, respectively). These findings are suggestive a of a

"characteristic" domain for biodiversity-herbivory dynamics (Wiens 1989, Thies et al. 2003, Germain et al. 2017), in which the effects of, for instance, plant height apparency or host concentration, are strongest at small scales (Hambäck et al. 2009). Yet the scaling of this relationship is not likely to be universal. We found, for example, that gall formation on oaks was best predicted by a combination of community composition and structure at both small (4 m^2) and large (16 m^2) scales. Since gall-forming wasps are small-bodied species specialists that can travel long distances (Hough 1951, Abrahamson et al. 1998), it may be the case that, in the FAB experiment, they can respond to community diversity across spatial scales (Stone et al. 2002, Vehvilainen et al. 2007, Sobek et al. 2009).

Though height apparency (Feeny 1976) did not always have a consistent effect on herbivore and pathogen damage in our study, it was frequently a predictor of these processes. Our variable selection protocol frequently resulted in inclusion of height apparency in final models, even if it was not a strong predictor of herbivore or pathogen damage. We did find that box elder and paper birch trees that were taller than their neighbors were generally more vulnerable to chewing herbivores, echoing past work on leaf mining in oak (*Q. robur*; Castagneyrol, Giffard, et al., 2013) and on gall formation in chestnuts (*Castanea sativa*; Guyot et al., 2015), and pine (*Pinus pinaster*; Damien et al., 2016). Yet we also documented the reverse pattern for other species: more apparent red maples, oaks, and basswoods were less vulnerable to herbivores. This pattern of apparency-driven resistance could result from one of two mechanisms. Taller plants could escape herbivores, especially those with limited mobility, producing a genuinely protective apparency effect. Or, alternately, trees that are much shorter than their neighbors (and thus have negative height apparency values) could be more visible, or apparent, to herbivores and thus more vulnerable. If the latter mechanism affects herbivore behavior, then herbivory may be highest at *either* high *or* low height apparency, rather than at only high apparency. Regardless, the frequent inclusion of plant height apparency in our models of herbivore and pathogen damage and its significant role in protecting some species from damage and exacerbating damage in others speaks to its potential importance as a mediator of herbivory and suggests avenues for further exploration of the concept. Previous research in which apparency has been invoked as a determinant of damage to plants has largely focused on the roles that focal and neighbor plant height play in regulating flying herbivores (e.g. Castagneyrol et al., 2013; Régolini et al., 2014); expectations for other herbivores and pathogens are underdeveloped. Whereas vulnerability to herbivory depends to some extent on insect choice (e.g. Bultman and Faeth 1986) and is mediated by chemical defenses, fungal infection depends instead on the probability that spores will come into contact with appropriate host leaves, with host distribution, landscape structure, and focal plant size and location all playing roles (Peay and Bruns 2014). As such, expectations of the consequences of plant apparency for herbivory and disease damage should reflect the particular biology of the hosts and natural enemies being examined.

Table 2.1 – Differences by study year, species, and leaf position (1 = newest fully expanded leaf) in mean per-leaf A) leaf removal, B) gall formation, C) leaf mine formation, and D) anthracnose intensity. Letters indicate grouping by post-hoc testing ($\alpha = 0.05$); non-significant relationships between natural enemy damage and year, species, and position are not shown. Study-wide incidence and intensity of gall rust (E) is also given.

A. Leaf Removal (Mean; % Area)		
Year		
2014	7.6%	a
2015	12.3%	c
2016	11.0%	b
Species		
Box elder	6.6%	a
Paper birch	7.3%	a
Bur oak	8.8%	ab
Basswood	10.7%	bc
White oak	10.9%	bc
Red oak	12.4%	c
Pin oak	12.4%	c
Red oak	16.7%	d
Leaf		
1 (youngest)	10.1%	b
2	12.2%	a
3	10.6%	ab
4	10.7%	ab
5 (oldest)	11.3%	ab

B. Galling (Mean; # Galls/Leaf)		
Year		
2014	0.07	a
2015	0.08	a
2016	0.53	b
Species		
Red oak	0.03	a
Pin oak	0.08	a
White oak	0.49	b
Bur oak	0.61	b

C. Leaf Mining (Mean; # Mines/Leaf)		
Species		
Pin oak	0.01	a
Bur oak	0.01	a
White oak	0.02	a
Paper birch	0.03	ab
Red oak	0.04	b

D. Anthracnose (Mean; Score/5)		
Leaf		
1 (youngest)	1.76	ab
2	1.72	a
3	2.02	abc
4	2.07	bc
5 (oldest	2.24	c

E.Gall Rust	
Incidence (% Trees Infected)	7.0%
Mean Intensity (Mean # Galls for Infected Trees)	2.5

Table 2.2 – Best models of leaf removal for all eight species surveyed (A) and for each individual species (B-I). The response variable is the maximum proportion (arcsin-square root transformed) of leaf removed per plant, pear year. All models are mixed-effects linear regression models. Each model is presented at the most explanatory spatial scale (# of trees in the neighbourhood) for a given species (and for all species).

Table 2. Best models of leaf removal for all eight species surveyed (A) and for each individual species (B-I). The response variable is the maximum proportion (arcsin-square root transformed) of leaf removed per plant, pear year. All models are mixed-effects linear regression models. Each model is presented at the most explanatory spatial scale (# of trees in the neighbourhood) for a given species (and for all species).

Fixed Terms	Estimate	SE	t	Random Terms	St. Dev.	Levels
A. All Species						
Intercept	0.050	0.053	7.110	Number of Obs.	NA	1225
Focal Tree Height	0.001	0.001	1.110	Tree/Plot/Block	<0.001	665
Height Apparency	<0.001	<0.001	-1.220	Plot/Block	0.051	105
				Block	0.068	8
				Species	0.049	3
				Year	0.072	3
Marginal R^2 = 0.002						
Conditional R^2 = 0.129						
8-tree scale						
B. Box elder (*Acer negundo*)						
Intercept	0.638	0.123	5.210	Number of Obs.	NA	84
Focal Tree Height	-0.002	0.003	-0.587	Tree/Plot/Block	0.101	58
SLA Trait Diversity	0.339	0.121	2.800	Plot/Block	<0.001	18
Lignin Trait Diversity	-0.344	0.106	-3.230	Block	<0.001	3
Basswood neighbours	-1.940	0.779	-2.490	Year	0.022	3
Marginal R^2 = 0.164						
Conditional R^2 = 0.282						
48-tree scale						
C. Red maple (*Acer rubrum*)						
Intercept	0.317	0.146	2.172	Number of Obs.	NA	151
Focal Tree Height	0.002	0.002	0.789	Tree/Plot/Block	0.067	85
Height Apparency	-0.002	0.001	-2.081	Plot/Block	0.037	29
Tannin Trait Mean	0.056	0.018	3.250	Block	0.064	3
Tannin Trait Diversity	-0.306	0.082	-3.710	Year	<0.001	3
Marginal R^2 = 0.095						
Conditional R^2 = 0.196						
8-tree scale						
D. Paper birch (*Betula papyrifera*)						
Intercept	0.442	0.090	4.910	Number of Obs.	NA	187
Focal Tree Height	-0.001	0.001	-1.060	Tree/Plot/Block	<0.001	98
Height Apparency	0.001	0.001	1.890	Plot/Block	<0.001	29
Red oak neighbours	-1.004	0.342	-2.930	Block	0.032	3
Maple neigbhours	0.941	0.250	3.770	Year	0.074	3
Marginal R^2 = 0.101						
Conditional R^2 = 0.162						
24-tree scale						

Fixed Terms	Estimate	SE	t	Random Terms	St. Dev.	Levels
E. White oak (*Quercus alba*)						
Intercept	0.325	0.095	3.410	Number of Obs.	NA	128
Focal Plant Height	0.005	0.003	1.750	Tree/Plot/Block	0.159	66
Height Apparency	-0.002	0.001	-1.440	Plot/Block	<0.001	29
				Block	<0.001	3
Marginal R^2 = 0.032				Year	<0.001	2
Conditional R2 = 0.257						
24-tree scale						
F. Pin oak (*Quercus ellipsoidalis*)						
Intercept	0.426	0.114	3.735	Number of Obs.	NA	194
Focal Plant Height	0.003	0.003	1.018	Tree/Plot/Block	<0.001	108
Height Apparency	-0.001	0.001	-1.009	Plot/Block	<0.001	32
				Block	0.071	3
Marginal R^2 = 0.009				Year	0.129	3
Conditional R^2 = 0.193						
8-tree scale						
G. Bur oak (*Quercus macrocarpa*)						
Intercept	0.331	0.116	2.860	Number of Obs.	NA	149
Focal Plant Height	0.001	0.003	0.359	Tree/Plot/Block	<0.001	78
Height Apparency	<0.001	0.001	0.154	Plot/Block	<0.001	31
Species Richness	0.026	0.013	2.080	Block	0.025	3
Marginal R^2 = 0.029				Year	0.004	2
Conditional R^2 = 0.094						
8-tree scale						
H. Red oak (*Quercus rubra*)						
Intercept	0.399	0.123	3.230	Number of Obs.	NA	154
Focal Plant Height	0.001	0.003	0.324	Tree/Plot/Block	<0.001	84
Height Apparency	<0.001	0.001	-0.438	Plot/Block	<0.001	28
Functional Diversity	0.050	0.023	2.170	Block	<0.001	3
Marginal R^2 = 0.034				Year	0.084	3
Conditional R^2 = 0.086						
8-tree scale						
I. Basswood (*Tilia americana*)						
Intercept	0.553	0.089	6.230	Number of Obs.	NA	212
Focal Plant Height	-0.001	0.002	-0.329	Tree/Plot/Block	<0.001	110
Height Apparency	0.001	0.001	0.908	Plot/Block	<0.001	33
				Block	0.048	3
Marginal R^2 = 0.004				Year	0.014	3
Conditional R^2 = 0.032						
8-tree scale						

Table 2.3 – Best models of oak gall formation (A), oak leaf mine formation (B), birch leaf mine formation (C), red maple leaf anthracnose (D), and juniper gall rust (E). The vulnerability of a tree to damage (left) and intensity of this damage (right) were modeled using fixed-effects zero-inflated negative binomial Poisson regresion models (A-C, E) and mixed-effects hurdle models (D). Baselines are given for categorical predictors and are arbitrary. | indicates 0.1 > p > 0.05; * indicates 0.05 > p > 0.01; ** indicates 0.01 > p > 0.001

Vulnerability: Zero-Inflation (Negative Binomial) Model					**Intensity:** Count (Gaussian) Model				
More negative estimates for vulnerability mean that a tree was at greater risk of herbivory (was not an excess zero).					*More positive estimate for intensity mean that a tree suffered a higher degree of herbivory.*				
	Term	**Estimate**	**SE**	**z**	**p**	**Term**	**Estimate**	**SE**	**z**	**p**
A. Oak Galls										
	Intercept	2.92	1	2.92	**	Intercept	3.46	1.92	1.8	|
	Pin oak (Species)	0.197	0.687	-0.287		Pin oak (Species)	-2.78	1.25	-2.24	*
	Bur oak (Species)	0.856	0.534	1.6		Bur oak (Species)	0.907	0.936	0.969	
	Red oak (Species)	0.664	0.605	1.1		Red oak (Species)	-2.22	0.841	-2.64	**
	Focal Tree Height	0.004	0.021	0.168		Focal Tree Height (24-tree)	0.018	0.045	0.393	
	Height Apparency (24-tree)	-0.016	0.013	-1.26		Height Apparency (80-tree)	-0.024	0.035	-0.7	
	Oak Neighbours (80-tree)	-2.11	0.915	-2.31	*	Oak Neighbours	-1.23	1.56	-0.787	
Baseline factor for Species is white oak.										
24- and 80-tree scale										
B. Oak Leaf Miners										
	Intercept	4.26	2.06	2.07	*	Intercept	-1.56	1.2	-1.31	
	Pin oak Species	0.338	0.964	0.351		Pin oak Species	-0.44	0.471	-0.934	*
	Bur oak Species	-0.799	1.54	-0.519		Bur oak Species	-1.14	0.45	-2.52	
	Red oak Species	1.44	1.102	1.3		Red oak Species	-0.035	0.541	-0.078	
	Focal Tree Height	-0.174	0.62	-2.79	**	Focal Tree Height	0.017	0.023	0.751	
	Height Apparency	0.009	0.011	0.793		Height Apparency	-0.004	0.005	-0.822	
	Oak Neighbours	-0.274	1.309	-0.21		Oak Neighbours	1.54	0.593	2.6	**
Baseline factor for Species is white oak.										
8-tree scale										

Table 2.3 (cont.)

C. Birch Leaf Miners									
	Intercept	0.164	1.52	0.108		Intercept	0.198	0.795	0.249	
	Focal Tree Height	-0.006	0.021	-0.293		Focal Tree Height	0.011	0.012	0.865	
	Height Apparency	0.024	0.016	-1.46		Height Apparency	-0.014	0.001	-2.34	*
	Paper birch neighbours	2.47	1.4	1.77		Paper birch neighbours	-1.12	0.833	-1.34	
8-tree scale										
D. Leaf Anthracnose									
Fixed	Intercept	2	3.64	0.55		Intercept	15.2	1.78	8.57	***
	Focal Tree Height	-0.023	0.03	-0.77		Focal Tree Height	-0.048	0.034	-1.41	
	Phylogenetic Diversity	-0.003	0.003	-0.86		Phylogenetic Diversity	-0.007	0.003	-2.24	*
Random	Year (2 Levels)		4.88			Year (2 Levels)		0.008		
24-tree scale										
E. Juniper Gall Rust									
	Intercept	2.34	2.65	0.885		Intercept	-1.31	0.528	-2.49	*
	Focal Tree Height	-0.108	0.07	-1.54		Focal Tree Height	0.01	0.006	1.62	
	Height Apparency	-0.064	0.052	-1.23		Height Apparency	-0.002	0.002	-0.919	
	E. red cedar neighbours	1.3	3.73	0.348		E. red cedar neighbours	-0.779	0.33	-2.36	*
8-tree scale										

Figure 2.1 – The best models of leaf removal herbivory were generally those fit at small (< 4 m^2) spatial scale. AIC model comparison indicated support for models at either 1 m^2 or 4 m^2 spatial scale for all species except box elder (*A. negundo*), for which a 9 m^2 model received more support. AIC values are presented in Supplementary Table 2.3.

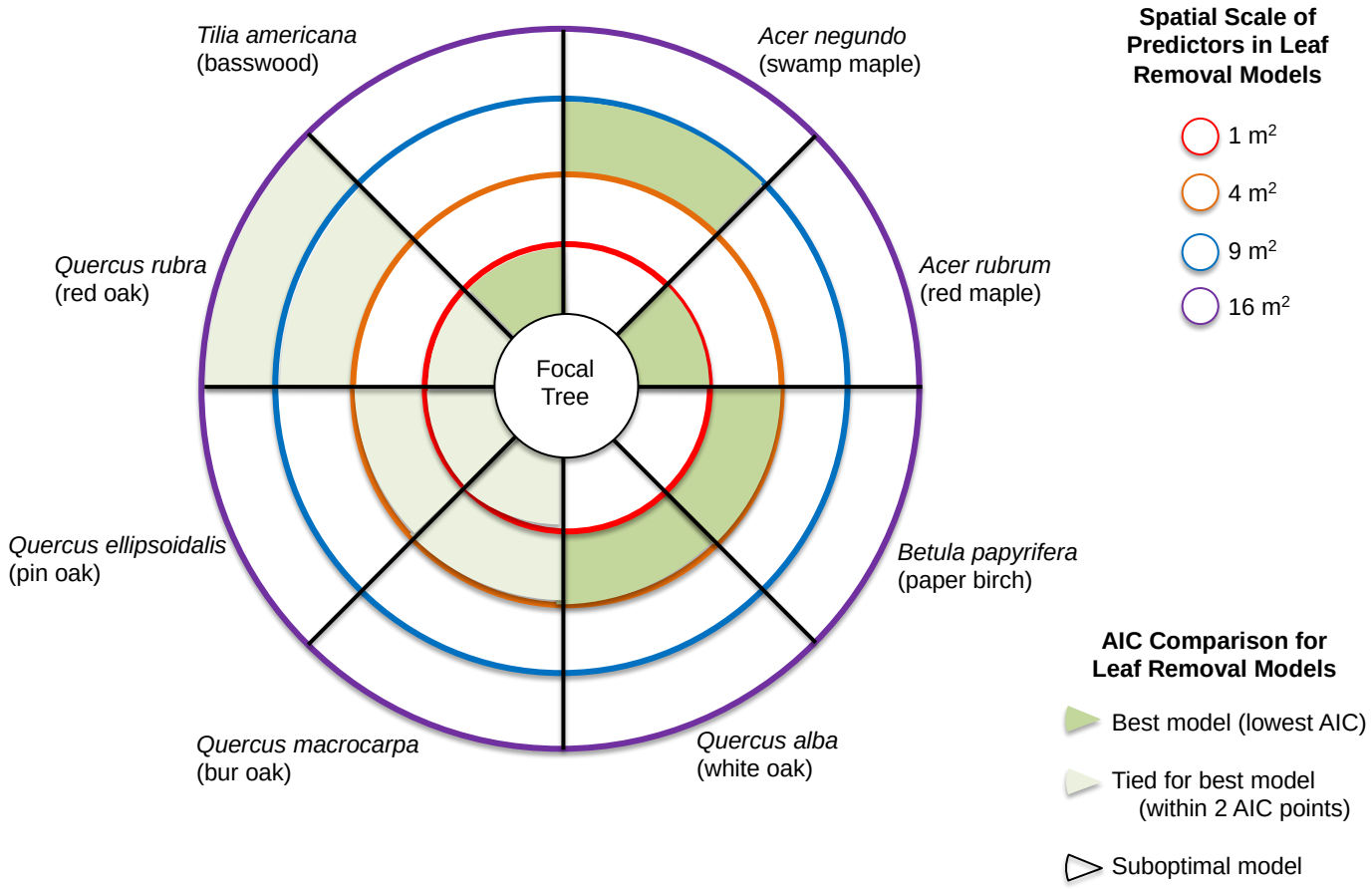


Figure 2.2 – Effects of neighborhood identity and diversity differed across specialist herbivores and pathogens. Effects of host density (proportion of conspecific or congeneric neighbors) on damage from oak (*Quercus* spp.) gall formers (A) and leaf miners (B), paper birch (*Betula papyrifera*) leaf miners (D), and eastern red cedar (*Juniperus virginiana*) apple gall rust (E) and effects of neighbourhood phylogenetic diversity (mean phylogenetic distance; MPD) on red maple (*Acer rubrum*) anthracnose (C) infection. Panels A-C reflect associational resistance (less damage at higher diversity) while Panels D and E demonstrate associational susceptibility (more damage at higher diversity). Plots display actual data (grey circles) and prediction curves from fixed-effects zero-inflated negative binomial Poisson regression models (A, B, D, E) and a mixed-effects Gaussian model (C). Prediction curves are derived from models presented in Table 2.3 and minimal random noise has been added to each point's abscissa in order for all points to be visible in plots.

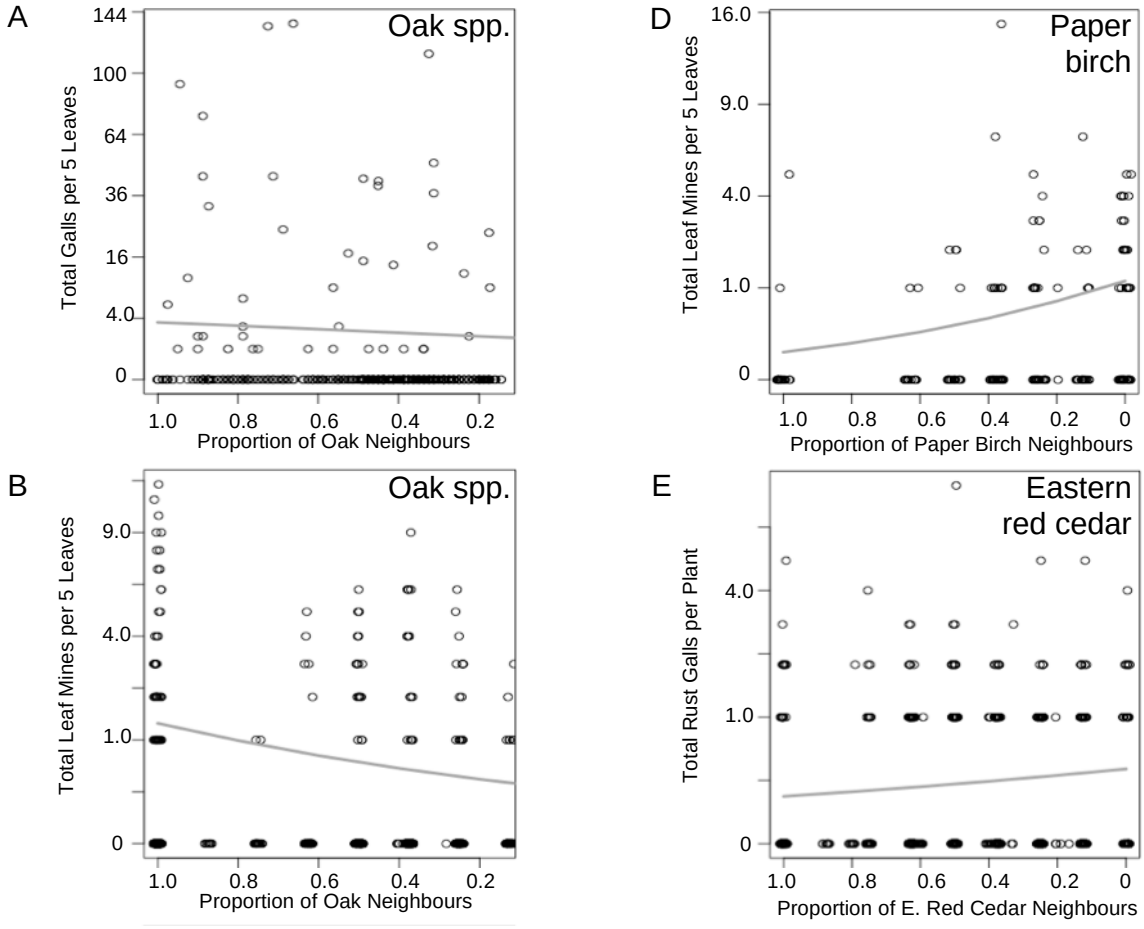
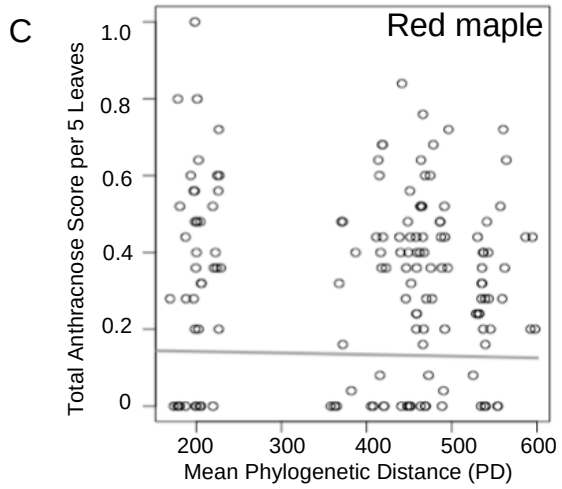


Figure 2.2 (cont.)



Chapter 3

Consequences of biodiversity for aspen and willow growth, fitness, and herbivory shift across phylogenetic scales [4]

[4] This chapter has been submitted for publication in the *Journal of Vegetation Science* (April 2018). The research presented here was conducted in collaboration with Jeannine Cavender-Bares.

Introduction

Human environmental impacts have contributed to striking biodiversity loss (Díaz et al. 2006, Ceballos et al. 2015), including threats to 20% of known plant species (Kew Gardens 2016). Designed experiments can improve our capacity to predict the effects of diminishing biodiversity for ecosystem functions (as reviewed in Cardinale et al. 2012, Hooper et al. 2012). Yet ecologists frequently rely on experiments in which only interspecific diversity – the composition and relative abundance of species – is manipulated. Intraspecific diversity is often neglected (Violle et al. 2012) and is rarely considered in the context of changes in interspecific diversity. In reality, biodiversity-ecosystem functioning (BEF) relationships can be described at multiple, hierarchical phylogenetic scales (*sensu* Cruz et al. 2005, Cavender-Bares et al. 2006; Silvertown et al. 2006). Evaluating BEF dynamics across phylogenetic scales requires biodiversity experiments to be designed to explicitly include multiple scales of variation within populations and communities (Eduardo 2016, Moreira et al. 2016).

The first generation of BEF experiments were designed to assess the consequences of biodiversity for primary productivity (Tilman et al. 1996, Spehn et al. 2005); subsequent work has broadened the field to include investigations of other functions. Besides productivity (or plant growth), damage from herbivores and pathogens has emerged as a key ecosystem function measured in BEF experiments (Grossman et al. 2018). Because herbivory results in the loss of tissue produced through primary production, these functions jointly affect fitness. Community biodiversity has been shown to have distinct consequences for plant productivity, herbivory, and fitness.

Past research on the consequences of both intraspecific and interspecific diversity for plant performance suggests that diversity at both scales can increase primary productivity. Intraspecific diversity has been shown to promote productivity in some experiments (Crutsinger et al. 2006, Hughes et al. 2008, Kotowska et al. 2010, Drummond and Vellend 2012, Bukowski and Petermann 2014) while having no effect in others (Fischer et al. 2017). Investigators have more frequently assessed the consequences of interspecific diversity for plant growth or productivity, often finding that more diverse ecosystems promote plant performance (Hooper et al. 2005, Reich et al. 2012, Zhang et al. 2012, Liang et al. 2016).

Research addressing the diversity-herbivory relationship is equivocal, with some studies showing increased damage with genetic diversity (Kotowska et al. 2010, Castagneyrol et al. 2012) and others showing damage decreasing (Parker et al. 2010, Abdala-Roberts et al. 2015a, 2016) or no response (Hambäck et al. 2010, Abdala-Roberts et al. 2015c). Research addressing the relationship between interspecific diversity and

herbivory, though also equivocal and context-dependent (Jactel and Brockerhoff 2007), has demonstrated the potential of diversity to increase herbivore damage (Haase et al. 2015, Schuldt et al. 2015, Staab et al. 2015, Damien et al. 2016, Wein et al. 2016). Among studies that distinguish between specialist and generalist herbivory, interspecific diversity has been shown to suppress specialist herbivory (Otway et al. 2005, Kaitaniemi et al. 2007, Lau et al. 2008, Alalouni et al. 2014, Abdala-Roberts et al. 2015c).

There have still been relatively few experiments that address the relationship between biodiversity and fitness through the systematic manipulation of biodiversity (Lau and Tiffin 2009, Cook-Patton et al. 2011, Duffy et al. 2015). Plants must expend resources to grow, to survive and reproduce, and to defend themselves from herbivores (Coley et al. 1985); therefore, both plant productivity and resistance to herbivory, along with other factors, affect fitness (Bazzaz et al. 1987). In predominantly clonal plants, such as willows and poplars, vegetative parts are themselves reproductive organs, magnifying the contributions of vegetative growth of and herbivore damage to plant fitness (Pan and Price 2002, Aarssen 2008). Thus, population and community-level diversity can affect the fitness of individual plants in complex ways, depending on whether their growth or vulnerability to herbivory are suppressed or enhanced by neighbors (Whitham et al. 2006, Johnson and Stinchcombe 2007).

Parallel research traditions investigating the consequences of intraspecific and interspecific diversity for plant growth, herbivory, and fitness have developed with a small, but growing number of experiments designed to assess both simultaneously (Booth and Grime 2003, Fridley et al. 2007, Fridley and Grime 2010, Cook-Patton et al. 2011, Crawford and Rudgers 2012, Moreira et al. 2014, Parachnowitsch et al. 2014, Abdala-Roberts et al. 2015b, c, Prieto et al. 2015, Schöb et al. 2015, 2017, Zeng et al. 2017, Hahn et al. 2017). This situation reflects two divisions in contemporary biology (Fig. 3.1A). First, despite progress toward greater integration (e.g. in community genetics, experimental evolution, and evolutionary ecology), ecologists and evolutionary biologists frequently fail to collaborate with each other. Second, within each field, investigators often focus on a particular phylogenetic scale, limiting integration of work by population and ecosystem ecologists or by micro- and macroevolutionary biologists (Cavender-Bares and Wilczek 2003). To promote greater synthesis of these research programs, we present our expectations for the present work and for future research as a novel, cross-scale conceptual framework (Fig. 3.1B; Supplementary Table 3.1) and apply this framework to findings from a tree diversity experiment.

To disentangle the consequences of interspecific and intraspecific diversity for forest tree productivity, fitness, and susceptibility to herbivores, we planted a high-density tree diversity experiment consisting of trees of three species in the family Salicaceae, each represented by three genotypes. The species used in the experiment – native quaking (*Populus tremuloides* Michx.) and exotic white (*P. alba* L.) aspen and native black willow (*Salix nigra* Marshall) – are all fast-growing, allowing us to rapidly document the

consequences of biodiversity during the first three years of stand establishment. We estimated incremental aboveground biomass season, fitness, and generalist and specialist herbivory for the 2015-2016 growing season. Our expectations are detailed in Fig. 3.1C.

Methods

In June 2014, we established the Biodiversity in Willows and Poplars experiment (BiWaP) at the Cedar Creek Ecosystem Science Reserve (Cedar Creek) in eastern Minnesota. The study site is described fully in the Methods section of Chapter 1.

Study Species

To produce plant material, we identified nine local source individuals (three each of quaking aspen, white aspen, and black willow), harvested cuttings from these donors, and grew plants out in the University of Minnesota Plant Growth Facilities (St. Paul, Minnesota, USA) for one to two years prior to outplanting. These species were included in the study because they were the three locally available species that were most conducive to propagation in the greenhouse. Propagation of other salicaceous species had a high failure rate. Quaking aspen and black willow are native to Minnesota; white aspen is a naturalized European species. All three can be found co-occurring naturally within 5 km of the BiWaP site. Salicaceous species in general, and these species in particular, have emerged as model systems for several research programs in tree and forest ecology. Considerable work has elucidated the role of phenolic glycosides and condensed tannins in Salicaceous trees in herbivore defense and downstream ecosystem processes (Palo 1984, Hwang and Lindroth 1997, Schweitzer et al. 2008, Boeckler et al. 2011, Lindroth and St. Clair 2013, Caseys et al. 2015, Madritch and Lindroth 2015). The herbivore communities and herbivory dynamics for a number of aspen and willow species have also been well-documented (Rowell-Rahier 1984, Roche and Fritz 1997, Shen and Bach 1997, Fearnside and Imbrozio Barbosa 1998, Barbosa et al. 2000, Bailey and Whitham 2003, Osier and Lindroth 2004, Wimp et al. 2005, Hillstrom and Lindroth 2008, Bangert et al. 2008). Finally, studies of the cold-adapted but relatively drought-intolerant Salicaceous species of North America and Europe have been central to recent research addressing plant genetic, physiological and fitness responses to changing environmental conditions (Lindroth et al. 1993, Guilloy-Froget et al. 2002, Li et al. 2005, Carpenter et al. 2008, Savage and Cavender-Bares 2012, Worrall et al. 2013, Stolting et al. 2015, Wei et al. 2017).

Site Preparation and Plant Propagation

The BiWaP site consists of two blocks surrounded by deer exclosure fences erected on an old agricultural field.

From 2013 to 2014, the site was mowed, burned, tilled, and sprayed three times with glyphosate to remove herbaceous vegetation. Trees and shrubs were removed by hand or cut to ground level and treated with

triclopyr. The experiment was planted over two weeks in June 2014 with greenhouse-grown potted trees. In May to June of 2015, trees that had died over the previous year were replaced. Mortality was less than 5% following planting. We collected cuttings from local populations to improve the likelihood that experimental plants would withstand environmental conditions in the common garden and to better simulate actual intra-/interspecific interactions at the site. For quaking aspen, we used the root cutting method (Luna 2003) and for white aspen and black willow, we used the semi-hardwood stem cutting method (Hartmann, et al. 2002). Stem cuttings were harvested from a single aboveground stem of one donor plant, so we were confident in the genetic identity of white aspen and black willow cuttings. Rhizome identity is more ambiguous, so we used microsatellite markers to determine the genetic identity of each quaking aspen genotype (methods in Deacon et al. 2017). Cuttings from a single stand were confirmed to be ramets of a single genotype, and each putative genotype was confirmed to be distinct.

Experimental Design

The BiWaP experiment consists of 885 trees in two blocks (Fig. 3.2). Each block consists of either 14 or 15 plots (29 total), arranged randomly within the block and interspersed with several unplanted control plots, which we included in order to monitor spontaneous establishment of Salicaceous species. The two blocks are separated by a distance of 10 m, but plots within a block are planted continuously (only 0.5 m separates the edge trees of two blocks). Trees are planted 0.5 m apart on a staggered grid such that each tree is surrounded by six neighbors in a hexagon; plots consist of 27-28 trees depending on their location within the block. There is no space between plots in a block. Plots fall into one of four treatments (and 17 unique compositions) described here and in Figure 3.2. Each of the nine genotypes are represented by monocultures (1S1G). These monocultures consist entirely of genetically identical trees; in contrast to the classical BEF literature, we use "monoculture" here to refer to a plot consisting of mono-genotypic trees instead of just mono-specific trees. The other treatment levels consist of plots with one species but three different genotypes (1S3G), three species each represented by only one genotype (3S3G), and high-diversity plots with all nine genotypes (3S9G). All possible species-genotype combinations are present in the experiment except at the 3S3G level; the three sets of genotypes used in plots in the 3S3G group were chosen randomly. All treatments (1S1G, 1S3G, 3S3G, and 3S9G) are replicated across both blocks and all compositions except three are duplicated at the plot level across both blocks. Failure to duplicate three plots occurred due to plant shortages following propagation.

We designed BiWaP so that composition (which genotypes and present in a plot), treatment (1S1G, 1S3G, 3S3G, 3S9G), species richness (SR; one or three), or genotype richness (GR; one, three, or nine) could be used as experimentally manipulated predictors of productivity, fitness, or herbivory. We also used publicly available chloroplast sequences for each species planted in the experiment to estimate the continuous

Faith's phylogenetic Diversity (PD; Faith 1992) metric for each plot (Appendix 3). We employed PD as an alternative, continuous predictor of molecular diversity alongside treatment, SR and GR.

Data Collection

We measured basal diameter and height to leader for all experimental plants in September 2015 and 2016. We treated basal diameter as diameter at 5 cm above the soil surface and stretched plants as needed to record height to leader. When plants had produced multiple stems, we measured only the diameter and height of the tallest, dominant stem. We used allometric equations from the literature to estimate incremental change in aboveground biomass of each sapling from 2015-16; equations were species-specific and developed for trees of equivalent size to ours (equations given in Appendix 3; Bond-Lamberty et al. 2002, Blujdea et al. 2012). Because genotypic differences in allometry were undetectable, we used the same published allometric equation for all trees of a given species.

In this study, we measured three forms of herbivore damage on all quaking aspen trees in the experiment. We focused on three specific types of herbivore damage, treating leaf removal as a form of generalist herbivory and leaf galling and mining as specialist herbivory. Quaking aspen is a foundation species in ecosystems across North America (Lindroth and St. Clair 2013), and it is fed upon by over 300 insect herbivores (Whitham et al. 1996). Invertebrate herbivory of aspen affects not only tree performance (Osier and Lindroth 2004, Stevens et al. 2007, Nabity et al. 2012), but also structures litter nitrogen and tannin content, altering ecosystem dynamics across trophic levels (Whitham et al. 2006, Schweitzer et al. 2008). We did not identify specific aspen herbivores, but instead surveyed the three common and distinct classes of herbivore damage that we observed to be most common (following Castagneyrol et al. 2013): leaf removal, galling, and mining. Though some specialist invertebrates remove aspen leaf tissue, leaf removal is the dominant form of feeding for the most significant polyphagous aspen herbivores, such as the Lepidopteran gypsy moth (*Lymantria dispar*; Lance 1983, Elkinton and Lebhold 1990) and forest tent caterpillar (*Malacossoma distria*; Futuyma and Wasserman 1981, Donaldson and Lindroth 2008). By comparison, endophagous leaf galling and mining insects are considered relatively specialized, feeding on only one host species or several related species. Gall-forming invertebrates, predominantly aphids (Hemiptera: Aphididae), mites (Trombidiformes: Eriophyidea), midges (Diptera: Cecidomyiidae), and sawflies (Hymenoptera: Symphyta) (Smith and Fritz 1996, Raman et al. 2004, Roslin and Roland 2005, Floate 2010), are believed to be so limited in diet breadth that the presence of their galls can be used to distinguish hybrid aspens from parental species (Floate and Whitham 1995). Similarly, though leaf mining is common in several insect orders (Coleoptera, Diptera, Hymenoptera, and Lepidoptera), the vast majority of leaf miner species are believed to be specialized to either one or a few related host species (Hesphenheide 1991, Davis and Deschka 2001). The diversity of leaf miners attacking quaking aspen has not been fully documented, with many North American studies focusing on damage from the lepidoteran

aspen leaf blotch miner moth (*Phyllonorycter apparella*; Auerbach and Alberts 1992, Kopper and Lindroth 2003). Comparison of damage by these three classes of herbivores with varying degrees of host specialization allows us to characterize how neighbourhood diversity and herbivore diet breadth influence quaking aspens' vulnerability to herbivory. To measure leaf removal, we estimated damage from leaf-chewing invertebrates on the five most recently fully expanded leaves on each quaking aspen individual in September 2016 using a four-class system in which 0 indicated no damage, 1 indicated less than 1% of leaf area removed, 2 indicated 1% to 25% of leaf area removed, and 3 indicated more than 25% of leaf area removed. To quantify specialist herbivory, we also counted all leaf and stem galls and all leaf miners on all quaking aspens in September 2016.

Data Analysis

In our analysis of productivity, we first modeled the effect of plot diversity on average tree relative growth rate (RGR) in each experimental plot (ln[2016 biomass – 2015 biomass]; g g^{-1}). We have employed this approach in this work and our analysis of tree growth in a different diversity experiment (Chapter 1; Grossman et al. 2017) because it allows us to assess tree growth independent of mortality. (In contrast to this earlier work, we model whole biomass rather than simply stem biomass, as adequate allometric equations for the prediction of whole plant biomass are available for all study species.) The standard approach in grassland diversity experiments (e.g. Tilman et al. 1996) is to sum all biomass production in a plot; doing so to compare plots with different numbers of living trees distorts actual patterns in growth rates. Measuring tree growth alone, however, does not account for the effect of diversity on plot productivity; to do so, we calculated overyielding in average tree RGR on a per-plot basis. Positive values indicate that a plot is performing better than would be expected, indicating a n-additive effect of biodiversity. Finally, we also partitioned overyielding into its constituent complementary effects (species facilitate one another or partition available resources) and selection effects (highly productive plants dominate polycultures). Overyielding, complementarity, and selection calculations are described in Chapter 1 and executed in this chapter with modificaitons described fully in Appendix 3.

For long-lived species that reproduce primarily through vegetative means, it can be challenging or impossible to measure lifetime fecundity and thus quantify fitness. Survival and growth are two related and critical components of fitness (Kozłowski 1992, Mangel and Stamps 2001). However, the joint effects of these factors are difficult to model, because they are characterized by different underlying statistical distributions (mortality is binomially distributed and growth is normally distributed). To estimate fitness for all trees in our experiment (in the absence of fecundity data) and model its relationship with planting treatment, we used aster modeling ("aster" package; Geyer et al. 2007, Shaw et al. 2008). Aster models represent fitness in terms of a response variable calculated based on the outcomes of earlier life history events. This technique has been used to assess the consequences of environmental variables for plant

fitness in a variety of species (Dechaine et al. 2009, Deacon and Cavender-Bares 2015, Center et al. 2016), including willows and aspens (Wei et al. 2017). We present here results from conditional aster models that treat an individual tree's 2015-16 absolute growth rate (AGR; 2016 biomass – 2015 biomass; g yr^{-1}) as a surrogate of fitness (modeled with a Gaussian distribution) contingent on that tree's survival from the prior growing season (modeled with a Bernoulli distribution):

Survival (2015) -> Growth (2016) (3.1)

For example, trees that died between measurements in 2015 and 2016 have a subsequent growth rate of 0 g, incorporating both the consequences of mortality for ultimate growth. Model comparison using the aster package's built-in likelihood ratio test allowed us to choose a preferred model of fitness among nested models. Because plants varied in initial size due to differences in propagation practices confounded with species, initial plant size was always included as a covariate. Preliminary analysis also indicated that species, but not genotypes, varied widely in fitness, so we also included species identity as a predictor in our fitness models. We then sequentially added SR and then GR nested within SR as predictors (Table 3.1). PD had equivalent effects on fitness to other variables, and so was excluded as a predictor from these models.

To model generalist herbivory on quaking aspen, we relied on logistic regression with plant height as a covariate (per Castagneyrol et al. 2013; "aod" package, Lesnoff and Lancelot 2012). Other diversity predictors included genotype identity, GR, SR, GR nested in SR, and PD (Table 3.1). Because we measured generalist herbivory using categorical damage classes and the distribution of scores was not zero-inflated, we used multinomial logistic regression to model the effects of diversity on leaf removal. Counts of specialist galls and leaf miners were zero-inflated. We therefore employed logistic regression with a zero-inflated negative binomial distribution ("pscl" package, Jackman et al. 2015) to model both the likelihood that a quaking aspen would experience damage at all (binomial data) as well as the intensity of that damage (count data). We compared all models of herbivory using AIC scores and report only the best-supported models here. Calculations and analyses were carried out in R (R Core Team 2016, ver. 3.3.1).

Results

Growth and Productivity

The species and genotypes of trees planted in this experiment varied in their growth rate (Appendix 3, Supplementary Figure 3.1). However, tree growth did not vary consistently with diversity treatment and we did not document transgressive overyielding at higher diversity – the most productive monocultures were more productive than the least productive polycultures (Fig. 3.3A). Overyielding in growth rate also did not vary consistently with diversity treatment. The best model of overyielding in productivity was an intercept-

only model without any predictors related to tree diversity (Table 3.1). Though estimated overyielding in productivity was positive for the 1S3G treatment ($t = 2.90$, $df = 5$, $p_{(2)} = 0.034$) and highest for the 3S9G treatment, it was not significantly different than zero for other treatment groups (Fig. 3.3B). Our findings therefore do not indicate a consistent positive or negative effect of diversity on tree growth or overyielding.

Diversity treatment was a strong predictor of both complementarity and selection in productivity at the plot level. More species-rich and genotype-rich plots showed higher complementarity and lower selection effects (Table 3.1). Complementarity and selection add to give total overyielding, so the opposed signs of the first two terms sum to eliminate any diversity-related signal in the gross overyielding (Fig. 3.3C,D). This pattern stems from differential species performance in different diversity treatments. White aspen trees grew the same regardless of the diversity of their neighborhood. But quaking aspen and black willow trees, which were much smaller than white aspens, performed much worse in any plot in which they had to compete with their dominant neighbor. The strong complementarity and selection signals that emerge through partitioning of total overyielding suggest that it was the dominance of white aspen that diminished the diversity-related signal in productivity. Furthermore, our observation that diversity, from the genotype- to the species-scale, increased complementarity (and reduced selection) suggests that diversity across phylogenetic scales may contribute to the diversity-productivity relationship.

Fitness

The best aster model of fitness included species identity and no other factors (Table 3.1). As such a given tree's species identity, but not its genetic identity or the genotypic or species diversity of its neighborhood contributed to fitness. Predicted fitness of experimental trees was highest in white aspen and lower in quaking aspen and black willow (Supplementary Figure 3.2).

Herbivory

Generalist leaf removal was abundant among quaking aspens, with 97% of trees undergoing some damage and 23% of trees having more than a quarter of their leaf area removed. Taller trees were more likely to incur moderate to heavy damage, while shorter trees were more likely to have less than 1% of their leaf area removed. Model comparison suggested that models including tree height and plot-level species richness best predicted leaf removal. The species richness of a tree's neighborhood was the best diversity- or identity-related predictor of leaf removal, but did not consistently affect leaf removal intensity (Table 3.1). Aspens in one-species plots were more likely to experience either no leaf removal or heavy leaf removal (greater than 25% of leaf area), while trees in three-species plots were more likely to experience light herbivory (<1% removed) (Supplementary Table 3.2).

Roughly a fifth of quaking aspen surveyed had at least one stem or leaf gall, and no plants in the highest diversity treatment (3S9G) had galls. We first assessed whether our failure to find galls in the highest-diversity treatment was due to the lower proportion of quaking aspens in high-diversity plots (nine per plot instead of 27 per monoculture). Though an independence test did indicate that number of aspens with galls was marginally positively associated with the number of aspens surveyed ($p = 0.05$; "coin" package, Hothorn et al. 2016), rarefaction indicated that we would still expect a survey of nine aspens to turn up at least two trees with galls (Supplementary Fig. 3.3). This suggests that 3S9G plots had fewer galls than expected given the number of quaking aspen trees in these plots. We also used zero-inflated logistic regression to model gall abundance and prevalence in 1S1G, 1S3G, and 3S3G plots (3S9G plots could not be included since we did not find any galled trees in them). The best model of gall abundance included plant height and genotype identity but not plot diversity (Table 3.2). Taller plants were significantly more likely to have galls in the first place and were also significantly likely to have more galls. Genetic identity also had an affect on both the likelihood of galling and its intensity. Quaking aspens of genotype #2 were less likely to have galls than were the other genotypes and had marginally fewer galls when they were present (Fig 3.4A, Supplementary Table 3.2).

The prevalence of leaf miners in quaking aspen (21%) was similar to that of galls. The best model of leaf miner abundance included plant height, plant genotype identity, and neighborhood genotypic richness (Table 3.1). Taller plants had significantly more leaf miners when at least one was present, and plants in more genotypically rich environments had fewer leaf miners (Fig 3.4B, Supplementary Table 3.2).

Discussion

The main objective of the work presented here was to use an experiment to assess the phylogenetic scale-dependence of multiple biodiversity-ecosystem function relationships. We conclude that the responses of community productivity, plant fitness, and herbivory to biodiversity change as scale varies from genetic to species diversity. We expected that both intraspecific and interspecific diversity would enhance tree productivity, generalist herbivory, and fitness, but decrease specialist herbivory, relative to trees in mono-genotypic stands. Only one of these expectations was conclusively demonstrated.

In contrast to past findings (Tobner et al. 2016, Grossman et al. 2017), interspecific diversity had no consistent effect on productivity, probably due to the dominant effect of one fast-growing species (Haggar and Ewel 1997). Similarly, genotypic diversity did not have a strong effect on productivity (Moreira et al. 2014, Fischer et al. 2017, Zeng et al. 2017, but see Parachnowitsch et al. 2014) and had no detectable effect on fitness. We also did not observe an interaction between genotypic and species diversity (but see Crawford and Rudgers 2012). Increased complementarity with greater diversity (Fig. 3.3) does suggest that

we may have seen a positive role of diversity if we had included more or different species for inclusion in the BiWaP experiment.

Diversity also had no consistent effect either on generalist herbivory (Abdala-Roberts et al. 2015b, but see Moreira et al. 2014) or on one measure of specialist herbivory, gall formation. But quaking aspens were subject to a lower intensity of leaf mining, another measure of specialist herbivory, in more genotypically diverse environments. This finding parallels Crawford and Rudgers' (2013) documentation of genotypic diversity contributing more strongly than species diversity to patterns of herbivore diversity in a dominant grass. This is sensible given past findings that genetic identity affects herbivore community dynamics *Populus* spp. (Whitham et al. 1999, Dungey et al. 2000, Wimp et al. 2005, 2007, Robinson et al. 2012). Taken together, these results echo past work suggesting that while interspecific biodiversity may be a strong determinant of forest productivity, genetic identity and diversity may play an important role in affecting individuals' susceptibility to herbivory (Hahn et al. 2017), with complex but important implications for other community and ecosystem patterns and processes (Madritch et al. 2006, Whitham et al. 2006, Bailey et al. 2009).

The design and implementation of the BiWaP experiment illustrates challenges to informative work in future biodiversity-ecosystem functioning experiments that explicitly scan phylogenetic scales. We present this work as a model for experiments and analysis that bridge two phylogenetic scales and allow for exploration of multiple ecosystem responses, but our findings are not meant to be extended widely to other biodiversity-ecosystem function relationships. Due to practical limitations, we only included nine genotypes of three species in this experiment. This fundamental limitation reduces the generalizability of our findings to more diverse forest communities and may have both amplified the role of the identity of dominant genotypes or species (e.g. white aspen) and reduced our capacity to detect the consequences of intraspecific or interspecific diversity. Inded, experiments in which diversity has been found to have strong ecological effects have generally consisted of more genotypes (Crutsinger et al. 2006) or species (Reich et al. 2012). However, the limited scope of our diversity manipulation (varying one to nine genotypes of three species, for a total of nine taxa) is not unprecedented. Past forest diversity experiments have entailed the manipulation of only three to five species and yielded important findings (Ewel et al. 1991, Haggar and Ewel 1997, Russell et al. 2004, Vehvilainen et al. 2007, Lang'at et al. 2013, Castagneyrol et al. 2013a, Muiruri et al. 2015).

We note that white aspen, in particular, may have been a problematic species to include in this experiment, and not only due to its much higher growth rate compared to quaking aspen and black willow. As an exotic, even if naturalized, species, white aspen may have attained its fast growth and competitive dominance due to release from its indigenous natural enemies (Keane and Crawley 2002). Indeed, during greenhouse

propagation and field measurements of trees in the BiWaP experiment, we never observed signs of herbivore or pathogen damage on white aspens; the same was not true for native quaking aspens and black willows.

Pathways toward biodiversity-ecosystem functioning research across phylogenetic scales

We believe that the use of integrated fitness modeling (Shaw et al. 2008) to probe the consequences of diversity across phylogenetic scales for natural selection can provide important insights into the reciprocal connections between ecological and evolutionary dynamics (Schoener 2011). Ecological species interactions may result in differences in fitness as noted here, but the story may be more complex, especially when proxies of sexual reproduction, which can incur a tradeoff against growth, are considered (Bazzaz et al. 1987). Some grassland BEF experiments are now decades old (Hooper et al. 2005, Reich et al. 2012) and forest BEF experiments are increasingly common (Zhang et al. 2012; http://www.treedivnet.ugent.be); these may serve as platforms for the exploration of the relationship between community biodiversity and plant fitness.

Our documentation of the different effects of genetic identity, intraspecific diversity, species identity, and interspecific diversity on productivity, fitness, and herbivory in aspens and willows underscores the importance of considering phylogenetic scale dependence when assessing BEF relationships. Some patterns and processes (e.g. leaf miner intensity) may be affected by intraspecific genetic identity and diversity whereas others (e.g. exploitation competition) may be driven by species-level identity and diversity (Bailey et al. 2009). Historically, evolutionary biologists have focused on intraspecific, genetic diversity, while ecologists have focused largely on interspecific, taxonomic diversity; limited integration of these perspectives has impeded critical progress (Cavender-Bares and Wilczek 2003; Violle et al. 2012). Contemporary advances in molecular techniques have made it feasible to genotype many individuals in a population of interest, allowing for a deeper understanding of molecular diversity and its phenotypic consequences (Dalziel et al. 2009). In parallel, recent advances in high-throughput phenotyping now make it possible to assess phenotypic diversity in time frames that are relevant to management (Cavender-Bares et al. 2016, Couture et al. 2016). Integration of these techniques promises to allow for a clearer and more mechanistic understanding of the relationship between biodiversity and ecosystem function across phylogenetic scales. Further controlled experiments that cross manipulation of intraspecific and interspecific diversity (Booth and Grime 2003, Fridley et al. 2007, Fridley and Grime 2010, Cook-Patton et al. 2011, Crawford and Rudgers 2012, Moreira et al. 2014, Parachnowitsch et al. 2014, Abdala-Roberts et al. 2015b, c, Prieto et al. 2015, Schöb et al. 2015, 2017, Zeng et al. 2017, Hahn et al. 2017) are essential, and should be designed to mimic diversity found in natural and managed systems of interest.

Table 3.1 – Models of ecosystem functioning in the Biodiversity in Willows and Poplars experiment. Model comparison for a) multiple linear regression models of overyielding (OY), complementarity effects (CE), and selection effects (SE) in relative growth rate, b) aster models of fitness, c) logistic regression models of leaf removal herbivory of quaking aspen, and d) zero-inflated negative binomial models of gall and leaf miner counts on quaking aspen. Bolded models are those deemed optimal via comparison of AIC (a,c,d) or Deviance (b); models within 2 AIC points are equivalent. We interpret the most parsimonious optimal model (shaded grey) except in Panel c, for which we also consider the model with Species Richness as a predictor.

a) Overyielding in Productivity Model Comparison

Model Predictors	Model DF	OY AIC	CE AIC	SE AIC
Block	1, 12	**37.9**	62.8	64.0
Block+GR	2, 11	**39.8**	**58.6**	**59.9**
Block+SR	2, 11	**39.0**	61.8	60.9
Block+SR/GR	3, 10	40.5	**59.4**	**58.7**
Block+PD	2, 11	**39.0**	**60.5**	**60.6**

b) Fitness Model Comparison

Model Predictors	Model DF	Deviance	d(Deviance)	p-value
log(Biomass)	3	-392.9		
log(Biomass)+Species ID	5	-383.1	9.7910	**0.0075**
log(Biomass)+Species ID+SR	6	-382.8	0.2520	0.6157
log(Biomass)+Species ID+SR/GR	7	-382.8	0.6640	0.7967
log(Biomass)+Species ID+SR/GR+PD	8	-382.7	0.0507	0.8219

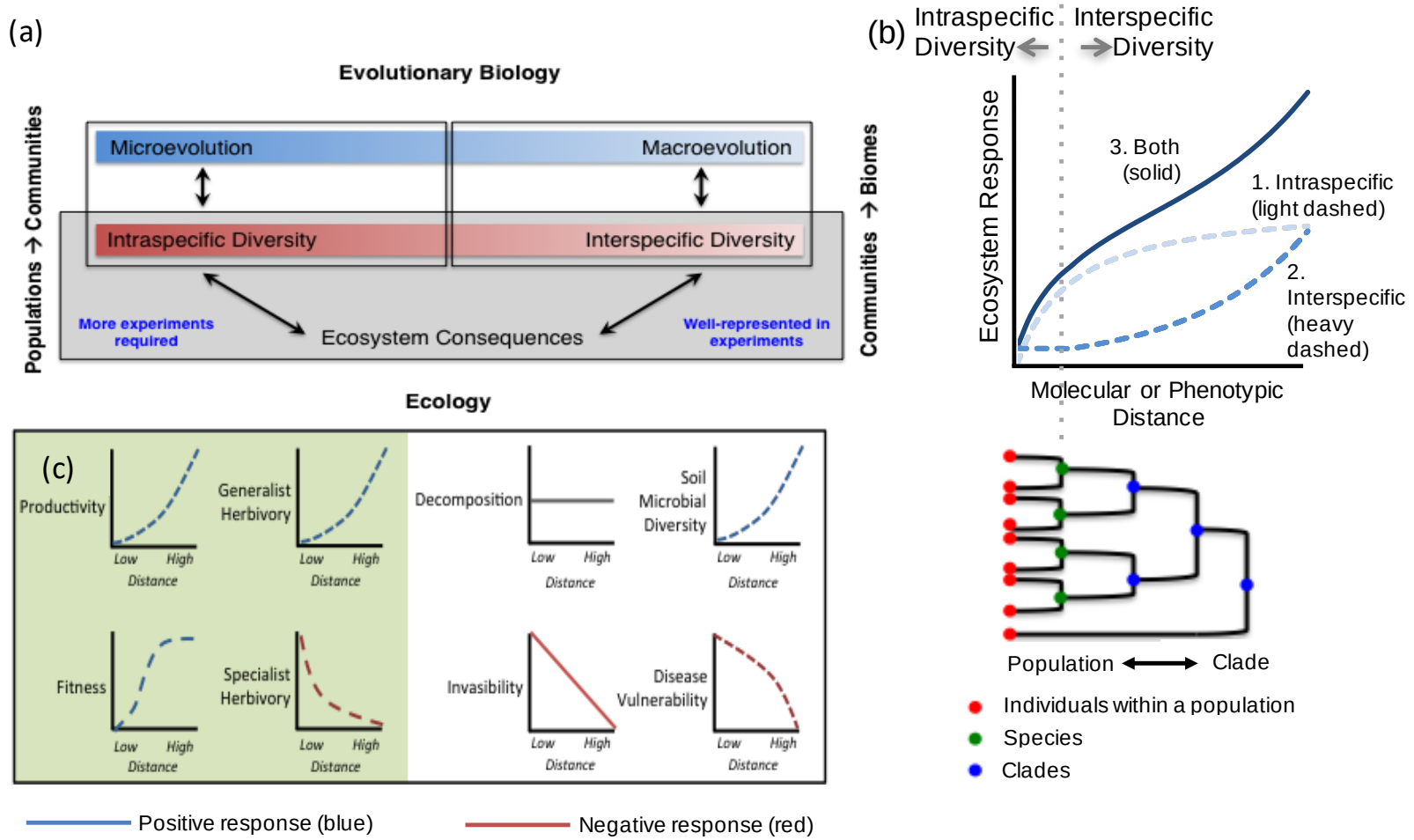
c) Leaf Removal Model Comparison

Model Predictors	Model DF	AIC
Plant Height	6	**562**
Plant Height+Genotype ID	12	568.6
Plant Height+Genotype ID+GR	15	569.4
Plant Height+Genotype ID+SR	15	**562**
Plant Height+Genotype ID+SR/GR	18	564.8
Plant Height+Genotype ID+PD	15	**562.6**

d) Gall and Leaf Miner Model Comparison

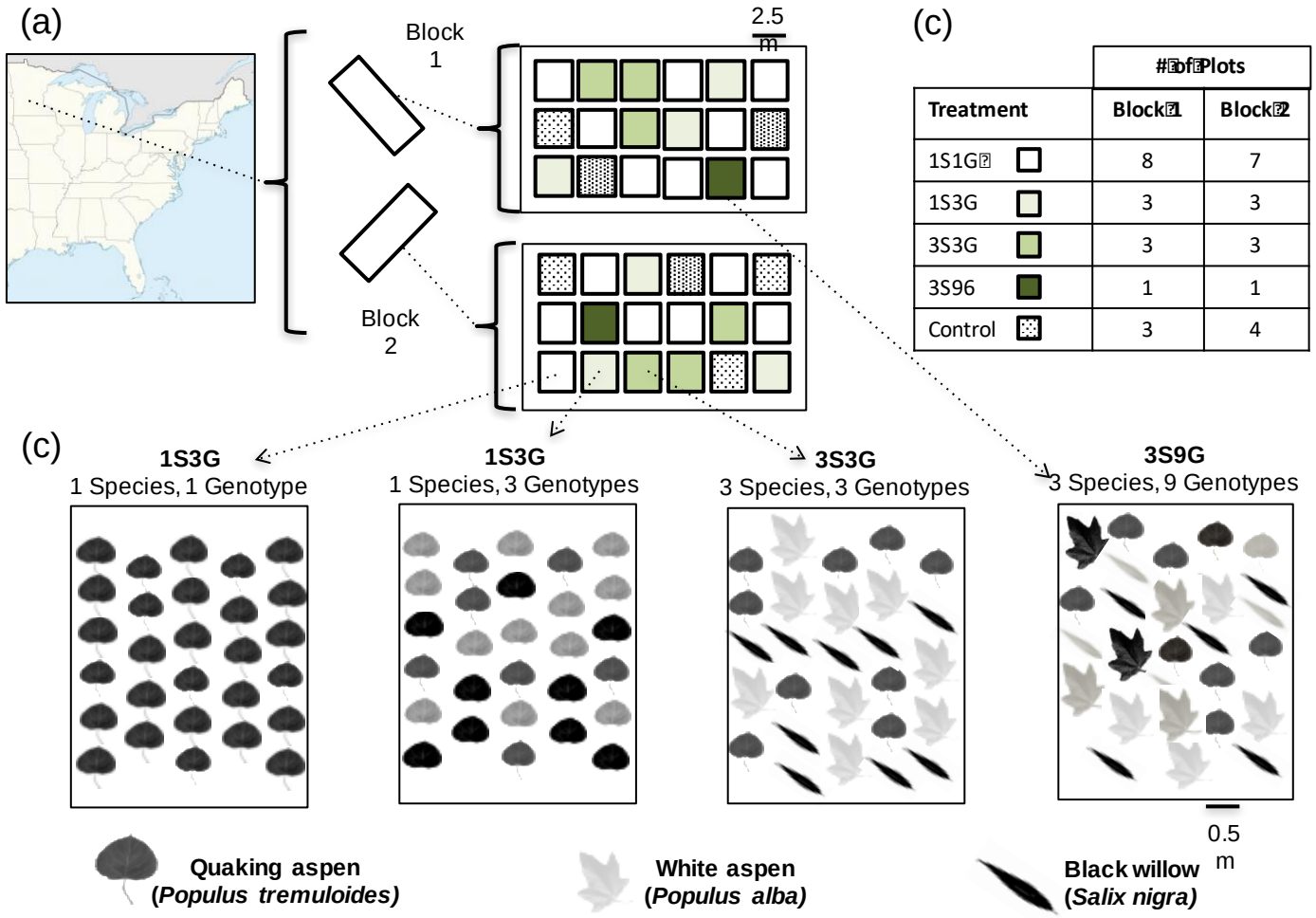
Model Predictors	Model DF	Galls AIC	Leaf Miners AIC
Plant Height	5	390.3	364.6
Plant Height+Genotype ID	9	**381.0**	355.3
Plant Height+Genotype ID+GR	11	384.8	**346.5**
Plant Height+Genotype ID+SR	11	384.9	350.8
Plant Height+Genotype ID+SR/GR	13	388.8	352.4
Plant Height+Genotype ID+PD	15	391.6	352.8

Figure 3.1 – Conceptual framework for biodiversity-ecosystem functioning research across phylogenetic scales. (a) The present research attempts to bridge disciplinary divisions in biological research through integrated assessment of the consequences of intraspecific and interspecific diversity for ecosystem



consequences (gray box). (b) A given ecological response will depend on diversity across phylogenetic scales. This diversity can be conceived of in terms of molecular distance (phylogenetic diversity) or phenotypic distance (functional diversity). Either distance can be represented cladistically based on either genetic or phenotypic information. When diversity among individuals in a population contributes to the relationship, but interspecific diversity does not (Type 1), the **Figure 3.1 (cont.)** response first increases rapidly with distance and then saturates. When diversity among species or clades contributes to the relationship, but intraspecific diversity does not (Type 2), the response does not increase with intraspecific diversity, but then increases with greater distance. When both phylogenetic scales contribute to the response, the relationship increases additively over phylogenetic scales (Type 3). All distance-response relationships shown here represent one set of potential responses to diversity. (c) Past work suggests the expected relationships between a continuous measure of molecular or phenotypic and a variety of ecological responses, including the four investigated here (in shaded box). The response to diversity may be positive, negative, or null and especially influenced by intraspecific diversity, interspecific diversity, or both. Supplementary Table 3.1 documents studies giving rise to these expectations

Figure 3.2 – The Biodiversity in Willows and Poplars (BiWaP) experiment with plots shaded by treatment group and (b) the number of plots per block corresponding to each treatment tabulated. The experiment consists of 29 plots and seven empty control plots. The 29 experimental plots are split into four treatment groups. Three one species, one genotype (1S1G) plots were removed from the experimental design due to seedling shortages. As a result, these monocultures are only planted once in the experiment. Other plot compositions are duplicated (one plot per block). (c) Leaves of the same shade and shape represent genetically identical ramets; different colored leaves of the same shape are different ramets of the same species.



(c)

Treatment	# of Plots Block 1	Block 2
1S1G	8	7
1S3G	3	3
3S3G	3	3
3S96	1	1
Control	3	4

Figure 3.3 – Consequences of diversity for growth and overyielding. Panels present (a) Relative growth rate (g g^{-1} yr^{-1}) and (b) net overyielding, (c) complementarity effects, and (d) selection effects on relative growth rate (g g^{-1} yr^{-1}) by treatment (1S1G = one species, one genotype; 1S3G = one species, three genotypes; 3S3G = three species, three genotypes; and 3S9G = three species, nine genotypes). Treatment means represented by light bars are significantly different than 0 (two-sided t-tests, $\alpha = 0.5$); dark bars indicate treatment means not different than 0. Letters above bars indicate significant differences among treatment means (post-hoc Tukey tests, $\alpha = 0.5$). Monocultural (1S1G) growth rates were used to calculate overyielding, complementarity, and selection, and so are not shown in panels b-d.

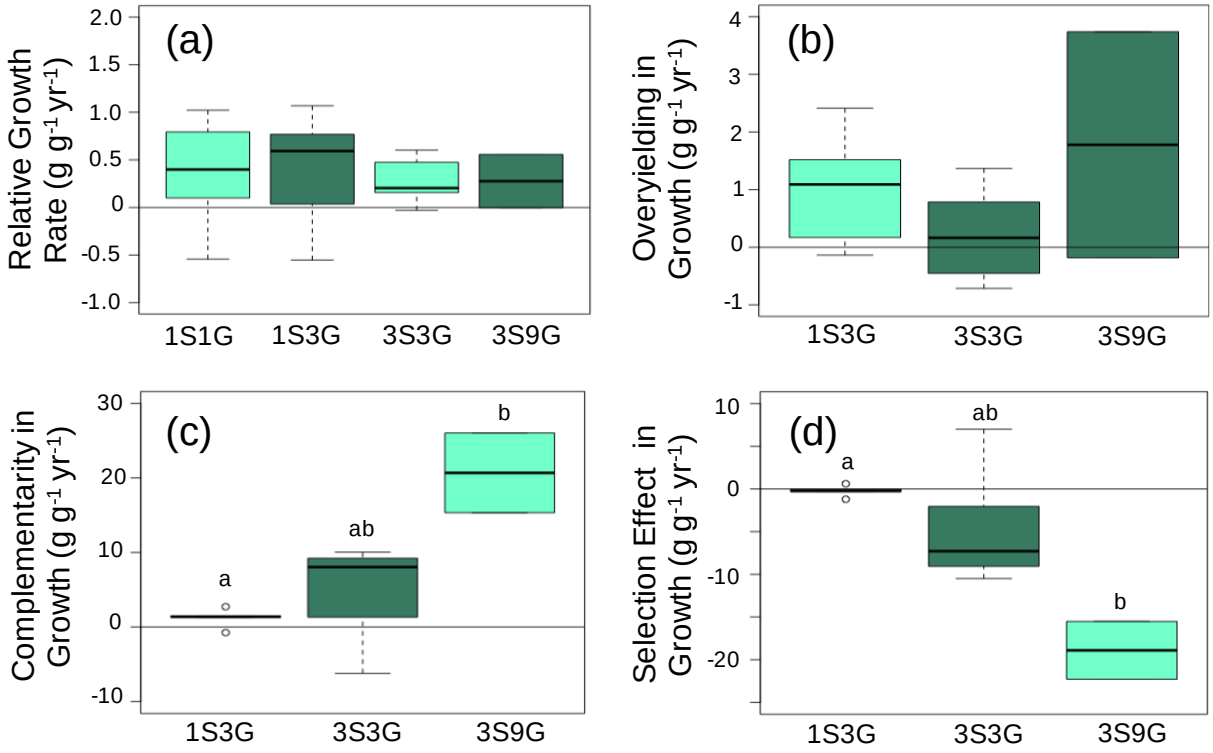
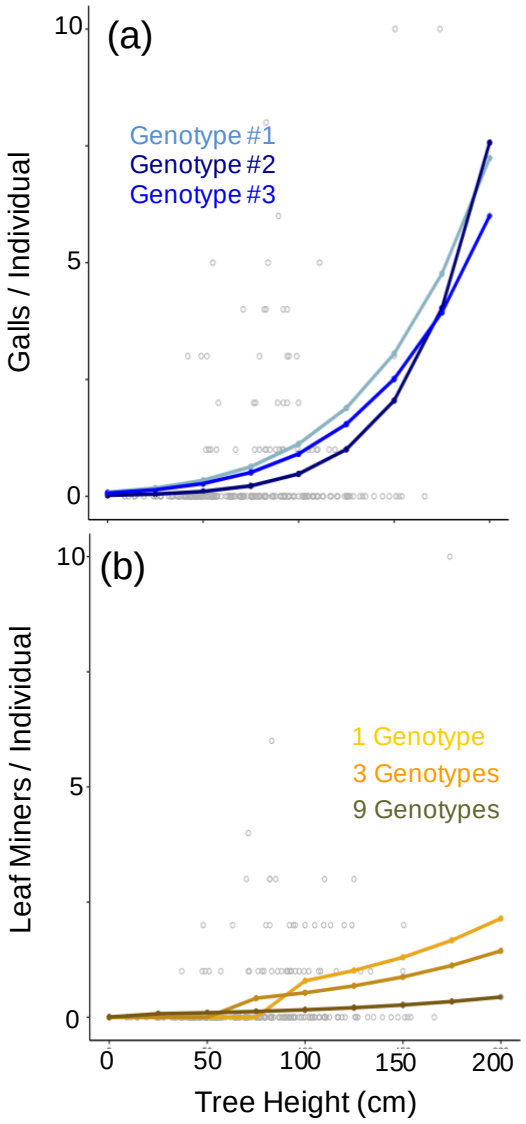


Figure 3.4 – Consequences of diversity for specialist herbivory. Predicted (closed circles) and actual (open circles) (a) gall and (b) leaf miner counts for quaking aspen vs. plant height based on the best models for each herbivore type. Genotypic identity was the best diversity-related predictor of gall intensity and plot genotypic richness was the best diversity-related predictor of leaf miner intensity.



Chapter 4

Functional diversity slows the decomposition of labile carbon in temperate forest litter[5]

[5] The research presented here was conducted in collaboration with Sarah E. Hobbie and Jeannine Cavender-Bares.

Introduction

Roughly 90% of the carbon fixed through terrestrial photosynthesis decomposes (Cebrian 1999). Yet understanding of the degree to which biodiversity regulates the "brown" ecosystem processes that begin with dead tissue pales in comparison to that of its role in the "green" food web centered around living tissue (Srivastava et al. 2009, Cardinale et al. 2011). Unsurprisingly, then, the study of the consequences of biodiversity for ecological functioning (BEF) has centered on plant growth as an exemplary ecological function, with most authors concluding that more diverse plant assemblages support greater primary production (e.g. Hooper et al. 2005, Cardinale et al. 2011, Reich et al. 2012). More recent BEF research has asked how the loss of primary producer diversity might affect ecosystem processes downstream of photosynthesis. These processes include consumption of living plant tissue by animals (herbivory; e.g. Jactel and Brockerhoff 2007) and microbes, i.e., disease (Zhu et al. 2000, Mitchell et al. 2002), and consumption of dead tissues by microbes, i.e., decomposition. Leaf litter decomposition, in particular, constitutes one of the main pathways through which temperate forests recycle nutrients, and thus develop and retain soil fertility (Berg 2000a, Augusto et al. 2002, Sayer 2006).

In an era of rapidly changing forest biodiversity (Vellend et al. 2017), it is crucial to understand the consequences of the loss of tree diversity for litter decomposition. Given that that species' leaf litter traits, and thus identity (Cornelissen 1996, Hobbie et al. 2006, Cornwell et al. 2008), strongly influence decomposition (along with climate and attributes of the decomposer community; Aerts 1997, Srivastava et al. 2009), two general hypotheses regarding the effects of leaf litter diversity on decomposition have emerged. The first, and more parsimonious, hypothesis stems from Grime's (1998) biomass-ratio hypothesis, which predicts that species will contribute to an ecosystem-level process proportionally to their presence in the community (Tardif and Shipley 2013). Under this purely additive scenario, nitrogen-rich and lignin-poor litter decomposes more quickly, regardless of forest diversity (Melillo et al. 1982). Alternately, the diversity hypothesis (Tilman et al. 1997b) predicts that either synergistic (positive) or antagonistic (negative) interactions between species can affect ecosystem processes. In this case, we might expect that translocation of nitrogen from nutrient-rich litter of one species to nutrient-poor litter of another, e.g., via fungal hyphae, would promote faster decomposition of the nutrient-poor litter than would be expected based on that litter decomposing by itself, a synergistic effect (Schimel and Hättenschwiler 2007). The extent to which either of these hypotheses can be generalized across forests is of applied concern (as in Prescott 2010). If the additive hypothesis better describes decomposition across forests, then carbon sequestration and nutrient release can be predicted given relatively accessible knowledge of forest composition. If the diversity hypothesis better predicts litter decomposition, then these processes may respond in more complex and less linear ways to the loss of biodiversity (Cardinale et al. 2011).

Empirical studies of the consequences of biodiversity for leaf litter decomposition have demonstrated support for both the additive and the diversity hypotheses. In a review of the first generation of such litter-mixing experiments, Gartner and Cardon (2004) found mixed results. In two-thirds of cases, changes in decomposition were non-additive, but idiosyncratic, with most authors reporting that species richness (one dimension of diversity) enhanced decomposition (synergism) and some suggesting that higher richness retarded decomposition (antagonism). Cardinale and colleagues (2011) found a similar pattern, although they noted that the high degree of variation in decomposition rates only weakly supports a pattern of synergistic, non-additive diversity effects. In their reviews, Hättenschwiler et al. (2005) and Srivastava et al. (2009) were less sanguine, arguing that such ambiguous evidence does not support the existence of a general, non-additive relationship between forest diversity and decomposition. More recent experiments have yielded similarly mixed results. In some cases, idiosyncratic effects of mixing have supported the additive biomass-ratio hypothesis (Scherer-Lorenzen et al. 2007a, Ball et al. 2008, Tardif and Shipley 2013, 2014, Jewell et al. 2016, Setiawan et al. 2016). In others, authors have found evidence consistent with the diversity hypothesis; interestingly, these tend to be synergistic rather than antagonistic (Vos et al. 2013, Barantal et al. 2014, Handa et al. 2014, Trogisch et al. 2016). Taken together, the presently available evidence suggests that decomposition of the whole litter responses to diversity (and particularly, species richness) inconsistently across study systems.

Despite this, repeated findings of non-additive effects indicate that mixing litters of different species may affect litter decomposition. Notably, non-additive effects of litter mixing may result in faster decomposition at increased functional diversity (Gessner et al. 2010, Barantal et al. 2014, Handa et al. 2014, but see Chapman and Koch 2007). For instance, mixtures that contain litter more diverse in its physical and chemical functional traits may decompose more quickly due to nutrient transfer (e.g. Schimel and Hättenschwiler 2007) or provision of complementary nutrients to soil fauna detritivores (e.g. Hättenschwiler and Gasser 2005). Additionally, because leaf litter consists of numerous chemical compounds arranged in complex physical structures, whole litter decomposition represents not one single biological process, but the sum of many simultaneous processes. These include the rapid leaching of soluble cell contents over days and weeks and the slow decay of lignin over years (Melillo et al. 1989, Berg 2014, Berg and McClaugherty 2014). These distinct processes of may respond in different ways to diversity in leaf litter, such that diversity may accelerate the decomposition of one class of compounds while having no effect on or even decelerating the decomposition of another.

To investigate the consequences of different axes of temperate forest litter diversity for decomposition, we carried out a two-year litterbag study using litter collected from 12 species. Litter was allowed to decompose in single-species monocultures and in 37 mixtures varying orthogonally in taxonomic, phylogenetic, and functional diversity. We quantified not only mass loss, but also changes in four carbon

fractions – soluble cell contents, hemicellulose and bound proteins, cellulose and acid non-hydrolyzable contents (e.g. lignin and similar compounds) over the study period. We expected that:

1) The four carbon fractions measured would display distinct profiles of decomposition over two years given their contrasting ease of breakdown and consumption by microbes (Melillo et al. 1989, Bray et al. 2012, Berg 2014).
2) Decomposition of whole litter mass and all four fractions would vary by species and that more nutrient-rich and lignin-poor litter would decompose more quickly (Hobbie et al. 2006, Cornwell et al. 2008).
3) As in previous work (Tardif and Shipley 2013, 2014, Jewell et al. 2016), litter decomposition would not deviate consistently from expected values based on monocultures.
4) If any metric of diversity did predict deviation from expected decomposition rates, multidimensional functional trait diversity would, by capturing information related to leaf chemical diversity, predict deviation better than would species richness or phylogenetic diversity (Chapman and Koch 2007, Barantal et al. 2014, Handa et al. 2014).

Methods

Litterbag construction

Litter from 12 temperate woody species native to eastern Minnesota was included in this study (Fig 4.1). In October 2014, we collected freshly senesced litter from adult trees of native provenance on private property in Hudson, WI, USA (44°98'N, 92°66'W; *Juniperus virginiana*; eastern red cedar) and at Cedar Creek Ecosystem Science Reserve in East Bethel, MN, USA (45°25′N, 93°10′W; all other species). Litter was air-dried and stored at room temperature in darkness. In spring 2015, litter was used to fill 20 cm by 20 cm square bags constructed of 1 mm fiberglass mesh. Bags were filled with 2.5 g of air-dried litter and heat-sealed. All weights were adjusted to reflect oven-dried (> 24 hours at 60°C) weight and loss-on-handling as estimated from one-species litterbags that had been assembled, deployed in the field, and immediately returned and weighed.

Litterbags contained one of 49 mixture types (or compositions): one monoculture for each study species, 28 bicultures, eight five-species mixtures, and a single twelve-species mixture (Supplementary Table 4.1). Bag compositions were chosen to align with composition of plots in the Forests and Biodiversity (FAB; Grossman et al. 2017) tree diversity experiment, a part of the IDENT network (Tobner et al. 2014), towards disentangling the effects of species richness, and phylogenetic and functional diversity. Briefly, 10 of the two-species mixtures were selected randomly from the available 12-species pool. The other 18 were chosen using a stratified sampling approach to ensure that, to the greatest extent possible, the two-species mixtures included in the experiment cover a range of possible values of both phylogenetic and functional diversity.

As such, two-species mixtures included in this experiment consisted of species pairs that vary widely and orthogonally in their phylogenetic and functional diversity. Five-species mixtures were assembled randomly, and a few randomly chosen species were replaced by others due to litter shortages during bag filling. Bags were filled with litter from one, two, five, or 12 species such that all bags were equiproportionally filled with litter of each constituent species (e.g. a two-species litterbag contained 1.25 g of litter from each species). Each one-, two-, and five-species mixture was replicated twelve times and the 12-species mixture was replicated 24 times, giving a total of 600 bags. Sets of four replicate bags were tied together with nylon string (N = 150). One of the four bags was harvested from each string at four different dates, as descried below, so replication per harvest date was three (unique one-, two-, and five-species mixtures) or six (12-species mixtures).

Measuring litter diversity

Bag composition varied not only in species richness (from one to 12), but also in phylogenetic diversity and functional trait identity and diversity (Fig. 4.1). The species included in the experiment span the seed plant phylogeny, including four gymnosperms and eight angiosperms. Phylogenetic diversity of mixtures was calculated as phylogenetic species variability (PSV; Helmus et al. 2007), which increases from zero to one independently of species richness and, as it nears one, reflects greater evolutionary divergence among species in a community. We calculated PSV using Zanne and colleagues' (2014) phylogeny and the "picante" package in R (Kembel et al. 2010).

We measured 18 leaf physical and chemical traits for all study species (Fig. 4.1; Supplementary Figure 4.1; Supplementary Table 4.2). Trait data were collected from litter used in this litterbag experiment or from sympatrically growing conspecifics. Fresh leaf area and dry mass for measurement of two physical traits, relative leaf water content and specific leaf area (SLA), were calculated through leaf scans with the SIOX ImageJ plug-in (Wang 2016) and balance measurements. We also measured a suite of 16 chemical traits potentially related to leaf litter decomposition. Leaf litter was first ground in a Wiley Mill at 0.425 mm, and then leaf carbon and nitrogen content were analyzed by dry combustion GC analysis on a Costech Analytical ECS 4010 (Valencia, CA, USA); carbon to nitrogen (C:N) ratios were calculated from these values. Leaf phosphorus, calcium, potassium, magnesium, manganese, molybdenum, zinc, and iron were measured through the multi-element, ICP-dry ash method on an iCap 7600 Duo ICP-OES Analyzer (Thermo Fischer Scientific, Waltham, MA, USA). We used an ANKOM 200 fiber analyzer (Macedon, NY, USA; Riggs et al. 2015) to measure the percent content by mass of four operational "carbon fractions" in ground litter: soluble cell contents, hemicellulose and bound proteins, cellulose, and acid non-hydrolyzable compounds (including and hereafter referred to as "lignin") on a mass basis in dried, ground leaves. Finally, we measured condensed tannin content for all species on freeze-dried, ground samples using the butanol-HCl method (Porter et al. 1986) and birch standards purified by the R. Lindroth lab

(Madison, WI, USA; Kopper et al. 2001); we were not able to measure hydrolyzable tannins, though they likely are also important contributors to microbial dynamics in decomposing litter.

For all litter mixture compositions, we estimated functional trait identity and diversity for each of these traits (Supplementary Table 4.1). We represent community-level trait identity as the community-weighted mean (CWM; Mokany et al. 2008) for a given trait and community. CWM for a given trait and community is the abundance-weighted mean of the trait value across all constituent species in a community. CWMs were calculated for all traits across all communities using the "FD" package (Laliberté and Legendre 2010). The same package was used to calculate functional dispersion, a metric of functional diversity, for all traits across all communities. For example, whereas the CWM for cellulose content increases in a community with species whose are richer in cellulose, the functional dispersion for cellulose is highest when species are maximally dissimilar for this trait, given the set of 12 species included in the study. Finally, we calculated multidimensional functional dispersion for all 18 traits across all communities. This multidimensional metric of functional diversity is highest when species in a community differ widely from each other across a broad suite of traits.

Litterbag deployment and collection

All litterbags were deployed in a common garden at Cedar Creek Ecosystem Science Reserve on 12 June, 2015. The common garden was located in a secondary, unmanaged stand of trees, primarily consisting of *Populus grandidentata* (bigtooth aspen) and *Pinus strobus* (white pine) interspersed with *Acer* spp. (maples). Understory growth was minimal and largely consisted of the seasonally abundant legume *Amphicarpaea bracteata* (hog peanut). A duff layer of roughly 0.25 cm in depth covered the mineral soil horizon in the common garden and was left intact. Each string of four litterbags was stretched to its full length so that bags were not touching and staked in place so that the entire bottom surface of each bag was in contact with the existing litter layer. Bags were not covered when deployed but became covered with a layer of freshly fallen litter from four months post-deployment onward. Because bags were deployed over an area large enough to vary in microtopography, overstory vegetation, exposure to deer trampling, etc., we divided bags into three blocks, with 50 strings arranged randomly within each block. Strings were assigned to blocks so that each bag composition was represented across all three blocks.

One litterbag from each of the 150 strings was collected at 62 days (two months), 124 days (four months), 363 days (one year), and 731 days (two years) following deployment. On collection, each bag was cleaned manually of mineral soil, allochthonous litter, ingrown plant material, and soil animals (including small earthworms). Litter was removed from each bag, cleaned further, oven dried at 60° for > 24 hours, and weighed. Dried litter was then ground and carbon fractions were measured as described above. Post-decomposition litter was ashed at 550 °C for four hours and all litter mass estimates and carbon fractions

are presented on an ash-free dry mass basis. Three bags were not recovered, giving a final sample size of 597 bags across 150 strings.

Data Analysis

Calculation of Decomposition Constants

To compare the consequences of litter chemistry for decomposition, we calculated the decomposition rate constant (*k*) for mass, soluble cell contents, hemicellulose and bound proteins, cellulose, and lignin for each string of four bags collected over two years (N = 150) and compared these values among strings. The percentage of mass remaining at a collection time for a given bag was calculated as the oven-dried weight of litter collected at that time divided by the pre-decomposition, oven-dried weight of the litter in that bag (multiplied by 100). Similarly, the pre-decomposition contributions of each carbon fraction to a litterbag's weight were estimated based on species composition and species-level carbon fraction measurements. Thus, it was possible to estimate the percentage of soluble cell contents, hemicellulose and bound proteins, cellulose, and lignin lost from each bag over the course of decomposition.

We then fit these data on proportion of mass or carbon fraction remaining from replicate bags of the same mixture composition (ignoring blocking) to exponential decay models, yielding a decomposition constant for each mixture (N = 49). Initially, we fit data to three different models: a 1) single-exponential, 2) double-exponential, and 3) asymptotic decomposition model (Wieder and Lang 1982; Riggs et al. 2015):

$$X = e^{-kt} \quad (4.1)$$

$$X = Ce^{-k_1 t} + (1 - C)e^{-k_2 t} \quad (4.2)$$

$$X = A + (1 - A)e^{-k_a t} \quad (4.3)$$

in which *X* is the proportion of initial mass or of a given carbon fraction remaining at *t* years after deployment. In thngle-exponential model (equation 4.1), *k* is the decomposition rate (yrs^{-1}). In the double-exponential model (equation 4.2), the decomposing litter is assumed to comprise two pools: a slow pool (C) decomposing at the rate of k_1 and a fast pool (1-C) decomposing at the rate of k_2. In the asymptotic model, the slow pool (*A*) is assumed to decompose at a rate of 0 and the fast pool decomposes at a rate of k_a. All models were fit using the R "bbmle" package (Bolker 2017) following the protocols of Riggs and colleagues (Riggs et al. 2015). We used the corrected Akaike Information Criterion (AICc) as a measure of model fit. Single-and double-exponential decay models fit most mixtures best, but the latter group frequently generated biologically unrealistic decomposition constants. Model fit (R^2) of both classes of models was similar across mixtures, so we used single-exponential models to assess litter decomposition (discussed below). We then refit all decomposition models on a per-string (rather than per-mixture) basis in

order to account for variability among replicate bags decomposing under different conditions. Thus, we calculated *k* values specific to mass and the four carbon fractions for each set of four replicate bags (N = 150). Constants calculated from monocultural bags only (N = 36) were compared using one-way ANOVA and post-hoc Tukey tests ("Agricolae" package; Mendiburu 2016) to assess species-level differences in decomposition rates.

Deviance from Predicted Decomposition (DFP)

To determine the extent to which litter diversity affected decomposition rate, we compared observed decomposition rates (*k*) of two-, five-, and 12-species mixtures to expected decomposition rates (k_e) for these mixtures based on litter decomposition in single-species bags. We did so by modeling the consequences of litter diversity in a given mixture for the deviance from predicted value (DFP; Jewell et al. 2016) of decomposition, calculated as $k - k_e$. Positive DFPs indicate faster decomposition than expected based on monoculture, while negative DFPs suggest that litter in mixture decomposed more slowly than expected based on single-species bags. These results can be shown graphically in plots of k_e vs. *k*, in which case points above a 1:1 line indicate a positive DFP and points below indicate a negative DFP.

To identify which of the 37 litter mixtures (two-, five-, and 12-species combinations) deviated from expected decomposition rates (DFP $\neq$ 0), we calculated confidence intervals of one standard error above and below the mean value for each mixture type (N = 6 for the 12-species mixture and 3 for all other mixtures). When a given mixture's confidence interval did not include zero, we concluded that that mixture deviated from expected, additive predictions of decomposition rates.

Decomposition Models

We used mixed-effects regression modeling to explore the relationship between both decomposition rates (*k*) and diversity-related changes in decomposition rates (DFP) and species richness, phylogenetic diversity, functional identity, and functional diversity. Models were fit using the *lmer* function in the "lme4" package (Bates et al. 2015) with a log-likelihood criterion. The structure of all models is as follows:

$$Y \sim X_i\beta_i + \text{Block/Mixture Type}\ \mu + \varepsilon \quad (4.4)$$

where *Y* is the dependent variable (either *k* or DFP for decomposition rate of mass or one of the four carbon fractions measured), X_i is the known vector of values for a given fixed predictor *i* (species richness, phylogenetic diversity, functional identity, or functional diversity), β is an unknown vector of fixed effects for predictor *i*, μ is an unknown vector of random effects corresponding to the random effect of mixture type nested in block, and ε is an unknown vector of random errors.

To assess the relationship between *k* (for mass loss and carbon fractions) and the chemical composition of litter, we used forward variable selection to determine which litter trait CWMs were most strongly associated with each decomposition constant. We then assessed multicollinearity of each candidate predictor set using Farrar-Glauber testing (a suite of multicollinearity measures incorporated into the *imcdiag* function of the "mctest" package; Ullah and Aslam 2018) and sequentially removed predictors from each set until remaining predictors were not collinear. Remaining predictors were then fit as fixed effects in mixed-effects linear regression models as in equation 4.4. We followed the same procedure to model the extent to which the DFP for mass or a given carbon fraction was predicted by the identity and diversity of particular traits, initiating variable selection with a predictor set consisting of CWMs and functional dispersion values for all 18 traits.

We also expected that DFP for mass loss and carbon fractions would vary with mixture species richness, phylogenetic diversity, and multidimensional functional trait identity, and functional trait diversity. To assess these relationships, for each dependent variable (DFP of mass loss and each carbon fraction) we first fit a maximal model in which species richness, phylogenetic diversity, and multidimensional functional diversity were included in that order as fixed predictors. We then used log-likelihood tests to compare these models to reduced models, sequentially removing each fixed predictor. When there was no difference between models, we chose the more parsimonious one. All statistical analyses were performed in R, Version 3.4.3 (R Core Team, 2017).

Results

Changes in mass, soluble cell contents, and hemicellulose and bound proteins were generally well-represented through single-exponential decomposition models. In some cases, double-exponential decay models generated lower AIC scores or fit decomposition data slightly better than did single-exponential decay models. However, in these double-exponential models, high k_2 values often caused these preferred models to collapse, functionally, into poorly-fitting asymptotic decay models. In other cases, and especially for slower-decomposing carbon fractions, estimated parameters in double-exponential models did not seem realistic or were hard to interpret. Since single-exponential decay models were almost as well-supported in model comparison and are more straightforward to interpret, we report the decomposition rate parameters from these models below as "*k"* or "decomposition" constants.

As expected, decomposition of total mass and carbon fractions varied widely among species included in this experiment (Table 4.2, Supplementary Figure 4.2). Mass loss over two years ranged from 41% (*Tilia americana*; basswood) to 8% (*Pinus strobus*; white pine; Fig. 4.2). The decomposition of soluble cell contents (losses ranging from 64% to 17%), hemicellulose and bound proteins (losses ranging from 69% to

6%), and cellulose (40% to 8%) demonstrated qualitatively similar patterns (Supplementary Figure 4.2, A-D). Only eastern red cedar lost appreciable amounts of lignin (12% of initial lignin content lost), while other species either did not show signs of lignin degradation or were enriched in lignin or chemically similar compounds (Supplementary Figure 4.3E).

As expected, pre-decomposition litter chemistry predicted mass loss and the decomposition of litter carbon fractions over two years (Table 4.3). Litter rich in nutrients, most notably calcium, and soluble cell contents tended to decompose faster. Lignin in nitrogen-enriched (low C:N ratio) litter decomposed more slowly than in nitrogen-poor litter. Litter traits explained mass loss (marginal $R^2 = 0.64$) and loss of soluble cell contents ($R_m^2 = 0.70$) and hemicellulose and bound proteins ($R_m^2 = 0.70$) better than loss of cellulose ($R_m^2 = 0.49$) or lignin ($R_m^2 = 0.28$; Supplementary Table 4.2).

Contrary to our expectations, litter mixtures decomposed non-additively, meaning that they decomposed more slowly or quickly than expected based on single-litter bags (Table 4.4, Supplementary Table 4.3). Mass decomposition was non-additive for 62% of the 37 mixtures we included in our study; eight mixtures decomposed more slowly than expected (antagonism) while 15 mixtures decomposed more quickly than expected (synergism). Change in carbon fractions showed different patterns depending on the fractions. Cellulose and lignin decomposed roughly as expected in mixture, showing antagonistic and synergistic deviations from expectations at roughly the same frequency. Antagonistic effects were much more common for soluble cell contents (54% of all mixtures), and to a lesser extent for hemicellulose and bound proteins (41% of all mixtures).

Though more diverse litter did not, overall, decompose differently than expected based on monoculture (Fig. 4.3), the two most labile litter carbon fractions decomposed more slowly than expected in functionally diverse litter (Table 4.4). The best models of DFP for soluble cell contents and hemicellulose and bound protein decomposition were those that included as a fixed effect only multidimensional functional diversity, and not species richness or phylogenetic diversity. As expected, functional diversity better predicted DFP than did other dimensions of diversity. (Species richness was somewhat predictive of DFP for these fractions, and phylogenetic diversity was not.) In both of these models, a negative coefficient for functional diversity indicates that litter with more diverse functional traits decomposed more slowly than expected based on single-species decomposition rates. Marginal R^2 values for these models indicate that functional diversity explained 11% of the variation in soluble cell contents DFP and 7% of the variation in hemicellulose and bound protein DFP. We did not find evidence for this pattern in models of total mass loss or cellulose or lignin decomposition DFPs, for which the best-supported model contained only an intercept and random effects (Supplementary Table 4.4).

Single-trait identity and diversity models of DFPs echoed our finding that functional trait diversity mediated the relationship between diversity and decomposition in our litterbag experiment (Table 4.5; Supplementary Table 4.4). Functional trait dispersion was far more important than litter identity (CWMs) in variable selection for these models of litter DFP; only one CWM, molybdenum, was retained as a predictor of DFP (for hemicellulose and bound proteins). And echoing our finding of the negative relationship between multidimensional functional diversity and decomposition, diversity in several litter chemical traits (calcium, magnesium, manganese, molybdenum, and zinc) also led to slower decomposition rates. In contrast, diversity in phosphorus, potassium, and iron was associated with faster than expected decomposition.

Discussion

We tracked decomposition of total mass and four carbon fractions in litter of 12 species and 37 polycultural mixtures over two years. Carbon fractions showed different decomposition profiles and species varied significantly in their decomposition rate, with more labile fractions and more nutrient-rich litter decomposing more quickly. Most notably, labile litter carbon decomposed more slowly in mixture than was expected, and this effect was stronger in litter from species with diverse chemical traits.

Carbon fractions varied in decomposition rate

As predicted by the mass-ratio hypothesis, the decomposition of our four measured litter carbon fractions varied with the chemical composition of the fraction. We expected that more labile fractions (e.g. soluble cell contents and hemicellulose and bound proteins) would decompose rapidly and that more recalcitrant fractions (e.g. cellulose and lignin) would decompose slowly, if at all, and stabilize within the two-year study period (Adair et al. 2008, Berg 2014, Berg and McClaugherty 2014, Riggs et al. 2015). Our expectations were confirmed; we documented rapid loss in the two labile carbon fractions and enrichment of litter with lignin and other compounds that resist acid hydrolysis (Melillo et al. 1989, Bray et al. 2012, Berg 2014). These patterns suggest rapid, physically and microbially mediated decomposition of labile carbon and relatively limited decomposition of more recalcitrant carbon (Berg et al. 2010, Bray et al. 2012, Chapman et al. 2013, Berg 2014). And limited cellulose loss is consistent with the expectation that, because some cellulose is physically enmeshed with lignin in leaf litter, unlignified cellulose will decompose relatively quickly, but that cellulose loss will then level off and keep pace with (slow) lignin decomposition (Herman et al. 2008, Berg 2014).

Litter chemistry predicted decomposition

Our findings confirm our expectations, based on the mass-ratio hypothesis, that leaf litter chemistry predicts whole mass and carbon fraction decomposition rates, although the particular chemical traits implicated in decomposition were not those we expected. Specifically, we found that whole litter

decomposed more quickly if it was initially higher in calcium, soluble cell contents, and zinc (Table 4.3). This finding is consistent with the current consensus that nutrient-rich litter with low lignin (and thus higher proportions of labile fractions such as soluble cell contents) decomposes more rapidly, especially in early stages of decomposition (Cornelissen 1996, Cornwell et al. 2008, Berg and McClaugherty 2014, Djukic et al. 2018). Interestingly, the community-weighted means of plant macronutrients such as nitrogen and phosphorus content were less frequently selected for inclusion in final models of *k*-values than were micronutrients such as calcium, zinc, and magnesium content. The absence of evidence of a strong effect of nitrogen on decomposition, in particular, suggests that litter decomposition in this particular study may have been limited primarily by micronutrients. However, patterns in litter quality across nutrient types were generally collinear (Supplementary Figure 4.1). Given this, we conclude that, though micronutrients were particularly predictive of decomposition in this experiment, our findings generally comport with the literature suggesting that higher-quality litter decomposes quickly.

Litter with higher initial calcium content lost not only mass, but also hemicellulose and bound proteins, cellulose, and lignin more rapidly than low-calcium litter, echoing past work that this nutrient contributes heavily to the first months and years of litter decomposition (Table 4.3; Davey et al. 2007, Berg et al. 2017). Whereas other nutrients such as nitrogen, phosphorus, and magnesium are generally thought to speed microbially mediated decomposition, calcium is believed to make litter more attractive to earthworms and other invertebrates, thus facilitating fragmentation and translocation of decomposing litter (Reich et al. 2005, Hobbie et al. 2006). Indeed, though the 1-mm mesh size of our litterbags likely prevented consumption of litter by adult earthworms, we found small earthworms inside litterbags; these may have migrated into the bags as juveniles and preferentially consumed high-calcium litter.

Past research suggests that condensed tannins may retard decomposition through chemical immobilization of nitrogen and toxicity to microbes (Hättenschwiler and Vitousek 2000, Kraus et al. 2003, Madritch and Lindroth 2015). In contrast, we found that initial condensed tannin content in litter was positively associated with whole mass and hemicellulose and bound protein decomposition. We did not measure changes in nitrogen content over decomposition, so we do not know if tannins immobilized litter nitrogen in this experiment. They may have, however, accelerated the decomposition of whole litter by serving as an alternative carbon source for microbial decomposers (e.g. Kraus et al. 2004). Finally, change in lignin was negatively associated with carbon to nitrogen ratios, a finding consistent with the expectation that nitrogen slows lignin decomposition (Melillo et al. 1982, Berg and Ekbohm 1993, Berg 2014).

Litter decomposition in mixture deviated from expectations

Based on the balance of current experimental evidence, we expected that litter diversity would not alter the decomposition rate of whole leaf litter non-additively or that its effects would be idiosyncratic (Gartner and

Cardon 2004, Hättenschwiler et al. 2005, Srivastava et al. 2009, Cardinale et al. 2011). This expectation was met: despite idiosyncratic deviations from predicted rates, whole litter in mixture did not generally lose mass faster or slower than expected.

Yet litter decomposition studies, including our own, continue to document measurable, if idiosyncratic or system-specific, non-additive decomposition of litter mixtures containing two or more species, as predicted by the diversity hypothesis (e.g. Vos et al. 2013, Barantal et al. 2014, Handa et al. 2014, Trogisch et al. 2016). Our findings suggest a new potential mechanism behind otherwise ambiguous previous findings of changes in decomposition across species richness gradients. We argue that more labile, or quickly decomposing, fractions of the whole litter may be disproportionately affected by functional diversity during early decomposition. Over half of the 37 litter mixtures included in our experiment showed significant, antagonistic, non-additive changes in soluble cell contents, a clear signal that the labile carbon fraction of mixed litter tended to decompose more slowly than it would have if separated into constituent species. Litter also lost soluble cell contents at a higher rate (17-64% of original mass) than was the case for any other fraction. The same patterns were exhibited, at smaller magnitude, by hemicellulose and bound proteins, the second most labile carbon fraction we measured. This leads us to conclude that, as the most actively decomposing carbon fractions, soluble cell contents and hemicellulose may have been most responsive to diversity over the first two years of litter decomposition. Yet, in our experiment, cellulose and lignin did not show high rates of mass loss and, to the extent that they did, did not deviate from expected values based on monoculture. Thus, the non-additive consequences of diversity for more labile fractions was masked by insensitivity to diversity in the decomposition of other fractions. Our findings thus provide one potential explanation for the past findings of idiosyncratic, non-additive decomposition of mixed leaf litter (e.g. Scherer-Lorenzen et al. 2007, Tardif and Shipley 2013, Jewell et al. 2016, Setiawan et al. 2016): the labile carbon in more functionally diverse litter may decompose more slowly than it would in the absence of leaf litter mixing.

Slower litter decomposition is associated with its functional diversity

Given the strong control of decomposition by litter chemistry, we expected that deviations from expected decomposition rates might be related to litter functional diversity (Barantal et al. 2014, Handa et al. 2014, Tardif and Shipley 2014, but see Chapman and Koch 2007). Indeed, we found that multidimensional functional dispersion of 18 leaf litter traits predicted deviance from predicted decomposition of labile carbon fractions better than did taxonomic or phylogenetic diversity (Fig. 4.3). In particular, litter mixtures that varied most in soluble cell contents and calcium and magnesium content showed the slowest decomposition compared to predictions from single-species bags (Table 4.5).

Our finding that more chemically diverse litter was associated with slower decomposition of labile carbon fractions may be attributable to the consequences of functional diversity for microbial decomposers. Early decomposition is mediated by rapidly shifting assemblages of bacterial and fungal decomposers (Aneja et al. 2006, Chapman et al. 2013, Voriskova and Baldrian 2013). The composition and functioning of these microbial decomposer communities is highly dependent on available resources, shifting rapidly to take advantage of high-quality litter (Strickland et al. 2009, Bray et al. 2012, Schneider et al. 2012). Thus, the physical proximity of nutritionally diverse litters is expected to have one of two effects. Diversity might, on one hand, facilitate decomposition through priming (e.g. transfer of nitrogen from rich-to poor-nitrogen litter; Schimel and Hättenschwiler 2007, Bonanomi et al. 2014) and/or niche complementarity (e.g. greater activity of detritivores in mixtures due to the availability of diverse nutrients and concomitant easing of nutrient limitation; Vos et al. 2013, Handa et al. 2014), leading to synergistic, faster than expected decomposition (Chapman and Koch 2007). Alternatively, and consistent with our findings, diverse litter might limit the abundance or disrupt the functioning of assemblages of the highly efficient, specialized decomposers that might thrive on single-species litter. This interpretation draws attention to the need for an additional focus on the mechanisms behind antagonistic, non-additive effects on mixed-litter decomposition to complement past work on synergistic effects (Vos et al. 2013, Barantal et al. 2014, Handa et al. 2014, Setiawan et al. 2016, Trogisch et al. 2016). It also contributes to evidence that for decomposition as well as for productivity, functional trait diversity may serve as an important predictor of ecosystem functioning (Tilman et al. 1997a, Diaz and Cabido 2001, Cadotte et al. 2009, Flynn et al. 2011, Eduardo 2016).

Conclusion

Our analysis of data from almost 600 litterbags indicates that functional traits are critical predictors of the decomposition of temperate forest litter. On the one hand, functional trait identity (community-weighted means) best predicted decomposition rates of total litter mass and carbon fractions (Mokany et al. 2008, Tardif and Shipley 2013, Jewell et al. 2016). Functional identity not only predicted decomposition of single-species litter, but also of changes in total mass and recalcitrant carbon fractions (cellulose and lignin) over two years. Yet functional diversity of leaf traits better predicted decomposition of labile carbon fractions (soluble cell contents and hemicellulose and bound proteins) in mixed litter due to largely antagonistic, non-additive interactions. Thus, in considering the effects of biodiversity on decomposition, we find evidence that the biomass-ratio hypothesis (Grime 1998) holds for changes in mass and recalcitrant carbon fractions of mixed litter while the diversity hypothesis (Tilman et al. 1997b) holds for labile carbon fractions of mixed litter. Longer-term studies (Melillo et al. 1989, Berg 2000b, 2014, Berg et al. 2010) may reveal that diversity alters the decomposition of cellulose and lignin in mixed litter as well, or the antagonistic, non-additive effect of diversity may be particular to labile carbon fraction decomposition.

Leaf litter decomposition contributes through multiple processes to the maintenance of soil fertility (Cotrufo et al. 2013, Hobbie 2015) and to the sequestration of carbon in forest soils (Prescott 2010). Both shorter-term inhibition of decomposition (as we found in our study) and long-term chemical stabilization (e.g. humification; Ponge 2013, Ni et al. 2016) of litter can lead to the sequestration of carbon, which would otherwise contribute to atmospheric greenhouse gas stocks, as soil organic matter (Mueller et al. 2015, Soong et al. 2015). Absent non-additive effects of litter mixing, the rate at which carbon and nutrients are sequestered in this way simply depends on species abundances. But given evidence from our work that litter mixing can depress labile carbon decomposition rates, it is possible that more biodiverse forests could lose these compounds at a slower rate than less diverse forests. Such non-additive diversity effects should be considered in the conservation and management of soil fertility in forests and plantations and in attempts to model carbon and nutrient cycles in tree-dominated landscapes.

Table 4.1 - Litterbag treatments and harvest design

Mixture Type	Number of Unique Mixtures	Replicates per Harvest	Number of Harvests	Total Bags
1-species	12	3	4	144
2-species (randomly choice)	10	3	4	120
2-species (stratified random choice)	18	3	4	216
5-species	8	3	4	96
12-species	1	6	4	24
Harvests took place 2, 4, 12, and 24 months after deployment.			**Total:**	**600**

Table 4.2 – Species means (and standard errors) for decomposition rates of total mass and carbon fractions. Within each column, values with the same superscript are not significantly different at the 0.10 level via post-hoc Tukey test.

Species	*k* (decomposition rate; year^{-1})				
	Mass Loss	Soluble Cell Contents	Hemicellulose and Bound Proteins	Cellulose	Lignin
Acer negundo	0.33 (0.03)^{bcd}	3.3 (0.13)^{a}	0.93 (0.15)^{bc}	0.27 (0.06)^{b}	None^{b}
Acer rubrum	0.32 (0.10)^{bcd}	2.0 (0.66)^{bc}	0.16 (0.09)^{c}	0.18 (0.07)^{b}	None^{b}
Betula papyrifera	0.47 (0.06)^{ab}	1.8 (0.26)^{bcd}	1.2 (0.17)^{b}	0.43 (0.11)^{ab}	0.07 (0.06)^{ab}
Juniperus virginiana	0.46 (0.16)^{abc}	1.5 (0.39)^{bcde}	0.83 (0.29)^{bc}	0.47 (0.18)^{ab}	0.19 (0.04)^{a}
Pinus banksiana	0.18 (0.03)^{cd}	0.39 (0.04)^{ef}	0.48 (0.07)^{bc}	0.22 (0.05)^{b}	0.05 (0.03)^{b}
Pinus resinosa	0.30 (0.08)^{bcd}	0.84 (0.17)^{cdef}	0.67 (0.08)^{bc}	0.20 (0.05)^{b}	0.01 (0.01)^{b}
Pinus strobus	0.12 (0.01)^{d}	0.25 (0.07)^{f}	0.26 (0.04)^{c}	0.30 (0.06)^{b}	0.05 (0.03)^{ab}
Quercus alba	0.31 (0.02)^{bcd}	0.75 (0.06)^{def}	0.63 (0.07)^{bc}	0.32 (0.05)^{b}	None^{b}
Quercus ellipsoidalis	0.16 (0.02)^{d}	0.34 (0.04)^{ef}	0.42 (0.05)^{bc}	0.23 (0.03)^{b}	0.03 (0.02)^{b}
Quercus macrocarpa	0.14 (0.03)^{d}	0.41 (0.04)^{ef}	0.48 (0.07)^{bc}	0.18 (0.01)^{b}	None^{b}
Quercus rubra	0.16 (0.02)^{d}	0.22 (0.02)^{f}	0.43 (0.02)^{bc}	0.39 (0.02)^{ab}	0.03 (0.02)^{b}
Tilia americana	0.67 (0.10)^{a}	2.4 (036)^{ab}	3.1 (0.44)^{a}	0.75 (0.12)^{a}	0.08 (0.05)^{ab}

Table 4.3 - Best models of decomposition constants (*k*) predicted by community-weighted means (CWMs) of trait values. Trait CWMS, chosen through forward selection, are included for loss of mass (A) and carbon fraction decomposition (B-E) as fixed predictors. Litter composition type, nested within block, is included as a random predictor. All estimates for fixed predictors are standardized.

Fixed Terms	Estimate	t	Random Terms	St. Dev.	Levels
A. Mass - *k*					
Calcium CWM	0.683	13.0	Number of Obs.	NA	150
Soluble Cell Contents CWM	0.262	5.08	Block/Composition	0.069	147
Zinc CWM	0.205	4.16			
Condensed Tannins CWM	0.182	3.59			
Marginal R^2 = 0.640					
Conditional R^2 = 0.894					
B. Soluble Cell Contents - *k*					
Water Content CWM	0.309	3.01	Number of Obs.	NA	150
Soluble Cell Contents CWM	0.609	6.73	Block/Composition	0.027	147
Cellulose CWM	0.250	2.68			
Magnesium CWM	0.233	2.54			
Manganese CWM	-0.150	-2.40			
Marginal R^2 = 0.700					
Conditional R^2 = 0.750					
C. Hemicellulose and Bound Proteins - *k*					
Calcium CWM	0.456	6.52	Number of Obs.	NA	150
Hemicellulose and Bound Proteins CWM	0.308	4.45	Block/Composition	<0.001	147
Condensed Tannins CWM	0.335	6.10			
Phosphorus CWM	0.261	4.11			
Marginal R^2 = 0.703					
Conditional R^2 = 0.703					
D. Cellulose - *k*					
Calcium CWM	0.777	11.8	Number of Obs.	NA	150
Molybdenum CWM	-0.171	-2.30	Block/Composition	0.012	147
Soluble Cell Contents CWM	-0.156	-2.23			
Marginal R^2 = 0.490					
Conditional R^2 = 0.968					
E. Lignin - *k*					
Lignin CWM	0.553	7.00	Number of Obs.	NA	150
Calcium CWM	0.511	5.51	Block/Composition	0.003	147
Carbon : Nitrogen CWM	0.252	2.89			
Marginal R^2 = 0.275					
Conditional R^2 = 0.749					

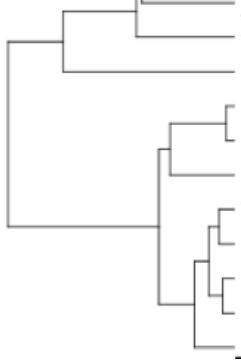
Table 4.4 – Non-additive and additive decomposition across carbon fractions. The number of each of 37 litter mixtures included in this experiment for which we observed antagonistic (slower than expected based on monoculture), synergistic (faster than expected), or additive (as expected) decomposition varied among whole litter mass and carbon fractions.

	Non-Additive		Additive
Decomposition Type	Antagonistic	Synergistic	
Mass Loss	8	15	14
Solube Cell Contents	20	7	10
Hemicellulose and Bound Proteins	15	9	13
Cellulose	12	12	13
Lignin	9	9	19

Table 4.5 – Best models of deviance from predicted (DFP) decomposition based on multidimensional functional diversity (A-B) or trait identity and univariate trait diversity (C-D). These metrics, chosen through forward selection, are included for soluble cell contents (A,C) and hemicellulose and bound protein decomposition (B,D) as fixed predictors. Litter composition type, nested within block, is included as a random predictor. In C and D, all estimates for fixed predictors are standardized. Models for mass, cellulose, and lignin are given in Supplementary Table 4.4.

Fixed Terms	Estimate	t	Random Terms	St. Dev.	Levels
A. Soluble Cell Contents - DFP - muldimensional trait diversity					
Functional dispersion	-2.62	-2.89	Number of Obs.	NA	114
			Block/Composition	< 0.001	111
Marginal R^2 = 0.115					
Conditional R^2 = 0.115					
B. Hemicellulose and Bound Proteins - DFP - multidimensional trait diversity					
Functional dispersion	-1.98	-2.88	Number of Obs.	NA	114
			Block/Composition	< 0.001	111
Marginal R^2 = 0.068					
Conditional R^2 = 0.068					
C. Soluble Cell Contents - DFP - CWMs and univariate trait diversity					
Molybdenum CWM	-0.436		Number of Obs.	NA	114
Soluble cell contents functional dispersion	-0.289		Block/Composition	< 0.001	111
Magnesium functional dispsersion	-0.380				
Carbon functional dispersion	0.249				
Marginal R^2 = 0.290					
Conditional R^2 = 0.290					
D. Hemicellulose and Bound Proteins - DFP - CWMs and univariate trait diversity					
Magnesium functional dispersion	-0.242	-3.24	Number of Obs.	NA	114
			Block/Composition	<0.001	111
Marginal R^2 = 0.085					
Conditional R^2 = 0.085					

Figure 4.1 – Species identity and chemical and physical characteristics of litter used in the study. Litter was collected from 12 species native to eastern Minnesota that span the seed plant phylogeny. Species-level trait means for eight traits thought to control decomposition are shown here; full trait information for these and 10 other traits is given in Supplementary Table 4.1. Percentages are given on a dry mass basis. The phylogenetic tree on the left side of the figure represents evolutionary relationships among the 12 species as in Chapter 1 and Grossman et al. (2017).



Species	Relative Water Content (%)	Specific Leaf Area (cm^2/g)	Soluble Cell Contents (%)	Lignin (%)	Carbon / Nitrogen	Phosphorus (%)	Calcium (%)	Condened Tannins (%)
Red pine *(Pinus resinosa)*	51.4%	26.2	53.0%	16.4%	156.2	0.048%	0.947%	22.10%
Jack pine *(Pinus banksiana)*	62.2%	35.1	45.0%	24.0%	100.1	0.103%	0.913%	18.32%
White pine (*Pinus strobus)*	53.6%	65.3	32.3%	30.0%	88.0	0.152%	1.227%	7.71%
Eastern red cedar *(Juniperus virginiana)*	63.6%	32.4	49.0%	25.8%	33.0	0.173%	3.169%	1.97%
Red maple *(Acer rubrum)*	60.4%	178.2	67.2%	12.5%	93.2	0.193%	1.020%	4.69%
Box elder *(Acer negundo)*	71.7%	166.6	61.8%	17.2%	33.1	0.217%	2.608%	6.99%
Basswood *(Tilia americana)*	72.9%	368.7	54.0%	13.9%	40.4	0.262%	4.525%	12.13%
White oak (*Quercus alba)*	58.0%	156.7	56.7%	16.2%	65.3	0.170%	1.994%	3.86%
Bur oak *(Quercus macrocarpa)*	59.3%	94.4	48.8%	20.8%	32.3	0.253%	1.215%	5.01%
Northern pin oak *(Quercus ellipsoidalis)*	58.6%	116.7	44.7%	26.6%	43.7	0.163%	1.079%	6.83%
Red oak *(Quercus rubra*)	54.9%	136.0	42.3%	22.0%	64.1	0.133%	1.403%	3.96%
Paper birch *(Betula papyrifera*)	69.5%	225.1	57.5%	20.4%	59.8	0.311%	1.841%	5.42%

Figure 4.2 – Decomposition constants (*k*) for monospecific litterbags. Letters above columns indicate the results of Tukey post-hoc testing at the 0.10 level; values of *k* for species that share a letter are not significantly different. Error bars reflect one standard error. Commensurate figures for all carbon fractions are shown in Supplementary Figure 4.1.

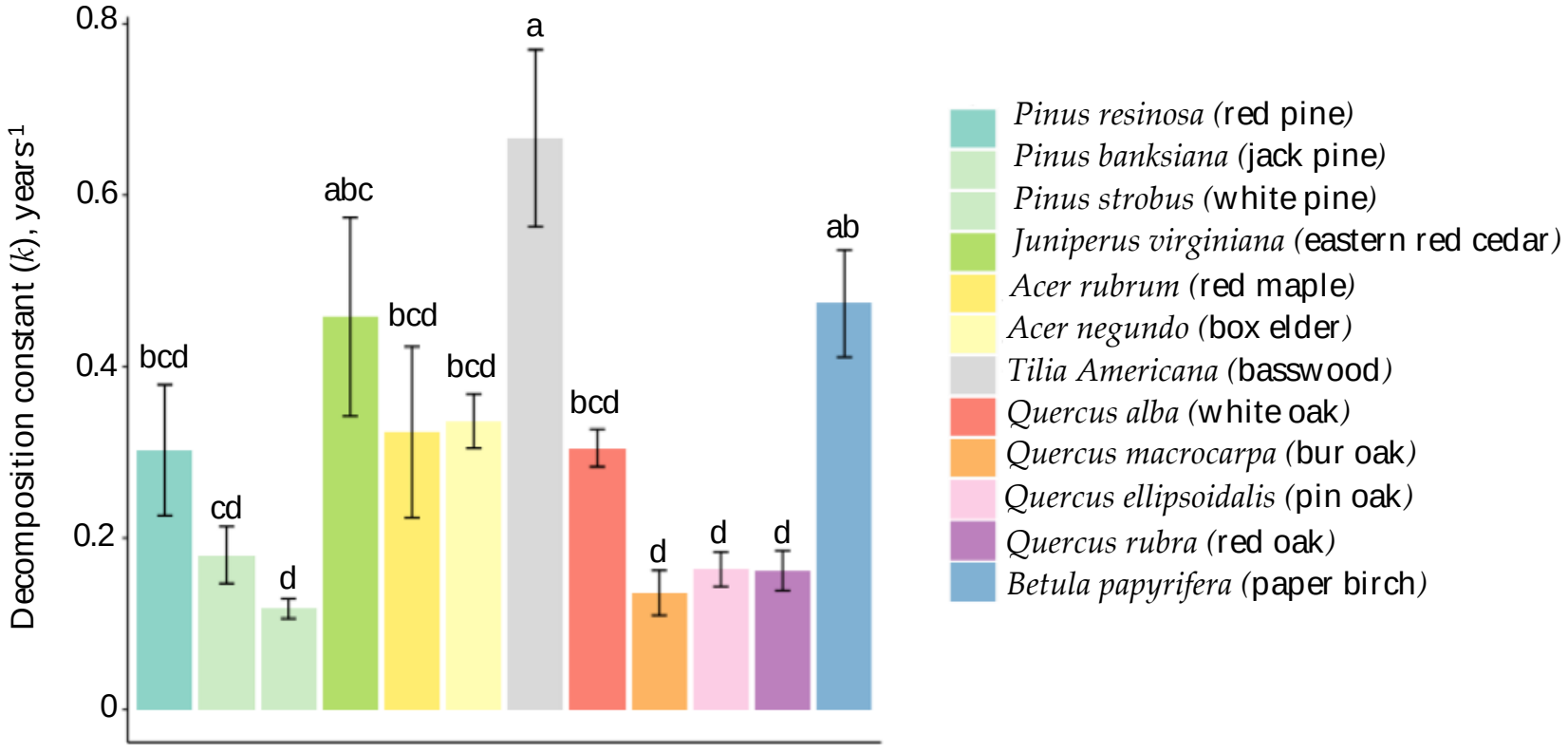
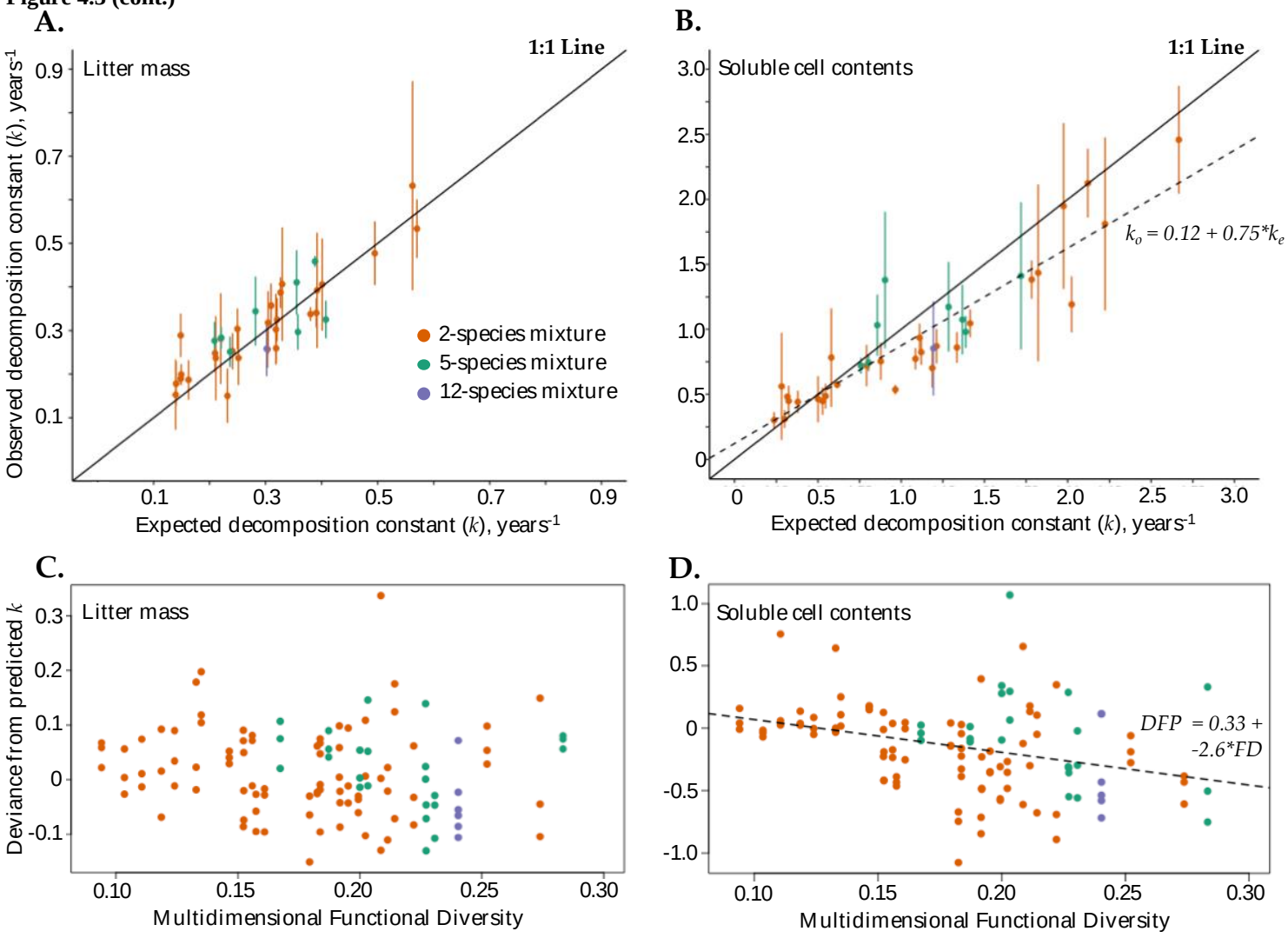


Figure 4.3 – Decomposition of total mass and soluble cell contents in mixed litter. A,B) Observed versus expected decomposition rates (*k*) of A) total mass and B) soluble cell contents in mixed litter. Error bars indicate standard error based on three- (or six-, for 12-species bags) replicate sets of bags with the same composition. In these plots, points that fall above a 1:1 line indicate a mixture that decomposed faster than expected based on monoculture and points that fall below the line indicate slower-than-expected decomposition. Total mass loss in mixtures did not deviate from expectations (A), but a simple linear regression shows that observed soluble cell contents decomposition rate in mixtures was roughly 75% of what would be expected based on monocultures (B). C) Deviance from expected decomposition (DFP; $k_{observed} - k_{expected}$) of total mass did not vary systematically with multidimensional functional diversity of mixed litter, but D) more functionally diverse litter lost soluble cell contents more slowly than would be expected. The regression slope in panel D corresponds to the model presented in Table 4.5A ($R^2_{Marginal} = 0.115$). All points are color-coded by thecies richness of the litter mixture as indicated in panel A.

Figure 4.3 (cont.)



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Appendices

Appendix S1: Methodological Appendix for Chapter 1

Stratified Random Selection of Bicultures

Half of the experimental bicultures were chosen using a stratified random approach as follows. We grouped all possible bicultures into four groups, representing each possible combination of low and high phylogenetic diversity (Phylogenetic Species Variability; PSV) and functional diversity (multidimensional Functional Dispersion; FDis) and randomly chose four bicultures from each group to include in the experiment. PSV and FDis are not correlated metrics of diversity (Supplementary Table 1.7). As such, their use in the design of the experiment allowed for disentanglement of PD and FD. Combined with the random bicultures, the stratified bicultures cover a wide range of possible values of PD and FD.

Classification of Mycorrhizal Association

Given the ecological importance of plant-mycorrhizal associations, we included dominant mycorrhizal type as a trait in this analysis. Most vascular plants associate with arbuscular mycorrhizae (AM), ectomycorrhizae (EM), neither, or both. Colonization with AM is the ancestral trait for mycorrhizal plants; many species that typically associate with EM also are colonized in part by AM (Maherali et al. 2016). Furthermore, mycorrhizal association can change ontologically or depending on external conditions (Dickie et al. 2002). All of the species included in the FAB experiment are mycorrhizal. Though there are records of dual infection with AM and EM (e.g. Wagg et al. 2008) for most of them, the preponderance of evidence suggests that both *Acer* species and *J. virginiana* tend to be colonized primarily by AM while the other species tend to be colonized primarily by EM (Maherali et al. 2016; http://datadryad.org/resource/doi:10.5061/dryad.n8bm9). For the purposes of this analysis, we wished to assess BEF dynamics based on species-level patterns in mycorrhizal association. In reality, however, most or all species considered (and certainly maples, pines, oaks, and birch) can associate with both classes of mycorrhizal fungi.

Calculation of Diversity Indices

Though we calculated a variety of plot-level PD and FD diversity metrics in our design and analysis of the experiment (Supplementary Table 1.3), we present our findings here in terms of two PD indices and two FD indices. Use of other indices in place of phylogenetic species variability for PD and FD yielded similar results in variable selection. We report PD as either Faith's (Faith 1992) Phylogenetic Diversity (FPD) or Phylogenetic Species Variability (PSV; Helmus et al. 2007). Faith's PD measures total branch length of a community's phylogeny and is thus correlated with SR, while PSV represents the degree of clumping within a phylogeny and is independent of the number of species in a community. We referred to Zanne and colleagues' (2014) phylogeny for the calculation of FPD and PSV. We report FD as either Scheiner and

colleagues' (2016) functional trait dispersion (FTD) or Laliberté and Legendre's (2010) functional dispersion (FDis). Scheiner and colleague's formulation of FTD is a metric of trait dispersion, and increases with species' functional distinctiveness based on the distance among them in a multidimensional space defined by scaled trait values. FTD is reported in units of SR, such that a community of five species with an FD value of two would only have two species if all species were equally distinct in their traits. Like FPD, it is inherently correlated with SR of a given community. FDis is the average distance to the centroid of all the species in a community, when those species are plotted in a multidimensional space defined by the traits considered. This value increases as species differ more in their traits, but is not dependent on the number of species in the community.

We also calculated unidimensional FDis for each of the nine traits included using the FDis method and a 9 x 1 trait matrix. Finally, we calculated community-weighted means (CWMs) for each trait based on mean trait values and species proportions within each community (Lavorel et al. 2008).

Mortality, Overyielding, CE, and SE

Mortality during the study period was year-, speciesand size-dependent, but not treatment-dependent. There was higher mortality from 2013-2014 (9%) than from 2014-2015 (4%). These patterns were also species dependent. From 2013-2014, mortality was highest (10-16%) for box elder, eastern red cedar, and all oaks; intermediate for paper birch (6%), red pine (7%) and red maple (8%); and low (<5%) for the other gymnosperms and basswood. From 2014-2015, mortality was still high for box elder (18%) and was moderate for pin oak (7%), with other species experiencing 3% or lower mortality. Smaller trees were also more likely to experience mortality than larger trees. From 2013-14, trees that died were 5 cm shorter and 1 mm smaller in diameter than the average experimental tree. The following year, the difference was 19 cm and 3 mm respectively. On the other hand, mortality did not vary consistently in either year by treatment, ranging from 8-12% in the first year of the study and from 3-5% in the second. Reflecting on these patterns in mortality, we feel confident that our conclusions regarding the relationship between diversity and biomass production are not highly biased by mortality *per se*, especially in the second year of our study, when mortality was generally low. We do acknowledge that data pertaining specifically to box elder and pin oak should be interpreted with some caution, since these species experienced somewhat high mortality across the study period. We are less concerned with size-related patterns in mortality, which reflect the tendency for newly transplanted (and thus smaller) plants to be more vulnerable to mortality than established ones. Furthermore, tree mortality was not correlated with diversity treatment: the number of trees that a given plot lost in a particular year was not related to the diversity of that plot (Appendix 1, Supplementary Fig. 1.8).

We excluded from calculations of biomass all trees that died between *t* and *t*-1, for which it was impossible to calculate incremental growth. In order to control for edge effects and unequal density of neighbors, we also excluded from both plotand neighborhood-level analyses trees that were on the edge of the experiment, or that had at least one (of eight) dead neighbor within 0.5 m. We excluded from plot-level analysis all trees on the edge of a plot, which, though they might have eight neighbors, bordered plots with different diversity levels. Thus, all analyses were conducted using measurements from a subset of the 8,960 trees in the whole experimental design (N_{plot} = 3,493 and $N_{neighborhood}$ = 5,765 for 2014-2015; N_{plot} = 3,661 and $N_{neighborhood}$ = 6,039 for 2015-2016).

We also report overyielding, the biomass of a tree or a plot less the biomass that would be expected based on constituent monocultures, for both individual trees and for plots (Trenbath 1974, Loreau and Hector 2001). For individual trees, we simply subtracted the average monocultural biomass of a given plant from its observed biomass. We did the same for mixture plots, calculating expected yield by multiplying average plot-level monocultural yield for each constituent species and proportion of living trees of each species in the plot in year *t*. In calculating monocultural biomass for each species, we averaged across all three monocultures of that species in the experiment, rather than comparing each polycultures's yield to the appropriate monocultural yields from plots in its block. We chose to follow this approach because, though stem growth did not vary importantly or consistently with block, there was moderate among-block variation in monocultural yield for some species.

At the plot-level, we partitioned overyielding into complementary (CE) and selection (SE) effects following Loreau and Hector (2001), such that

$$CE = SR * \overline{\Delta RY_{ij}} * \overline{M_i} \qquad \text{(S1.1)}$$

$$SE = SR * cov(RY_{ij}, M_i). \qquad \text{(S1.2)}$$

where *SR* is species richness of a plot, M_i is the average plot-level monocultural yield for species *i* (averaged across all monocultures of *i*), and RY_{ij} is the relative yield for species *i* in plot *j*. Averages used in the calculation of CE are across species in the plot and the covariance of M_i and RY_{ij} used to calculate SE is the population (denominator *N*) rather than the sample (denominator *n-1*) covariance (as in Loreau and Hector 2001). Relative yield is calculated as observed yield less expected yield, where observed yield is the measured plot-level biomass increment of a given species in a given plot divided by *M* for that species and expected yield is the species planted proportional abundance (e.g. 0.5 for either species in a biculture). The

mean relative and monocultural yield values used to calculate CE are the means of relative and monocultural yield for each species present in the plot.

For a given plot, CE and SE must sum to overyielding. We interpret CE as the amount of biomass in excess of expected yield that results from interactions (e.g. facilitation, resource partitioning) among species and SE as the overyielding biomass produced when highly productive monocultural species benefit from reduced intraspecific density in mixture (Huston 1997, Hector 1998, Fargione et al. 2007). Put differently, complementary effects are often treated as the results of non-additive species interactions while selection effects are treated as the result of influential species contributing additively to productivity. Mathematically, SE as calculated using the Loreau and Hector (2001) method also includes the "sampling effect" (Aarsen 1997) – the effect of chance inclusion of highly influential species in polycultures. We report overyielding, CE, and SE in the same units as biomass (kg/year); or alternatively, in order for models to meet the regression assumption of normality, we take the square root of their absolute values and then return the positive or negative sign of the original value, giving the sign-retaining square root of overyielding, CE, or SE (as in Loreau & Hector 2001).

Reverse Empirical Variable Selection (REVS)

REVS fits a simple linear regression model for each variable from a pool of potential predictors and orders these models by AIC. It then builds a multiple linear regression model consisting of the predictors from the best and second-best simple linear regressions. The protocol then adds the predictor from the next-best simple linear regression, continuing until adding a new variable does not improve the AIC score of the multiple linear regression model. This process generates a model with predictors added in order of decreasing importance and thus helps us to disentangle the effects of various indices of diversity on productivity. It also excludes variables from the reduced model that do not improve model fit.

Block Effects

When block had been retained in a model as a fixed effect, we refit the model using the *nlme* package in R as a restricted maximum likelihood (REML) mixed-effects model with block removed as a fixed effect and added as a random intercept. If the mixed-effects model had a lower AIC than a fixed-effects only model without block (fit using generalized least squares and REML for the purpose of comparison), we would have kept it as our final model. This was never the case, so block was excluded as a predictor from final mixed-effects models (Zuur et al. 2009).

Appendix S2: Supplementary Information for Chapter 2

Methods: Experimental Platform

Each species in a plot is at equal abundance (e.g. 32 trees of each species in a biculture) and each unique planting location in a plot was randomly assigned a species from those in the assigned plot composition. In fiveand 12-species polycultures, some species are represented, at random by one extra tree compared to others. As such, species abundances are either 0.19 or 0.20 in five-species plots and either 0.08 or 0.09 in 12-species plots.

Dead trees were replaced with conspecifics across the study period. Additionally, trees with dead near-neighbours were excluded from herbivory analysis. As such, all species in a tree's neighbourhood are, generally speaking, equally abundant. Pilot analysis with abundance-weighted diversity metrics did not differ considerably from analyses in which species abundances were not included. For this reason, we calculated diversity metrics in absolute, rather than-abundance weighted terms.

We surveyed a subset of individuals in the FAB experiment in the work presented here. Surveyed individuals ("focal trees") were chosen as follows: we selected the three individuals closest to the center of their plot with eight living neighbours. In cases in which individuals located at the core of a plot had dead neighbours, we moved toward the plot edge until a tree of the appropriate species with living neighbours was encountered. On each tree surveyed, the five newest, fully expanded leaves on the leading stem were measured, ensuring that measurements took place on leaves of equal age within a given species. Since oaks (*Quercus* spp.) leafed out in several flushes per summer and the other FAB angiosperms leafed continuously, oak leaves were probably slightly older (by two to four weeks) than leaves of other species.

Methods: Tree Size and Community Structure

We follow Castagneyrol et al. (2013) in calculating height apparency relative to neighbours as:

$$\Delta H = \frac{1}{8} \times \sum_{i=1}^{8} \frac{HF - HN_i}{dF,N_i} \quad \text{(S2.1)}$$

where HF is the height of the focal tree, HN_i is the height of neighbour tree i, and dF,N_i is the distance between the focal tree and its neighbour i.

Methods: Community Diversity Characteristics

Diverse metrics have been developed to represent phylogenetic (PD) and functional diversity (FD). Here, we use the same analytical method (mean pairwise distance; Webb et al. 2002) to calculate both PD and FD. PD is calculated as the average pairwise branch-length between all members of a given tree's neighbourhood. FD is calculated as the mean pairwise distance in unior multidimensional trait space for all

species pairs in a community. Both of these are conceptually independent from and empirically only weakly correlated with species richness. Both increase from 0 as diversity increases.

Unlike height apparency, which varies based on a focal plant's height and the height of its neighbours, the metrics of phylogenetic and functional diversity that we used are independent of the identity of a focal plant. In preliminary analysis, we also assessed the consequences for herbivory of phylogenetic and functional distance from neighbours, which increase as a focal plant is more phylogenetically or functionally distinct than its neighbourhood. These metrics were generally correlated with absolute phylogenetic and functional diversity (phylogenetic and functional MPD) and were not explanatory of observed responses, so they were not included in our formal analysis.

It was not logistically feasible to measure functional traits of the over 7,000 leaves assessed in this study – relevant trait measurements such as those described below are destructive and time-consuming. Instead, we opted to collect local species-level trait data and assess species-level trait means as potential predictors of herbivory and pathogen damage. Though functional information was useful in some cases, it was not a strong predictor of damage by herbivores or pathogens. This absence of evidence linking plant traits to herbivory may be the result of study design limitations or may corroborate past findings that leaf traits are only of limited value in predicting herbivory (Carmona et al. 2011, Schuldt et al. 2012, Kozlov et al. 2015). New techniques for high-throughput phenotyping, including leaf-level spectroscopy, will allow investigators to collect real-time measurements of, for instance, leaf nitrogen, phosphorus, or water content, and assess the relationships between these traits and observed patterns of herbivory or disease in the future (Cavender-Bares et al., 2017; Couture et al., 2016; Fahlgren, Gehan, & Baxter, 2015; Serbin, Kingdon, & Townsend, 2014).

In the present work, we measured species means of six leaf traits we deemed potentially important for herbivory: specific leaf area (SLA) and leaf water content, and concentrations of lignin, nitrogen, phosphorus, and condensed tannins.

Specific leaf area (SLA), leaf Nitrogen, and leaf Phosphorus are considered central traits to the leafand whole plant-economic spectra (Wright et al. 2004, Reich 2014). SLA is calculated as leaf area (cm^2) divided by fresh weight (g); leaves with a higher SLA have a greater surface area per unit mass and are often described as "softer." In global meta-analysis (Wright et al. 2004), high SLA has been shown to correlate with high leaf nutrient (Nitrogen and Phosphorus) content on a mass basis. Soft plant leaves with high nutrient content are generally "faster," with a more acquisitive, competitive growth strategy and shorter leaf lifespans. Fast plants are also thought to be more vulnerable to herbivores (Coley et al. 1985, Fine, P. V., Mesones, I., Coley 2004, Züst and Agrawal 2017).

Leaf water, lignin, and condensed tannins all are believed to play a role in plant defense against herbivory and disease. Leaves with higher water content and lower lignin content are generally believed to be more palatable or accessible and thus more susceptible to herbivores and pathogens (Coley 1983, War et al. 2012). Tannins play complex roles in regulating leaf vulnerability to enemies, and the classical consensus around their role as feeding deterrents for herbivores has been undermined (Madritch and Lindroth 2015). Generally speaking, tannins are expected to affect particular herbivores and pathogens in distinct ways and to alter ecosystem-level nutrient cycling (Schweitzer et al. 2008).

All trait measurements were conducted at the species level on leaves collected from FAB trees or adjacent conspecifics. Fresh leaf area for SLA and relative leaf water content calculations were measured through leaf scans with the SIOX ImageJ plug-in (Wang 2016) and balance measurements. Leaf nitrogen was analyzed by dry combustion GC analysis on a Costech Analytical ECS 4010 (Valencia, CA, USA). Phosphorus was measured through the multi-element, ICP-dry ash method on an iCap 7600 Duo ICP-OES Analyzer (Thermo Fischer Scientific, Waltham, MA, USA). We assessed percent lignin on a mass basis in dried, ground leaves using an ANKOM 200 fiber analyzer (Macedon, NY, USA; Riggs et al. 2015). Condensed tannins were measured on freeze-dried, ground samples using the butanol-HCl method (Porter et al. 1986) and birch standards purified by the R. Lindroth lab (Madison, WI, USA; Kopper et al. 2001); we were not able to measure hydrolysable tannins, though they likely are also important anti-herbivore defenses in the species studied.

Methods: Herbivory and Anthracnose Measurements

Insect herbivores from many orders remove leaf tissue through chewing, skeletonizing, and other means (Fig. 2.1E). We did not systematically observe which herbivores removed leaf tissue in FAB, and so followed past investigators in preliminarily treating it as generalist herbivory (Schuldt et al. 2010, Castagneyrol et al. 2013a). We measured each leaf using a translucent grid divided in one cm^2 and recorded leaf size and estimated leaf area removed by herbivores to the nearest estimated 0.5 cm^2. When a large portion of a leaf had been removed, adjacent leaves were used to help estimate its original size. Very limited herbivory (< 0.5 cm^2 leaf area removed) was recorded as 0.1 cm^2 of leaf removal.

We considered leaf galling and mining damage to be the result of specialist herbivory. Oak galls are formed by larvae of highly species-specialized wasps (Hymenoptera) in the family Cynipidae (Abrahamson et al. 1998, Price et al. 2004, Hayward and Stone 2005). Leaf mines, on the other hand, are formed by larvae of moths (Lepidoptera), flies (Diptera), beetles (Coleoptera), and sawflies (Hymenoptera, suborder Symphyta), which are variously considered to be specialized to species (Opler 1974) or capable of successfully reproducing on a few related host species (Auerbach and Simberloff 1988, Castagneyrol et al.

2013b). In both groups of herbivores, gravid females locate appropriate hosts and oviposit (Quiring and McNeil 1987, Stone et al. 2002). Their larvae form galls or leaf mines in order to feed and develop into adults.

Symptoms of maple leaf anthracnose include necrotic leaf spotting and abscission of highly damaged leaves (Stanosz 1993, Pijut 2005). Though a variety of ascomycete fungi cause anthracnose, their effects are considered species-specific regardless of the causal agent(s) (Myren and Davis 1991, Sinclair and Lyon 2005). Indeed, we did not observe any anthracnose infection on surveyed box elder trees (red maple's congener).

Methods: Eastern Red Cedar Gall Rust Measurements

Cedar apple gall rust (*Gymnosporangium juniperae-virginiae* Schwein.) is caused by a basidiomycete fungus that requires two hosts to complete its life span. Air-borne teleospores infect and form roestelia on leaves of species in the apple genus (*Malus* spp.), giving rise to rust-colored lesions. These rust patches produce aesciospores that then infect species in the juniper genus (*Juniperus* spp.), forming distinctive red-orange galls that are the source of new, wind-dispersed teleospores (Crowell 1934, Money and Fischer 2009). Eastern red cedar is the only suitable host for either life stage in the FAB experiment. Naturalized and native apples are common at low density across Cedar Creek and grow close enough to the FAB experiment to infect junipers therein (MacLachlan 1935).

Methods: Data Analysis

To assess the effect of diversity and plant size on leaf removal we treated the maximum proportion of a single leaf removed from a given plant in a given year as our response variable. We modeled the proportion of total leaf area removed, which was correlated with total leaf area ($r_p = 0.723$, $t = 92.5$, $df = 7{,}800$, $p < 0.001$). Because maximum and median leaf area removal rates were also reasonably well-correlated ($r_p = 0.678$, $t = 36.4$, $df = 1{,}555$, $p < 0.001$), and modeling of each yielded similar qualitative results, we present maximum removal here. For instance, if, for a given tree, we recorded leaf removal of 4%, 45%, 25%, 1% and 1% on its five newest, fully expanded leaves in 2014, then we treated 0.45 as the removal rate for that tree in that year. Once arcsin-square root transformed, maximum leaf removal proportions were normally distributed, and far enough from 0 that their distribution was not substantially truncated; this was not the case for mean or median leaf removal.

Since we did not know the identity and diet breadth of leaf removers and, therefore, had competing *a priori* expectations about which factors would predict leaf removal, we used automated variable selection from a wide range of candidate predictors to build both neighbourhoodand plot-level models of leaf removal across all species and for each species surveyed (*glmulti* function of the eponymous R package; Calcagno

and de Mazancourt 2010). Candidate predictors included all focal tree, structural, compositional, and diversity metrics described above. We then built four neighbourhood-level (one for each spatial scale) fixed-effects linear regression model including the variables returned in >80% of potential models assessed in variable selection. We then compared the AIC scores of all models for herbivory in a single species (or for the all-species dataset). The model with the lowest AIC score was then refit with random intercepts for tree, nested within plot, nested within block, and for study year ("lme4" R Package; Bates et al. 2015). The all-species model also included a random intercept for species. When AIC scores were within two points of the lowest score for a given species, the models were deemed equivalent and the smaller-scale model was selected as "best." This process yielded, for each angiosperm species in FAB and for all of them combined, an optimal mixed-effects multiple linear regression model of leaf removal including any treeor community-related predictors identified in variable selection as fixed effects (Supplementary Tables 2.1 and 2.2). We then repeated this procedure on models of leaf removal in which height apparency was included as the only fixed effect (along with the height covariate and random effects as described above). This yielded a second set of models alongside those with the "best" fixed predictors as determined through variable selection (Supplementary Table 2.3).

Because counts of galls and leaf miners were very low across species and years, we summed them on a per-plant basis and modeled these forms of herbivory using zero-inflated negative binomial Poisson regression (*zeroinfl* function in the "pscl" package; Jackman et al. 2015). These models consist of two parts. The first is a logistic regression component that gives the likelihood of finding any galls or miners at all on a plant; coefficients from this model component can be interpreted in terms of odds ratios (OR; $e^{coefficient}$) giving the *vulnerability* of a particular plant to herbivory. The second model component is a typical Gaussian regression on a log scale, which predicts the number of galls or leaf miners on a particular plant given that herbivory has taken place there. Predictors from this model component describe the *intensity* of galling or leaf mining.

Because variable selection for zero-inflated negative binomial Poisson regression models is less straightforward than for linear regression models, we performed variable selection manually in R. We built models for each response including the following predictors across all four spatial scales: height apparency, neighbourhood conspecific (or, for oaks, congener) abundance, PD, and multidimensional FD. Plant height was always included as a covariate. We then manually conducted backward variable selection using a one-tailed log-likelihood approach, settling on a reduced model when removing an additional variable did not result in a significant improvement in log-likelihood score. We then compared models across spatial scales using AIC scores as described above. Finally, we added in study year (when applicable) and, for pooled models across all oaks, species, as covariates in order to arrive at final models of galling and leaf mining.

Because variability in anthracnose score was high among leaves of individual plants, we ultimately modeled it as total score on a per-plant basis, ranging from zero for unaffected plants to 25 for plants with all leaf area covered on all five leaves. These total plant anthracnose scores were normally distributed and continuous, but still zero-inflated, so we used hurdle models (Martin et al. 2005) to assess anthracnose infection. Hurdle modeling, like the integrated models used for galling and leaf mining, represents infection vulnerability and intensity as distinct processes. In hurdle modeling, however, these models are built separately. Our hurdle models consisted of two generalized linear mixed-effects models built using the *glammadmb* function in the "glmmADMB" R package (Skaug et al. 2016). Both were mixed-effects models including fixed effects chosen through variable selection (as described for galling and leaf-mining above) and year as a random effect. The binomial model of vulnerability was built using a logit link function, while the Gaussian model of intensity was built using an identity link function. Model selection was as for the zero-inflated Poisson models used for galling and leaf mining. The results of these models are also interpreted in parallel to the results from the zero-inflated Poisson models, which is to say in terms of vulnerability to and intensity of damage.

Results: Species-level Traits and Herbivory

Several plant traits emerged as predictors of maximum leaf removal at the species level. Across the eight angiosperms in FAB, leaf removal was marginally negatively associated with leaf water content (r_s = -0.714, p = 0.058) and phosphorus (r_s = -0.690 p = 0.069). We were not able to assess the species-level relationships of these traits with other forms of herbivory or disease since these responses were not measured across more than a few species. Finally, we note that it is reasonable to expect leaf removal rates to vary with tree size. We included tree diameter and height as candidate predictors in variable selection for all leaf removal models. As such, height was included in a covariate of all herbivory models.

Results: Relationships between leaf removal, galling, and mining

We observed both speciesand leaf-level relationships among vulnerability to leaf removal, vulnerability to galling, and vulnerability to mining. At the species level, galls were marginally negatively associated with maximum leaf removal (r_s = -1.0, p = 0.083). Red oak, which had the highest average leaf removal rate of the four oaks (11%), had the lowest rate of gall formation (one gall in every eighth tree). The reverse was true for pin oak (5% average leaf removal, two of every three trees galled). Leaf mining was not correlated with either leaf removal or galling at the species level. When we considered herbivory of individual leaves, however, leaves with some tissue removed were significantly more likely to be attacked by a leaf miner as well. In a leaf-level logistic regression model of risk of leaf miner attack based on year, tree species, and percent of leaf area, leaves with more area removed were significantly more likely to have a leaf miner (OR = 3.63).

Results: Specialist Damage on Red vs. White Oaks

Furthermore, an oak's proximity to neighbours of a different oak lineages (Sect. *Lobatae* vs. *Quercus*) did not decrease specialist herbivore damage, despite the hypothesis that contrasting enemies might account for complementarity in the two major lineages (Supplemental Figure 2.3; Cavender-Bares *et al.* 2004). This may be due to low phylogenetic conservativism of chemical defense traits within species-rich genera such as *Quercus* (Sedio 2017) or host dilution (Otway et al. 2005) in plots with many white oaks.

Appendix S3: Supplementary Information for Chapter 3

Calculation of Faith's Phylogenetic Diversity

Though we designed the BiWaP experiment to include four treatments varying in species richness and, nested within it, genotypic richness, we also were able to distinguish among plots based on their continuous molecular distance (phylogenetic diversity). We used Faith's (1992) phylogenetic diversity (PD), which measures branch length across a community phylogeny, to describe molecular distance. Since we did not have molecular information about genotypes of white aspen and black willow, we calculated PD based on a phylogeny built from publicly available sequences from GenBank.[1] We selected at random three large subunit RUBP sequences from GenBank for each species in the experiment and used Geneious (ver. 9.1.3, Biomatters Ltd., City) to build a neighbor-joining consensus tree of all nine genotypes. This tree reflected the deep phylogenetic split between the *Salix* and *Populus* genera and the shallow split between *P. alba* and *P. tremuloides*. We then used the Picante package in R to calculated PD from this tree. As genotypic diversity contributes far less to PD than does interspecific diversity, plot PD was highly correlated with species richness in the BiWaP experiment. Because we designed BiWaP based on plot species richness rather than PD, we used the former of the two correlated measures as a predictor of ecosystem function in our analyses.

[1]Accessions HM850277.1, JF429909.2, and KC485205.1 (*P. alba*); JX949535.1, KC483598.1, and KF940825.1 (*P. tremuloides*); and AB012790.1, HQ590257.1, and KX016459.1 (*S. nigra*)

Allometric Equations

Allometric equations were used to estimate total plant biomass (g) on a species-level basis as follows:

$$Biomass_{\text{P.alba}} = 1000 * e^{-1.2947+2.1367*\ln\left(\frac{D}{10}\right)} \quad \text{(S3.1)}$$

$$Biomass_{\text{P.tremuloides}} = 10^{1.462+2.687*\log_{10}\left(\frac{D}{10}\right)} \quad \text{(S3.2)}$$

$$Biomass_{\text{S.nigra}} = 10^{1.534+2.733*\log_{10}(\frac{D}{10})} \quad \text{(S3.3)}$$

where *D* is basal stem diameter in cm. The allometric equation for *P. alba* ($r^2 = 0.873$) is drawn from Blujdea et al. (2012), while the euqations for *P. tremuloides* ($r^2 = 0.991$) and *S. nigra* ($r^2 = 0.962$) are drawn from Bond-Lamberty et al. (2002).

Overyielding

Diversity is expected to affect plant growth through "complementarity" (*sensu* Loreau and Hector 2001) when species facilitate one another or partition available resources (Fichtner et al. 2017; e.g. Cardinale et al. 2007, Fargione et al. 2007, Morin et al. 2011, Forrester and Bauhus 2016, Williams et al. 2017) or through "selection" when some highly productive plants dominate polycultures (Fox 2005, Jiang et al. 2008; e.g. Kirui et al. 2012, Tobner et al. 2016, Peng et al. 2017). A given plot's overyielding can further be broken down into complementary and selection effects (*sensu* Loreau and Hector 2001). For analysis of data from the BiWaP experiment, we adapted the classical equations presented in Appendix S1 as follows:

$$CE = GR * \Delta RY_{ij} * M_i \quad \text{(S3.4)}$$

$$SE = GR * cov(RY_{ij}, M_i) \quad \text{(S3.5)}$$

where *GR* is the genotypic richness of a plot, M_i is the average plot-level monocultural yield for genotype *i* (averaged across all monocultures of *i*), and RY_{ij} is the relative yield for genotype *i* in plot *j*. Averages used in the calculation of CE are across genotypes in the plot and the covariance of M_i and RY_{ij} used to calculate SE is the population (denominator *N*) rather than the sample (denominator *n-1*) covariance (A. Hector, *personal communication*). Relative yield is calculated as observed yield less expected yield, where observed yield is the measured plot-level biomass increment of a given genotype in a given plot divided by *M* for that genotype and expected yield is the species planted proportional abundance (e.g. 0.33 for all genotypes in a 3S3G plot). The mean relative and monocultural yield values used to calculate CE are the means of relative and monocultural yield for each genotype present in the plot.

Complementary and selection effect values must sum to the overyielding value for a plot. A high complementarity value indicates that diversity affects productivity through non-additive interactions among different species; a high selection value indicates that those species that are highly productive in monoculture take advantage of diverse environments, suppressing neighbors but boosting plot overyielding. Typically, overyielding, complementarity, and selection are calculated assuming that each species in an experiment is distinct and treating monocultures as monospecific stands regardless of their genetic

composition. In this analysis, we treat genotypes as distinct, regardless of their species identity, and treat mono-genotypic plots as monocultures (see Abdala-Roberts et al. 2015). As such, all expected values for growth come from 1S1G plots. We constructed models of RGR and overyielding, complementarity, and selection in RGR as follows: block was always included as a predictor along with one of the following diversity-related predictors: GR, SR, GR nested within SR (Martins and Hansen 1996), or PD (Table 3.1). We compared these models using AIC, selecting the model with the lowest AIC score as our preferred model for a response. When appropriate, we used post-hoc Tukey testing ("agricolae" package, de Mendiburu 2016) of preferred models to compare differences among treatment groups.

Species and Genotypic Differences in Growth Rate

Species differed in the growth rate of individual trees, both in terms of absolute biomass gain from 2015 to 2016 and in relative growth rate during that time (Supplementary Figure 3.1). White aspen gained an average of 828 g yr^{-1} in biomass, significantly more than quaking aspen (21.5 g $yr^{=1}$) and black willow (15.7 g yr^{-1}). Yet white aspen individuals were larger at the start of 2015, so relative growth rate was similar between white (0.672 g g^{-1}) and quaking (0.656 g g^{-1}) aspen, but significantly lower for black willow (-0.119 g g^{-1}). Many black willow individuals, in fact, lost biomass from 2015 to 2016 as stems died back due to freezing or small herbivore damage, leading to its net negative relative growth rate. Because size at the start of the study period clearly influenced performance over the next year, we present and model relative, rather than absolute, growth rate in our overyielding analysis. Furthermore, aboveground biomass of experimental trees integrates qualitatively similar patterns in growth in height and basal diameter, which are not presented separately here.

Genotype identity predicted differences in absolute growth rate among white aspens only and in relative growth rate among all three species. In terms of absolute growth rate, white aspen genotype #2 was more productive than #1 or #3 (Supplementary Figure 3.1B); genotypes of the other species did not differ significantly in absolute growth. Relative growth rate varied by both species and genotype, ranging from 0.798 g g^{-1} (quaking aspen genotype #3) to -0.213 g g^{-1} (black willow genotype #3).

Supplementary Table 1.1 - Richness, phylogenetic and functional diversity, and composition of experimental plots in FAB. Plots are numbered based on position in blocks. Subsequent columns provide the species richness (SR), phylogenetic species variability (Helmus et al. 2007; PSV), Faith's (1992) Phylogenetic Diversity (FPD), Laliberté and Legendre's (2010) functional dispersion (FDis), Scheiner and colleagues' (2016) multidimensional functional trait dispersion (FTD), and presence/absence (x=present) of each species (per codes from Fig. 1.2) in all plots. Bicultures chosen through stratified random sampling are also indicated in the appropriate column.

Plot	SR	Stratified	PSV	FPD	FDis	FTD	ACNE	ACRU	BEPA	JUVI	PIBA	PIRE	PIST	QUAL	QUEL	QUMA	QURU	TIAM
1	5		0.7606	1118	2.646	2.86					x	x	x		x			x
2	5		0.7361	1066.4	3.191	3.41		x			x	x		x				x
3	2		0.036	364.9	1.063	1.22	x	x										
4	2		0.432	504.4	1.546	1.27					x		x					
5	2	x	0.0681	376.2	0.367	1.07								x		x		
6	1		NA	352.2	0	1							x					
7	1		NA	352.2	0	1										x		
8	2		1	704.5	3.506	2				x								x
9	2	x	0.1769	414.5	1.552	1.32			x							x		
10	2	x	1	704.5	1.63	1.41							x				x	
11	1		NA	352.2	0	1			x									
12	1		NA	352.2	0	1		x										
13	2	x	0.3337	469.8	1.832	1.46	x							x				
14	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
15	2		0.0511	370.2	0.673	1.12									x		x	
16	2	x	1	704.5	1.865	1.5							x		x			
17	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
18	5		0.5797	984.8	2.746	2.99	x		x			x					x	x
19	2	x	1	704.5	1.975	1.51							x	x				
20	1		NA	352.2	0	1	x											
21	2	x	0.1769	414.5	1.338	1.29			x						x			
22	1		NA	352.2	0	1								x				
23	2	x	0.2854	452.7	2.544	1.59		x										x
24	2	x	0.3337	469.8	1.821	1.48	x								x			
25	2	x	1	704.5	3.09	1.93		x			x							
26	2		1	704.5	2.348	1.61						x		x				
27	1		NA	352.2	0	1											x	
28	1		NA	352.2	0	1				x								
29	2	x	1	704.5	2.485	1.58							x					x
30	5		0.5296	886	2.001	2.43		x					x	x	x	x		

Supplementary Table 1.1 (cont.)

Plot	SR	Stratified	PSV	FPD	FDis	FTD	ACNE	ACRU	BEPA	JUVI	PIBA	PIRE	PIST	QUAL	QUEL	QUMA	QURU	TIAM
31	2		1	704.5	2.059	1.51						x					x	
32	2	x	1	704.5	3.004	1.78		x		x								
33	2		0.432	504.4	1.155	1.21						x	x					
34	2		0.4084	496.1	0.662	1.1					x	x						
35	2		0.1136	392.2	0.311	1.07									x	x		
36	1		NA	352.2	0	1						x						
37	2		0.7572	619	1.612	1.34				x		x						
38	2	x	1	704.5	2.11	1.51			x		x							
39	2		0.1136	392.2	0.806	1.15										x	x	
40	2		0.3337	469.8	2.322	1.5										x		x
41	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
42	2		0.3337	469.8	2.282	1.37			x									x
44	2		0.7572	619	1.295	1.27				x	x							
45	1		NA	352.2	0	1									x			
46	1		NA	352.2	0	1												x
47	1		NA	352.2	0	1					x							
48	2	x	1	704.5	2.498	1.73				x							x	
50	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
51	1		NA	352.2	0	1										x		
52	1		NA	352.2	0	1							x					
53	5		0.7225	1073.5	2.395	2.78			x	x	x				x	x		
54	2		1	704.5	2.348	1.61						x		x				
55	2	x	0.1769	414.5	1.552	1.32			x							x		
56	2		1	704.5	2.059	1.51						x					x	
57	1		NA	352.2	0	1												x
58	5		0.7168	998.2	2.551	2.92		x				x	x	x		x		
59	2		0.432	504.4	1.546	1.27					x		x					
60	5		0.7189	1005.8	2.593	2.96		x			x	x			x	x		
61	1		NA	352.2	0	1											x	
62	1		NA	352.2	0	1								x				
63	2	x	1	704.5	2.11	1.51			x		x							
64	2	x	1	704.5	3.004	1.78		x		x								
65	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
66	2		0.1136	392.2	0.311	1.07									x	x		
67	1		NA	352.2	0	1				x								
68	1		NA	352.2	0	1					x							
69	2	x	0.3337	469.8	1.821	1.48	x								x			
70	1		NA	352.2	0	1	x											
71	2		0.1136	392.2	0.806	1.15										x	x	
72	2		0.7572	619	1.295	1.27				x	x							
73	2		0.036	364.9	1.063	1.22	x	x										
74	2		0.3337	469.8	2.282	1.37			x									x
75	2	x	0.1769	414.5	1.338	1.29			x						x			
76	2		0.7572	619	1.612	1.34				x		x						
77	2		0.3337	469.8	2.322	1.5										x		x
78	1		NA	352.2	0	1			x									
79	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
80	2	x	1	704.5	1.865	1.5							x		x			

Supplementary Table 1.1 (cont.)

Plot	SR	Stratified	PSV	FPD	FDis	FTD	ACNE	ACRU	BEPA	JUVI	PIBA	PIRE	PIST	QUAL	QUEL	QUMA	QURU	TIAM
81	2		0.432	504.4	1.155	1.21						x	x					
82	1		NA	352.2	0	1									x			
83	2	x	0.2854	452.7	2.544	1.59		x										x
84	2	x	1	704.5	1.63	1.41							x				x	
85	2	x	1	704.5	2.498	1.73				x							x	
86	2	x	0.0681	376.2	0.367	1.07								x		x		
87	1		NA	352.2	0	1						x						
88	2		0.4084	496.1	0.662	1.1					x	x						
89	2		0.0511	370.2	0.673	1.12									x		x	
90	2	x	1	704.5	2.485	1.58							x					x
91	2	x	1	704.5	1.975	1.51							x	x				
94	2		1	704.5	3.506	2				x								x
95	2	x	0.3337	469.8	1.832	1.46	x							x				
96	1		NA	352.2	0	1		x										
97	2	x	1	704.5	3.09	1.93		x			x							
99	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
100	2	x	0.1769	414.5	1.552	1.32			x							x		
101	1		NA	352.2	0	1					x							
102	1		NA	352.2	0	1				x								
103	2	x	0.3337	469.8	1.832	1.46	x							x				
104	2		0.0511	370.2	0.673	1.12									x		x	
105	2		0.1136	392.2	0.311	1.07									x	x		
106	1		NA	352.2	0	1									x			
107	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
108	1		NA	352.2	0	1												x
109	5		0.2692	650.6	2.32	2.5		x	x						x		x	x
110	1		NA	352.2	0	1										x		
111	2		0.3337	469.8	2.322	1.5										x		x
113	1		NA	352.2	0	1			x									
114	5		0.5423	908.3	2.663	2.92			x	x				x		x		x
115	2		1	704.5	3.506	2				x								x
116	2	x	0.1769	414.5	1.338	1.29			x						x			
117	2	x	1	704.5	2.11	1.51			x		x							
118	2		1	704.5	2.059	1.51						x					x	
120	2	x	1	704.5	3.09	1.93		x			x							
121	2	x	0.2854	452.7	2.544	1.59		x										x
122	1		NA	352.2	0	1						x						
123	2		0.1136	392.2	0.806	1.15										x	x	
124	2		0.7572	619	1.295	1.27				x	x							
125	2	x	1	704.5	3.004	1.78		x		x								
126	2		0.036	364.9	1.063	1.22	x	x										
127	2	x	1	704.5	1.865	1.5							x		x			
128	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x
129	2		0.432	504.4	1.546	1.27					x		x					
130	2		0.432	504.4	1.155	1.21						x	x					

Supplementary Table 1.1 (cont.)

131	2	x	0.3337	469.8	1.821	1.48	x								x					
132	2	x	1	704.5	2.498	1.73				x								x		
133	2		0.7572	619	1.612	1.34				x		x								
134	2	x	1	704.5	1.63	1.41							x					x		
135	1		NA	352.2	0	1							x							
136	1		NA	352.2	0	1								x						
137	2	x	1	704.5	2.485	1.58							x							x
138	2		0.4084	496.1	0.662	1.1					x	x								
139	2	x	1	704.5	1.975	1.51							x	x						
140	12		0.643	1642.2	2.742	6.19	x	x	x	x	x	x	x	x	x	x	x	x		x
141	1		NA	352.2	0	1			x											x
142	2		0.3337	469.8	2.282	1.37								x		x				
143	2	x	0.0681	376.2	0.367	1.07								x		x				
144	1		NA	352.2	0	1		x			x	x		x						x
145	5		0.7361	1066.4	3.191	3.41						x		x						
146	2		1	704.5	2.348	1.61	x													
147	1		NA	352.2	0	1		x												

Supplementary Table 1.2 - Functional trait values used to calculate FDs and CWMs: wood density (g cm-3), leaf mass per area (LMA; g cm-2), leaf N concentration (%), mycorrhizal type (arbuscular – AM [0], ecotomycorrhizal – ECM [1]), leaf habit (deciduous [0], evergreen [1]), leaf calcium concentration (ppm), shade tolerance, drought tolerance, and waterlogging tolerance (all tolerances range from 1-4). Species mean traits values were obtained from previously collected data in the region (Reich *et al.* 1997; Holdsworth *et al*. 2008; Cavender-Bares & Reich 2012; Grossman, *unpublished data*) and, in the case of shade, drought and waterlogging tolerance, from Niinemets and Valladares (2006).

Species	Wood_Density	LMA	Leaf_N_Mass	Mycorrhizae	Leaf_Habit	Leaf_Ca	Shade_Tol	Drought_Tol	Waterlog_Tol
Acer_negundo	2	1.57	0.398	0	0	26084	3.47	3.03	2.75
Acer_rubrum	3	1.84	0.28	0	0	10195	3.44	1.84	3.08
Betula_papyrifera	2	1.88	0.36	1	0	18409	1.5	2.02	1.25
Juniperus_virginiana	1	2.52	0.215	0	1	31690	1.28	4.65	1.19
Pinus_banksiana	1	2.39	0.093	1	1	9126	1.36	4	1
Pinus_resinosa	1	2.47	0.068	1	1	9473	1.89	3	1
Pinus_strobus	1	2.09	0.18	1	1	12270	3.21	2.29	1.03
Quercus_alba	4	1.89	0.366	1	0	19937	2.85	3.56	1.43
Quercus_ellipsoidalis	3.5	2.02	0.322	1	0	10787	2.5	3.7	1.7
Quercus_macrocarpa	4	1.97	0.355	1	0	12148	2.71	3.85	1.82
Quercus_rubra	3.5	1.91	0.311	1	0	14032	2.75	2.88	1.12
Tilia_americana	2	1.78	0.468	1	0	45253	4	2.25	1.5

Supplementary Table 1.3 - A variety of community diversity metrics were calculated in preliminary data analysis. Representative and non-collinear metrics of functional and phylogenetic were chosen for final analyses as reported in the main text.

Scale	Index	Description	Package	Source
Plot	SR	Species Richness, the number of species in the plot		Magurran 1988
Neighborhood	LSR	Local Species Richness, the number of species among a focal tree's eight closest neighbors		Authors, Magurran 1988
Plot/Neighborhood	PSV	Phylogenetic Species Variability, increases with community phylogenetic diversity, not correlated with species richness	Picante (Helmus et al. 2014)	Helmus et al. (2007)
Plot/Neighborhood	FPD	Faith's Phylogenetic Diversity, increaes with community phylogenetic diversity, correlated with species richness, calculated with and without branch lenghts set to 0.	Picante	Faith (1992)
Plot/Neighborhood	MPD	Phylogenetic Mean Pairwise Distance, increases with community phylogenetic diversity, not correlated with species richness	Picante	Webb et al. (2008)
Plot/Neighborhood	PSE	Phylogenetic Species Evenness, abundance-weighted form of PSV	Picante	Helmus et al. (2007)
Plot/Neighborhood	MPD.A	Abundance-weighted phylogenetic MPD	Picante	Webb et al. (2008)
Plot/Neighborhood	PSV.t	Functional PSV calculated for all nine traits	Picante	Helmus et al. (2007)
Plot/Neighborhood	NTI.t	Functional Nearest Taxon Index calculated for traits, decreases with increasing community trait diversity	Picante	Webb et al. (2002)
Plot/Neighborhood	NRI.t	Functional Net Relatedness Index calculated for traits, descreases with increasing community trait diversity	Picante	Webb et al. (2002)
Plot/Neighborhood	TD.t	Functional Taxonomic Diversity, calculted for traits, increases with increasing community trait diversity	Vegan (Okansen et al. 2015)	Clarke and Warwick (1998, 2001)
Plot/Neighborhood	PSE.t	Functional PSE, calculated for traits	Picante	Helmus et al. (2007)
Plot/Neighborhood	NTI.t.A	Abundance-weighted NTI.t	Picante	Webb et al. (2002)
Plot/Neighborhood	NRI.t.A	Abundance-weighted NRI.t	Picante	Webb et al. (2002)
Plot/Neighborhood	FDis	Functional Dispersion, an abundance-weighted metric that increases with increasing community functional diversity	FD (Laliberte et al. 2014)	Laliberte and Legendre (2010)
Plot/Neighborhood	FDis_Trait	FDis as calculated for each of the nine traits considered, increases as the as the community functional diversity of that trait increases.	FD (Laliberte et al. 2014)	Laliberte and Legendre (2010)
Plot/Neighborhood	RaoQ	Rao's Q, an abundance-weighted metric that increases with increasing community functional diversity	FD	Bokka-Dukat (2005)
Plot/Neighborhood	FGR	A posteriori Functional Group Richness, splits species into functional groups based on trait values, higher numbers indicate more functional groups, set to four groups based on post hoc inspection	FD	Petchey and Gaston (2006)
Plot/Neighborhood	FTD	Functional Trait Dispersion, increases with species' functional distinctiveness based on the distance among them in a multidimensional space defined by scaled trait values. Units are the same as Species Richness, and values can be interpreted as the number of species that would be present in the community if all species were equally distinctive in trait space.		Scheiner et al. (2016)
Plot/Neighborhood	CWM_trait	Community-Weighted Mean of each of the nine traits considered, increases as the abundance-weighted mean community value of that trait increases	FD	Lavorel et al. (2008)
Plot/Neighborhood	MPD.t.trait	MPD calculated for each of the nine traits considered, increases as the community functional diversity of that trait increases	Picante	Webb et al. (2008)
Neighborhood	MPD.dist	Phylogenetic Distance from Neighbors, average MPD of a focal tree and each of its eight closest neighbors	Picante	Authors, Webb et al. (2008)
Neighborhood	MPD.dist.t	Functional Distance from Neighbors, average MPD, calculated using all nine traits considered, between a focal tree and each of its eight closest neighbors	Picante	Authors, Webb et al. (2008)

Trait Abbreviations

Density = Wood Density, Nitrogen = Leaf Nitrogen, LMA = Leaf Mass per unit Area, Myco = Mycorrhizal Association, Habit = Leaf Habit, Calcium = Leaf Calcium Content, Drought = Drought Tolerance, Shade = Shade Tolerance, Waterlog = Waterlogging Tolerance

Supplementary Table 1.4 – Allometric equations used to calculate stem biomass for experimental plants. AB = aboveground biomass in kg, BA = basal area in mm2, D = basal diameter in mm, r = basal radius in cm, H = height in cm. All logs are base *e*. Sources for equations are drawn from the BAAD database (Anninghoefer et al. 2016), Peichl and Arain (2007), or harvested FAB trees (*unpublished data*).

Species	Equation	r^2	Source
ACNE	AB = e^(-7.0(	0.97	FAB
ACRU	AB = e^(-5.7!	0.99	BAAD
BEPA	AB = 0.1533*	0.96	BAAD
JUVI	AB = e^(log(:	0.94	FAB
PIBA	AB = -74.074	0.96	BAAD
PIRE	AB = -43.510	0.96	FAB
PIST	AB = 0.0377*	1	P&A
QUAL	AB = 0.10092	0.82	FAB
QUEL	AB = e^(-4.3'	0.95	FAB
QUMA	AB = e^(-4.5(	0.95	FAB
QURU	AB = e^(-3.8!	0.95	FAB
TIAM	AB = e^(2.13	0.84	FAB

Supplementary Table 1.5 - Best models of Net Biodiversity Effects (A-D), Complementarity Effects (E-G), and Selection Effects (H-J) for the first (2013-14; A, B, D-F, H, I) and second (2014-15; C, G, J) years of the study, as determined by reverse empirical variable selection and model comparison with AIC. Models are given for the random-draw polycultures (A, E, H) and bicultures vs. monocultures (B, C, F, G, I, J) subsets of plots and for focal tree neighborhoods (D).

A 2013-2014 Conditional r^2 = 0.839
All Polycultures - NBE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Species Richnesss	0.743	11.695	18	***
Mycorrhizal Association CWM	0.871	5.431	18	***
Leaf Calcium CWM	0.94	4.761	18	***
Waterlogging Tolerance CWM	0.901	4.908	18	***
Tree Diameter	0.506	3.407	35	**
Leaf Nitrogen CWM	-1.42	-3.174	18	**
Number of Trees	0.091	1.185	35	
Leaf Habit CWM	-0.604	-1.576	18	

Mixed-effects Model with random intercept
based on plot composition, which consists of 25 levels and yieldd a residual of 0.063.

B 2013-2014 Conditional r^2 = 0.873
Bicultures Only - NBE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Tree Diameter	0.945	10.833	54	***
Mycorrhizal Association CWM	1.314	11.768	22	***
Waterlogging Tolerance CWM	0.996	7.521	22	***
Leaf Nitrogen CWM	-1.195	-0.122	22	***
Leaf Calcium CWM	0.967	11.464	22	***
LMA CWM	-0.51	-3.829	22	***

Mixed-effects Model with random intercept
based on plot composition, which consists of 28 levels and yielded a residual of 0.036.

E 2013-2014 Conditional r^2 = 0.731
All Polycultures - CE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Faith's Phylogenetic Diversity	0.743	10.084	23	***
Tree Height	0.256	3.307	35	**
Number of Trees	0.11	1.466	35	

Mixed-effects Model with random intercept
based on plot composition, which consists of 25 levels and yielded a residual of 0.095.

F 2013-2014 Conditional r^2 = 0.575
Bicultures Only - CE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Tree Diameter	1.721	7.204	49	***
J. virginiana abundance	-1.253	-6.079	49	***
P. banksiana abundance	-0.52	-3.337	49	**
P. strobus abundance	-0.322	-2.692	49	**
A. rubrum abundance	-0.213	-2.253	49	*
P. resinosa abundance	-0.187	-1.903	49	|
B. papyrifera abundance	-0.143	-1.412	49	

Mixed-effects Model with random intercept
based on plot composition, which consists of 28 levels and yielded a residual of 0.088.

Supplementary Table 1.5 (cont.)

C 2014-2015 Conditional r^2 = 0.835
Bicultures Only - NBE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
J. virginiana abundance	-0.634	-8.725	43	***
A. rubrum abundance	-0.635	-7.932	43	***
P. resinosa abundance	-0.462	-7.054	43	***
Q. alba abundance	-0.478	-6.755	43	***
Q. ellipsoidalis abundance	-0.6	-6.986	43	***
Q. rubra abundance	-0.456	-7.088	43	***
Q. macrocarpa abundance	-0.541	-6.637	43	***
Tree Diameter	0.002	0.113	43	
B. papyrifera abundance	-0.559	-3.654	43	***
P. strobus abundance	-0.212	-3.385	43	**
Number of Trees	0.002	1.09	43	
Tree Height	0.005	1.521	43	
A. negundo abudnance	-0.366	-2.394	43	*

Mixed-effects Model with random intercept
based on plot composition, which consists of 28 levels and yielded a residual of 0.058.

D 2013-2014 Conditional r^2 = 0.059
Neighborhoods - NBE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Tree Diameter	0.285	7.345	5484	***
J. virginiana abundance	-0.217	-8.755	5484	***
P. banksiana abundance	-0.102	-4.661	5484	***
Q. alba abundance	0.058	3.053	5484	**
A. negundo abundance	0.002	0.164	5484	
Tree Height	-0.016	-0.507	5484	
Q. macrocarpa abundance	-0.004	-0.225	5484	

Mixed-effects Model with random intercepts based on species (with 12 levels
and a residual estimate of 0.856) and a spherical correlation
structure based on easting and northing location in the experiment.

G 2014-2015 Conditional r^2 = 0.838
Bicultures Only - CE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Q. rubra abundance	-0.637	-6.019	51	***
P. banksiana abundance	0.199	1.776	51	|
Number of Trees	0.159	2.28	51	*
P. resinosa abundance	-0.14	-1.372	51	
Q. alba abundance	-0.082	-0.792	51	

Mixed-effects Model with random intercept
based on plot composition, which consists of 28 levels and yielded a residual of 0.109.

H 2013-2014 Conditional r^2 = 0.160
All Polycultures - SE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Tree Height	-0.793	-2.41	35	*
Tree Diameter	0.831	2.697	35	*
Shade Tolerance Diversity	0.285	1.988	22	|
Mycorrhizal Association Diversit	-0.266	-1.697	22	

Mixed-effects Model with random intercept
based on plot composition, which consists of 25 levels and yielded a residual of 0.144.

Supplementary Table 1.5 (cont.)

Significance of predictors in the models given is non-significant (p > 0.10; blank), significant (0.5 > 0 > 0.01; *), highly significant (0.01 > 0 > 0.001; **), or very highly significant (p < 0.001; ***). A brief description of model structure is given below each panel. Regression coefficients are standardized. Numerator degrees of freedom are 1 in all cases as predictors are continuous.

I 2013-2014 Conditional r^2 = 0.259
Bicultures Only - SE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Shade Tolerance Diversity	0.278	3.168	24	**
Tree Height	-0.354	-3.129	54	**
Tree Diameter	0.268	2.055	54	*
LMA Diversity	-0.124	-1.515	24	
Leaf Calcium Diversity	0.091	1.41	24	

Mixed-effects Model with random intercept
based on plot composition, which consists of 28 levels and yielded a residual of 0.091.

J 2014-2015 Conditional r^2 = 0.617
Bicultures Only - SE

Predictor	Std. Coefficient	t-Statistic	DF	Significance
Q. rubra abundance	0.515	4.23	53	***
Q. ellipsoidalis abundance	-0.298	-2.344	53	*
Number of Trees	-0.133	-1.307	53	

Mixed-effects Model with random intercept based on
plot composition, which consists of 28 levels and yielded a residual of 0.156.

Supplementary Table 1.6 – Simple linear regression models of NBE at the plot level. Models are given for all random-draw polycultures (A) and bicultures vs. monocultures (B) for the 2014-15 growing season. Results from 2013-14 are consistent with those presented here. For each model, the single predictor of diversity is provided, along with its standardized regression coefficient, the significance of the predictor (as in Table 1.1), and r^2 for the model. Models are ranked in order of descending ^{r2}. Abbreviations are as in Fig. 1.1, and also include Faith's (1992) PD, Scheiner and colleagues' (2016) multidimensional functional trait dispersion (FTD), Laliberté and Legendre's (2010) functional dispersion (FDis), and phylogenetic species variability (Helmus et al. 2007; PSV). All plots in panel B have the same species richness (SR=2), so SR, FPD, and FTD are included only in Panel A.

A	Predictor	Coefficient	p-value	r^2
	Faith's Phylogenetic Diversity (FPD)	0.0004	***	0.614
	Scheiner's Functional Diversity (FTD)	0.103	***	0.571
	Species Richness	0.049	***	0.541
	Functional Dispersion (FDis)	0.174	***	0.341
	Waterlogging Tolerance Diversity	0.418	***	0.235
	Shade Tolerance Diversity	0.281	***	0.227
	Leaf Habit Diversity	0.252	***	0.224
	Mycorrhizal Association Diversity	0.247	***	0.199
	Drought Tolerance Diversity	0.301	**	0.149
	LMA Diversity	0.258	**	0.127
	Leaf Nitrogen Diversity	0.269	**	0.125
	Phylogenetic Species Variability (PSV)	0.279	**	0.104
	Wood Density Mean	-0.086	*	0.081
	Wood Density Diversity	0.168	*	0.072
	Leaf Calcium Diversity	0.151	*	0.055
	Leaf Habit Mean	0.132		0.026
	Leaf Calcium Mean	0		0
	Drought Tolerance Mean	-0.035		0
	Waterlogging Tolerance Mean	-0.051		0
	LMA Mean	0.113		0
	Mycorrhizal Association Mean	-0.023		0
	Leaf Nitrogen Mean	-0.272		0
	Shade Tolerance Mean	-0.048		0

Supplementary Table 1.6 (cont.)

B	Predictor	Coefficient	p-value	r^2
	Wood Density Mean	-0.113	***	0.486
	Leaf Habit Mean	0.209	***	0.293
	Waterlogging Tolerance Mean	-0.123	***	0.162
	Leaf Nitrogen Mean	-0.585	***	0.138
	Phylogenetic Species Variability (PSV)	0.139	***	0.129
	LMA Mean	0.248	***	0.123
	Leaf Nitrogen Diversity	0.144	***	0.12
	Shade Tolerance Diversity	0.106	**	0.088
	Functional Dispersion (FDis)	0.045	*	0.047
	Wood Density Diversity	-0.074	*	0.038
	Shade Tolerance Mean	-0.047	|	0.032
	Leaf Habit Diversity	0.056	|	0.027
	Drought Tolerance Mean	-0.05	|	0.022
	Waterlogging Tolerance Diversity	-0.065	|	0.022
	Mycorrhizal Association Mean	0.08		0.02
	Drought Tolerance Diversity	0.048		0.009
	Leaf Calcium Mean	0		0.008
	Leaf Calcium Diversity	0.036		0.003
	LMA Diversity	0.027		0
	Mycorrhizal Association Diversity	0.001		0

Supplementary Table 1.7 - Correlations between traits as presented in Table 1.2. The lower diagonal gives correlations calculated from the random-draw polycultures dataset and the upper diagonal gives correlations from the bicultures vs. monocultures dataset. Abbreviations are as in Supplementary Table 1.3.

	SR	FPD	FTD	PSV	FDis	FDis_Density	FDis_LMA	FDis_Nitrogen	FDis_Myco	FDis_Habit	FDis_Calcium	FDis_Shade	FDis_Drought	FDis_Waterlog
SR		x	x	x	x	x	x	x	x	x	x	x	x	x
FPD	0.96		x	x	x	x	x	x	x	x	x	x	x	x
FTD	0.991	0.978		x	x	x	x	x	x	x	x	x	x	x
PSV	0.207	0.456	0.296		0.716	0.528	0.6	0.727	0.179	0.901	0.068	0.287	0.294	0.05
FDis	0.566	0.72	0.658	0.724		0.532	0.706	0.626	0.45	0.652	0.45	0.622	0.488	0.468
FDis_Density	0.51	0.613	0.565	0.512	0.687		0.415	0.334	0	0.662	-0.066	0.11	0.198	0.27
FDis_LMA	0.363	0.533	0.46	0.712	0.759	0.678		0.503	0.244	0.645	0.018	0.536	0.41	0.223
FDis_Nitrogen	0.349	0.561	0.45	0.845	0.86	0.74	0.862		0.112	0.685	0.298	0.15	-0.003	-0.03
FDis_Myco	0.497	0.59	0.537	0.536	0.626	0.167	0.288	0.417		-0.023	0.287	0.18	0.142	0.366
FDis_Habit	0.563	0.732	0.641	0.746	0.802	0.829	0.871	0.868	0.412		-0.063	0.247	0.282	0.125
FDis_Calcium	0.206	0.242	0.253	0.183	0.549	0.195	0.038	0.312	0.398	0.056		0.18	-0.046	0.138
FDis_Shade	0.259	0.348	0.338	0.404	0.67	0.193	0.559	0.469	0.233	0.419	0.354		0.47	0.222
FDis_Drought	0.305	0.338	0.353	0.209	0.516	0.134	0.322	0.225	0.544	0.244	0.26	0.404		0.262
FDis_Waterlog	0.748	0.731	0.761	0.108	0.565	0.568	0.309	0.382	0.446	0.562	0.188	0.139	0.297	
CWM_Density	0.097	-0.029	0.071	-0.464	-0.181	0.324	-0.161	-0.19	-0.305	0.043	-0.121	-0.322	-0.229	0.404
CWM_LMA	-0.182	-0.033	-0.175	0.528	-0.051	-0.262	0.006	0.085	0.305	-0.013	-0.206	-0.096	0.044	-0.395
CWM_Nitrogen	0.131	0.025	0.149	-0.363	0.171	0.225	-0.023	-0.037	-0.06	0.042	0.409	0.218	0.064	0.346
CWM_Myco	-0.099	-0.101	-0.117	-0.065	-0.219	0.024	-0.11	-0.186	-0.513	-0.028	-0.335	0.141	-0.388	-0.09
CWM_Habit	-0.138	-0.002	-0.13	0.485	0.006	-0.287	0.099	0.119	0.244	-0.037	-0.176	0.041	0.141	-0.413
CWM_Calcium	0.009	0.062	0.088	0.23	0.526	0.045	0.22	0.292	0.407	0.129	0.736	0.609	0.407	0.027
CWM_Shade	0.108	-0.007	0.122	-0.421	0.117	0.315	0.16	0.036	-0.351	0.062	0.158	0.188	0.116	0.316
CWM_Drought	-0.117	-0.049	-0.125	0.235	-0.177	-0.173	-0.196	-0.125	0.394	-0.065	-0.147	-0.422	0.101	-0.187
CWM_Waterlog	0.175	0.046	0.161	-0.461	0.012	0.226	-0.034	-0.04	-0.053	-0.022	0.195	-0.22	0.114	0.348

Supplementary Table 1.7 (cont.)

	CWM_Density	CWM_LMA	CWM_Nitrogen	CWM_Myco	CWM_Habit	CWM_Calcium	CWM_Shade	CWM_Drought	CWM_Waterlog
SR	x	x	x	x	x	x	x	x	x
FPD	x	x	x	x	x	x	x	x	x
FTD	x	x	x	x	x	x	x	x	x
PSV	-0.532	0.476	-0.448	-0.094	0.572	0.097	-0.216	0.029	-0.4
FDis	-0.375	0.082	-0.002	-0.457	0.168	0.505	0.066	-0.201	0.111
FDis_Density	0.201	-0.209	0.13	-0.056	-0.154	-0.028	0.216	-0.168	0.105
FDis_LMA	-0.283	0.183	-0.176	-0.384	0.22	0.182	-0.102	0.042	0.036
FDis_Nitrogen	-0.436	0.179	-0.194	0.001	0.32	0.276	0.086	-0.298	-0.209
FDis_Myco	-0.208	0.129	-0.005	-0.58	0.107	0.399	-0.082	0.318	0.22
FDis_Habit	-0.222	0.197	-0.214	-0.034	0.272	0.036	-0.016	-0.115	-0.234
FDis_Calcium	-0.173	-0.158	0.358	-0.355	-0.119	0.788	0.295	-0.236	0.234
FDis_Shade	-0.335	0.105	0.025	-0.183	0.133	0.423	-0.02	-0.185	-0.034
FDis_Drought	-0.259	0.27	-0.169	-0.378	0.206	0.053	-0.356	0.167	0.059
FDis_Waterlog	0.211	-0.324	0.237	-0.508	-0.309	0.085	0.295	-0.184	0.649
CWM_Density		-0.683	0.707	0.16	-0.862	-0.1	0.421	0.041	0.43
CWM_LMA	-0.725		-0.879	0.029	0.893	-0.254	-0.779	0.531	-0.668
CWM_Nitrogen	0.707	-0.88		-0.039	-0.919	0.537	0.634	-0.298	0.544
CWM_Myco	0.215	0.073	-0.071		0	-0.337	-0.07	-0.113	-0.656
CWM_Habit	-0.885	0.926	-0.923	-0.025		-0.216	-0.547	0.273	-0.624
CWM_Calcium	-0.11	-0.246	0.567	-0.332	-0.238		0.351	-0.166	0.184
CWM_Shade	0.599	-0.904	0.756	-0.053	-0.769	0.237		-0.597	0.541
CWM_Drought	-0.11	0.639	-0.376	-0.059	0.401	-0.136	-0.695		-0.242
CWM_Waterlog	0.51	-0.765	0.602	-0.583	-0.672	0.124	0.708	-0.369	

Supplementary Table 2.1 – Fixed terms included in mixed-methods multiple linear regression models of maximum leaf removal herbivory for all species and for particular species and across four spatial scales. Fixed terms are given for the "Best" model as determined by variable selection. All models include as random effects year and tree position nested within plot, nested within block. The all-species model includes species as an additional random effect. Tree height is included as a covariate in all models (including those with no other fixed terms).

	# of Trees in Neighbourhood			
Species	**8**	**24**	**48**	**80**
All	Height Apparency	Height Apparency	Height Apparency; *B. papyrifera* Neighbours	Height Apparency; *P. payrifera* Neighbours
A. negundo	Height Apparency	Height Apparency	SLA Trait Diversity; Lignin Trait Diversity; *T. americana* Neighbours	Height Apparency; *P. banksiana* Neighbours
A. rubrum	Height Apparency; Condensed Tannin Trait Mean; Condensed	None	Condensed Tannin Trait Diversity	Height Apparency; *P. banksiana* Neighbours
B. payrifera	Height Apparency	Height Apparency; *Q. rubra* Neighbours; Maple Neighbours	None	None
Q. alba	Height Apparency	Height Apparency	None	None
Q. ellipsoidalis	Height Apparency	Height Apparency; *A. rubrum* Neighbours	Height Apparency	Height Apparency; Lignin Trait Mean; Lignin Trait Diversity
Q. macrocarpa	Height Apparency; Species Richness	Height Apparency	Height Apparency	Height Apparency; Species Richness
Q. rubra	Height Apparency; Multidimensional Trait Diversity	Height Apparency; *P. strobus* Neighbours	Height Apparency; Nitrogen Trait Diversity; *A. negundo* Neighbours;	Height Apparency; Lignin Trait Mean; Lignin Trait Diversity
T. americana	Height Apparency	Height Apparency	None	*Q. ellipsoidalis* neighbours

Supplementary Table 2.2 – Height apparency models of leaf removal for all eight species surveyed (A) and for each individual species (B-I). The response variable is the maximum proportion (arcsin-square root transformed) of leaf removed per plant, pear year. All models are mixed-effects linear regression models. Each model is presented at the most explanatory spatial scale (# of trees in the neighbourhood) for a given species (and for all species).

Fixed Terms	Estimate	SE	t	Random Terms	St. Dev.	Levels
A. All Species						
Intercept	0.450	0.063	7.110	Number of Obs.	NA	1225
Focal Tree Height	0.001	0.001	1.113	Tree/Plot/Block	<0.001	665
Height Apparency	<0.001	<0.001	-1.220	Plot/Block	0.051	105
				Block	0.068	8
				Species	0.049	3
				Year	0.072	3
Marginal R^2 = 0.002						
Conditional R^2 = 0.129						
8-tree scale						
B. Box elder (*Acer negundo*)						
Intercept	0.559	0.174	3.220	Number of Obs.	NA	65
Focal Tree Height	-0.004	0.005	-0.711	Tree/Plot/Block	0.173	44
Height Apparency	<0.001	0.002	0.001	Plot/Block	<0.001	18
				Block	<0.001	3
				Year	0.007	3
Marginal R^2 = 0.012						
Conditional R^2 = 0.319						
8-tree scale						
C. Red maple (*Acer rubrum*)						
Intercept	0.538	0.116	4.626	Number of Obs.	NA	151
Focal Tree Height	<0.001	0.003	0.106	Tree/Plot/Block	0.064	85
Height Apparency	-0.001	0.001	-1.370	Plot/Block	0.099	29
				Block	0.032	3
				Year	<0.001	3
Marginal R^2 = 0.015						
Conditional R^2 = 0.168						
8-tree scale						
D. Paper birch (*Betula papyrifera*)						
Intercept	0.362	0.087	4.179	Number of Obs.	NA	177
Focal Tree Height	0.001	0.001	0.551	Tree/Plot/Block	0.089	96
Height Apparency	<0.001	0.001	0.432	Plot/Block	<0.001	29
				Block	0.049	3
				Year	0.053	3
Marginal R^2 = 0.006						
Conditional R^2 = 0.131						
8-tree scale						

Fixed Terms	Estimate	SE	t	Random Terms	St. Dev.	Levels
E. White oak (*Quercus alba*)						
Intercept	0.325	0.095	3.411	Number of Obs.	NA	128
Focal Plant Height	0.005	0.003	1.745	Tree/Plot/Block	0.159	66
Height Apparency	-0.002	0.001	-1.440	Plot/Block	<0.001	29
				Block	<0.001	3
Marginal R^2 = 0.032				Year	<0.001	2
Conditional R2 = 0.257						
24-tree scale						
F. Pin oak (*Quercus ellipsoidalis*)						
Intercept	0.426	0.114	3.740	Number of Obs.	NA	194
Focal Plant Height	0.003	0.003	1.020	Tree/Plot/Block	<0.001	108
Height Apparency	-0.001	0.001	-1.010	Plot/Block	<0.001	32
				Block	0.071	3
Marginal R^2 = 0.008				Year	0.129	3
Conditional R^2 = 0.193						
8-tree scale						
G. Bur oak (*Quercus macrocarpa*)						
Intercept	0.385	0.116	3.314	Number of Obs.	NA	149
Focal Plant Height	0.002	0.003	0.661	Tree/Plot/Block	<0.001	78
Height Apparency	<0.001	0.001	-0.438	Plot/Block	0.014	31
				Block	0.600	3
Marginal R^2 = 0.003				Year	0.065	2
Conditional R^2 = 0.082						
8-tree scale						
H. Red oak (*Quercus rubra*)						
Intercept	0.517	0.114	4.552	Number of Obs.	NA	154
Focal Plant Height	0.002	0.003	0.835	Tree/Plot/Block	<0.001	84
Height Apparency	-0.001	0.001	-0.741	Plot/Block	0.056	28
				Block	0.087	3
Marginal R^2 = 0.006				Year		3
Conditional R^2 = 0.084						
8-tree scale						
I. Basswood (*Tilia americana*)						
Intercept	0.553	0.089	6.230	Number of Obs.	NA	212
Focal Plant Height	-0.001	0.002	-0.329	Tree/Plot/Block	<0.001	110
Height Apparency	0.001	0.001	0.908	Plot/Block	<0.001	33
				Block	0.048	3
Marginal R^2 = 0.004				Year	0.014	3
Conditional R^2 = 0.032						
8-tree scale						

Supplementary Table 2.3 – AIC values for mixed-methods multiple linear regression models of maximum leaf removal herbivory for all species and for particular species and across four spatial scales. AIC values are given for the "Best" model at each spatial scale as determined by variable selection (and as reported in Supplementary Table 2.2) and for a model with only tree height and height apparency as fixed predictors. All models include as random effects year and tree position nested within plot, nested within block. The all-species model includes species as an additional random effect. Bolded values indicate the model(s) for each species with the lowest AIC and all models for that species with an AIC within 2 points of the lowest value.

Species	# Trees in Neighbourhood	AIC "Best" Model	AIC Height Apparency Model
All	8	**738.49**	**738.49**
	24	770.29	770.29
	48	835.53	837.61
	80	835.82	837.51
A. negundo	8	46.07	**46.07**
	24	45.32	**45.32**
	48	**40.23**	**46.04**
	80	47.78	**45.90**
A. rubrum	8	**78.31**	**85.88**
	24	101.71	101.41
	48	98.92	102.42
	80	99.53	99.53
B. papyrifera	8	115.72	**115.72**
	24	**104.43**	**116.35**
	48	118.06	120.03
	80	118.06	119.97
Q. alba	8	105.95	105.95
	24	**91.66**	**91.66**
	48	114.18	114.50
	80	114.18	114.72
Q. ellipsoidalis	8	**120.67**	**120.67**
	24	**118.60**	**122.46**
	48	141.77	141.77
	80	143.15	141.60
Q. macrocarpa	8	**88.43**	**90.64**
	24	**89.05**	**89.05**
	48	98.98	98.98
	80	98.36	98.75
Q. rubra	8	**138.07**	**140.57**
	24	140.31	144.26
	48	**139.81**	153.24
	80	**138.93**	152.96
T. americana	8	**101.33**	**101.33**
	24	116.20	116.20
	48	120.31	122.13
	80	117.04	121.63

Supplementary Table 3.1 - Predictions of the consequences of diversity across phylogenetic scales for a variety of ecological responses, as in Fig. 3.1C. For each ecological response, the expected direction of the BEF relationship (positive, negative, or null) is given, along with the phylogenetic scale(s) (intraspecific, interspecific, or both) expected to contribute to the relationship and key references informing these predictions.

Ecological response	Direction of relationship	Which scale contributes?	Literature informing prediction
Productivity	Positive	Interspecific	Crutsinger et al. (2006), Haase et al. (2015)
Fitness	Positive	Intraspecific	Johnson et al. (2006)
Generalist Herbivory	Positive	Interspecific	Abdala-Roberts et al. (2015), Haase et al. (2015)
Specialist Herbivory	Negative	Intraspecific	Lau et al. (2008)
Decomposition	Null	Neither	Madritch et al. (2006), Hattenschwiler et al. (2005)
Invasibility	Negative	Both	Tilman (1997), Crutsinger et al. (2008)
Soil Microbial Diversity	Positive	Interspecific	Schweitzer et al. (2008), Nguyen et al. (2016)
Disease Vulnerability	Negative	Interspecific	Pautasso et al. (2005)

Supplementary Table 3.2 – Model structure and coefficients for best models of a) leaf removal, b) gall, and c) leaf miner herbivory. Coefficients and standard errors for the multinomial model of leaf removal are given, as are coefficient estimates and p-values for the zero-inflated negative binomial models of gall and leaf miner counts.

a) Leaf Removal

Best Model: Leaf Removal ~ Plant Height + Species Richness

Coefficients

Category	(Intercept)	Plant Height	Species Richness
1	-5.603	0.0279	5.693
2	-5.862	0.0427	5.446
3	-5.420	0.0344	5.131

Standard Errors

Category	(Intercept)	Plant Height	Species Richness
1	0.5370	0.0161	0.4554
2	0.5270	0.0159	0.4526
3	0.5553	0.0161	0.4610

b) Galls

Best Model: Gall Count ~ Plant Height + Genotype ID | Plant Height + Genotype ID

Count Model Predictors

Predictor	Estimate	p-value
(Intercept)	-0.7840	0.1938
Plant Height	0.0144	0.0135
Genotype2	0.7448	0.0582
Genotype3	-0.1792	0.6664
Log(theta)	0.7229	0.3390

Zero-inflation Model Predictors

Predictor	Estimate	p-value
(Intercept)	1.4520	0.0926
Plant Height	-0.0178	0.0319
Genotype2	2.3410	<0.0001
Genotype3	0.0694	0.9166

c) Leaf Miners

Best Model: LM Count ~ Plant Height + Genotype ID + Genotypic Richness +
Plant Height + Genotype ID + Genotypic Richness

Count Model Predictors

Predictor	Estimate	p-value
(Intercept)	-1.0360	0.0592
Plant Height	0.0010	0.0374
Genotype2	-0.2406	0.4510
Genotype3	0.6032	0.1632
Genotypic Richness	-0.1984	0.0211
Log(theta)	-0.3286	0.3438

Zero-inflation Model Predictors

Predictor	Estimate	p-value
(Intercept)	566.3	0.4690
Plant Height	-6.440	0.4740
Genotype2	-269.1	0.4740
Genotype3	63.91	0.4870
Genotypic Richness	-62.65	0.4820

Supplementary Table 4.1 - Bags were filled with one of 49 mixtures of litter. Litter composition and diversity metrics for each litter type are given here.

	Species	Phylogenetic	Multidimensional	Proportion of litter composed of each species											
Mixture	Richnes	Species Variability	Functional Dispersion	ACNE	ACRU	BEPA	JUVI	PIBA	PIRE	PIST	QUAL	QUEL	QUMA	QURU	TIAM
M1	1	0	0	1											
M2	1	0	0		1										
M3	1	0	0			1									
M4	1	0	0				1								
M6	1	0	0						1						
M5	1	0	0					1							
M7	1	0	0							1					
M8	1	0	0								1				
M9	1	0	0									1			
M10	1	0	0										1		
M11	1	0	0											1	
M12	1	0	0												1
B1	2	0.04	0.21	0.5	0.5										
B2	2	0.33	0.18	0.5							0.5				
B3	2	0.33	0.19	0.5								0.5			
B4	2	1.00	0.19		0.5		0.5								
B5	2	1.00	0.15		0.5			0.5							
B6	2	0.29	0.22		0.5										0.5
B7	2	1.00	0.25			0.5		0.5							
B8	2	0.18	0.18			0.5						0.5			
B9	2	0.18	0.20			0.5							0.5		
B10	2	0.33	0.21			0.5									0.5
B11	2	0.76	0.16				0.5	0.5							
B12	2	0.76	0.20				0.5		0.5						
B13	2	1.00	0.16				0.5							0.5	
B14	2	1.00	0.21				0.5								0.5
B15	2	0.41	0.10					0.5	0.5						
B16	2	0.43	0.13					0.5		0.5					
B17	2	0.43	0.18						0.5	0.5					
B18	2	1.00	0.16						0.5		0.5				
B19	2	1.00	0.18						0.5					0.5	
B20	2	1.00	0.15							0.5	0.5				
B21	2	1.00	0.12							0.5		0.5			
B22	2	1.00	0.12							0.5				0.5	
B23	2	1.00	0.27							0.5					0.5
B24	2	0.07	0.13								0.5		0.5		
B25	2	0.11	0.09									0.5	0.5		
B26	2	0.05	0.11									0.5		0.5	
B27	2	0.11	0.15										0.5	0.5	
B28	2	0.33	0.20										0.5		0.5
F1	5	0.58	0.28	0.2		0.2			0.2					0.2	0.2
F10	5	0.54	0.23			0.2	0.2				0.2		0.2		0.2
F2	5	0.27	0.23		0.2	0.2						0.2		0.2	0.2
F3	5	0.74	0.23		0.2			0.2	0.2		0.2				0.2
F5	5	0.72	0.19		0.2			0.2	0.2			0.2	0.2		
F6	5	0.72	0.20		0.2				0.2	0.2	0.2		0.2		
F7	5	0.53	0.17		0.2					0.2	0.2	0.2	0.2		
F8	5	0.72	0.20			0.2	0.2	0.2				0.2	0.2		
T	12	0.64	0.24	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083	0.083

Supplementary Table 4.1 (cont.)

	Community Weighted Means (CWMs) of Functional Traits (%/mass)																	
Mixture	Rel. Water Content	Sp. Leaf Area	Sol. Cell Contents	Hemicellulose & BP	Cellulose	Lignin	Carbon	Nitrogen	Carbon : Nitrogen	Phosphorus	Calcium	Potassium	Magnesium	Manganese	Molybdenum	Zinc	Iron	Condensed Tannins
M1	0.72	166.59	61.78	16.29	17.71	17.20	45.25	1.47	33.09	0.22	2.61	1.55	0.35	1.09E-02	1.34E-04	2.12E-03	5.31E-02	6.99
M2	0.60	178.22	67.24	9.60	15.81	12.46	57.31	0.67	93.18	0.19	1.02	0.75	0.23	3.77E-02	2.28E-05	4.03E-03	8.11E-03	4.69
M3	0.69	225.07	57.52	15.50	14.45	20.42	49.77	0.90	59.78	0.31	1.84	1.51	0.47	9.64E-02	4.74E-06	2.81E-02	1.16E-02	5.42
M4	0.64	32.44	48.97	15.55	19.08	25.75	52.19	1.69	33.00	0.17	3.17	0.35	0.28	3.72E-02	5.17E-05	3.58E-03	4.48E-02	1.97
M6	0.51	26.22	52.98	13.95	19.50	16.36	51.42	0.35	156.21	0.05	0.95	0.20	0.16	2.48E-02	1.65E-05	3.63E-03	2.58E-02	22.10
M5	0.62	35.13	45.02	13.19	20.86	24.04	56.12	0.60	100.08	0.10	0.91	0.23	0.13	3.25E-02	1.85E-05	3.27E-03	2.42E-02	18.32
M7	0.54	65.31	32.29	15.92	25.68	30.03	59.76	0.74	87.98	0.15	1.23	0.42	0.23	4.24E-02	3.02E-06	8.69E-03	1.05E-02	7.71
M8	0.58	156.67	56.73	16.58	17.87	16.19	49.33	0.81	65.33	0.17	1.99	0.46	0.21	5.97E-02	1.65E-05	1.79E-03	8.59E-03	3.86
M9	0.59	116.65	44.69	15.13	17.32	26.64	53.24	1.32	43.65	0.16	1.08	0.76	0.26	4.43E-02	6.72E-06	3.10E-03	1.52E-02	6.83
M10	0.59	94.40	48.81	16.90	18.39	20.78	57.00	1.96	32.34	0.25	1.21	0.91	0.24	4.42E-02	3.46E-05	2.94E-03	2.59E-02	5.01
M11	0.55	135.96	42.27	16.92	22.50	21.98	52.35	0.90	64.06	0.13	1.40	0.33	0.30	9.33E-02	4.68E-06	4.79E-03	7.91E-03	3.96
M12	0.73	368.70	54.04	24.67	20.53	13.89	45.49	1.21	40.41	0.26	4.53	0.76	0.59	2.66E-02	3.77E-05	2.39E-03	1.44E-02	12.13
B1	0.66	172.41	64.51	12.95	16.76	14.83	51.28	1.07	63.13	0.21	1.81	1.15	0.29	2.43E-02	7.82E-05	3.07E-03	3.06E-02	5.84
B2	0.65	161.63	59.26	16.43	17.79	16.70	47.29	1.14	49.21	0.19	2.30	1.00	0.28	3.53E-02	7.50E-05	1.95E-03	3.09E-02	5.43
B3	0.65	141.62	53.24	15.71	17.51	21.92	49.24	1.40	38.37	0.19	1.84	1.16	0.30	2.76E-02	7.02E-05	2.61E-03	3.42E-02	6.91
B4	0.62	105.33	58.10	12.58	17.45	19.10	54.75	1.18	63.09	0.18	2.09	0.55	0.26	3.74E-02	3.72E-05	3.80E-03	2.65E-02	3.33
B5	0.61	106.68	56.13	11.39	18.34	18.25	56.71	0.64	96.63	0.15	0.97	0.49	0.18	3.51E-02	2.06E-05	3.65E-03	1.62E-02	11.51
B6	0.67	273.46	60.64	17.14	18.17	13.17	51.40	0.94	66.80	0.23	2.77	0.75	0.41	3.21E-02	3.02E-05	3.21E-03	1.13E-02	8.41
B7	0.66	130.10	51.27	14.34	17.66	22.23	52.94	0.75	79.93	0.21	1.38	0.87	0.30	6.45E-02	1.16E-05	1.57E-02	1.79E-02	11.87
B8	0.64	170.86	51.11	15.32	15.88	23.53	51.50	1.11	51.72	0.24	1.46	1.14	0.36	7.03E-02	5.73E-06	1.56E-02	1.34E-02	6.13
B9	0.64	159.74	53.17	16.20	16.42	20.60	53.38	1.43	46.06	0.28	1.53	1.21	0.36	7.03E-02	1.97E-05	1.55E-02	1.87E-02	5.21
B10	0.71	296.88	55.78	20.09	17.49	17.15	47.63	1.06	50.09	0.29	3.18	1.13	0.53	6.15E-02	2.12E-05	1.52E-02	1.30E-02	8.78
B11	0.63	33.79	47.00	14.37	19.97	24.90	54.15	1.14	66.54	0.14	2.04	0.29	0.21	3.48E-02	3.51E-05	3.43E-03	3.45E-02	10.15
B12	0.57	29.33	50.98	14.75	19.29	21.06	51.80	1.02	94.61	0.11	2.06	0.27	0.22	3.10E-02	3.41E-05	3.61E-03	3.53E-02	12.03
B13	0.59	84.20	45.62	16.24	20.79	23.87	52.27	1.29	48.53	0.15	2.29	0.34	0.29	6.52E-02	2.82E-05	4.18E-03	2.64E-02	2.97
B14	0.68	200.57	51.51	20.11	19.80	19.82	48.84	1.45	36.71	0.22	3.85	0.55	0.44	3.19E-02	4.47E-05	2.99E-03	2.96E-02	7.05
B15	0.57	30.68	49.00	13.57	20.18	20.20	53.77	0.48	128.14	0.08	0.93	0.21	0.15	2.86E-02	1.75E-05	3.45E-03	2.50E-02	20.21
B16	0.58	50.22	38.66	14.55	23.27	27.03	57.94	0.67	94.03	0.13	1.07	0.32	0.18	3.75E-02	1.08E-05	5.98E-03	1.73E-02	13.01
B17	0.52	45.76	42.64	14.93	22.59	23.19	55.59	0.55	122.10	0.10	1.09	0.31	0.19	3.36E-02	9.78E-06	6.16E-03	1.81E-02	14.90
B18	0.55	91.44	54.86	15.26	18.68	16.28	50.37	0.58	110.77	0.11	1.47	0.33	0.18	4.22E-02	1.65E-05	2.71E-03	1.72E-02	12.98
B19	0.53	81.09	47.63	15.43	21.00	19.17	51.88	0.62	110.14	0.09	1.18	0.27	0.23	5.90E-02	1.06E-05	4.21E-03	1.68E-02	13.03
B20	0.56	110.99	44.51	16.25	21.77	23.11	54.55	0.78	76.66	0.16	1.61	0.44	0.22	5.11E-02	9.74E-06	5.24E-03	9.52E-03	5.78
B21	0.56	90.98	38.49	15.53	21.50	28.33	56.50	1.03	65.82	0.16	1.15	0.59	0.24	4.34E-02	4.87E-06	5.90E-03	1.28E-02	7.27
B22	0.54	100.63	37.28	16.42	24.09	26.00	56.05	0.82	76.02	0.14	1.32	0.38	0.26	6.79E-02	3.85E-06	6.74E-03	9.18E-03	5.83
B23	0.63	217.00	43.17	20.30	23.10	21.96	52.63	0.98	64.20	0.21	2.88	0.59	0.41	3.45E-02	2.04E-05	5.54E-03	1.24E-02	9.92
B24	0.59	125.54	52.77	16.74	18.13	18.48	53.17	1.39	48.84	0.21	1.60	0.68	0.23	5.19E-02	2.55E-05	2.36E-03	1.72E-02	4.44
B25	0.59	105.53	46.75	16.02	17.85	23.71	55.12	1.64	38.00	0.21	1.15	0.84	0.25	4.42E-02	2.07E-05	3.02E-03	2.05E-02	5.92
B26	0.57	126.30	43.48	16.03	19.91	24.31	52.79	1.11	53.86	0.15	1.24	0.55	0.28	6.88E-02	5.70E-06	3.95E-03	1.15E-02	5.40
B27	0.57	115.18	45.54	16.91	20.44	21.38	54.67	1.43	48.20	0.19	1.31	0.62	0.27	6.87E-02	1.96E-05	3.87E-03	1.69E-02	4.49
B28	0.66	231.55	51.43	20.79	19.46	17.33	51.25	1.59	36.38	0.26	2.87	0.83	0.42	3.54E-02	3.62E-05	2.67E-03	2.02E-02	8.57
F1	0.64	184.51	53.72	17.47	18.94	17.97	48.85	0.97	70.71	0.19	2.27	0.87	0.37	5.04E-02	3.95E-05	8.20E-03	2.26E-02	10.12
F10	0.65	175.46	53.22	17.84	18.06	19.41	50.76	1.31	46.17	0.23	2.55	0.80	0.36	5.28E-02	2.90E-05	7.76E-03	2.11E-02	5.68
F2	0.63	204.92	53.15	16.37	18.12	19.08	51.63	1.00	60.22	0.21	1.97	0.82	0.37	5.96E-02	1.53E-05	8.48E-03	1.14E-02	6.61
F3	0.61	152.99	55.20	15.60	18.91	16.59	51.93	0.73	91.04	0.16	1.88	0.48	0.26	3.63E-02	2.24E-05	3.02E-03	1.62E-02	12.22
F5	0.58	90.13	51.75	13.75	18.38	20.05	55.02	0.98	85.09	0.15	1.03	0.57	0.20	3.67E-02	1.98E-05	3.40E-03	1.98E-02	11.39
F6	0.57	104.16	51.61	14.59	19.45	19.16	54.96	0.91	87.01	0.16	1.28	0.55	0.21	4.18E-02	1.87E-05	4.22E-03	1.58E-02	8.67
F7	0.58	122.25	49.95	14.83	19.01	21.22	55.33	1.10	64.50	0.19	1.31	0.66	0.23	4.57E-02	1.67E-05	4.11E-03	1.36E-02	5.62
F8	0.63	100.74	49.00	15.25	18.02	23.53	53.66	1.29	53.77	0.20	1.64	0.75	0.28	5.09E-02	2.32E-05	8.19E-03	2.43E-02	7.51
T	0.61	133.45	51.03	15.85	19.14	20.48	52.44	1.05	67.43	0.18	1.83	0.69	0.29	4.58E-02	2.92E-05	5.70E-03	2.08E-02	8.25

Supplementary Table 4.1 (cont.)

	Single-trait Functional Dispersion																	
Mixture	Rel. Water Content	Sp. Leaf Area	Sol. Cell Contents	Hemicellulose & BP	Cellulose	Lignin	Carbon	Nitrogen	Carbon : Nitrogen	Phosphorus	Calcium	Potassium	Magnesium	Manganese	Molybdenum	Zinc	Iron	Condensed Tannins
M1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M9	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
M12	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
B1	0.80	0.06	0.29	0.97	0.32	0.44	1.32	0.83	0.81	0.16	0.72	0.88	0.46	0.52	1.53	0.13	1.52	0.19
B2	0.98	0.05	0.27	0.04	0.03	0.09	0.45	0.68	0.44	0.33	0.28	1.20	0.54	0.94	1.62	0.02	1.50	0.25
B3	0.93	0.26	0.91	0.17	0.07	0.87	0.87	0.15	0.14	0.38	0.69	0.86	0.36	0.64	1.75	0.07	1.28	0.01
B4	0.23	0.75	0.97	0.86	0.54	1.22	0.56	1.06	0.81	0.14	0.97	0.44	0.21	0.01	0.40	0.03	1.24	0.22
B5	0.13	0.73	1.18	0.52	0.84	1.06	0.13	0.07	0.09	0.62	0.05	0.57	0.37	0.10	0.06	0.05	0.54	1.10
B6	0.89	0.97	0.70	2.18	0.78	0.13	1.29	0.57	0.71	0.48	1.58	0.01	1.38	0.22	0.21	0.11	0.21	0.60
B7	0.52	0.97	0.66	0.33	1.07	0.33	0.69	0.31	0.55	1.44	0.42	1.40	1.30	1.23	0.19	1.71	0.43	1.04
B8	0.78	0.55	0.68	0.05	0.48	0.57	0.38	0.44	0.22	1.02	0.34	0.81	0.83	1.01	0.03	1.72	0.12	0.11
B9	0.73	0.67	0.46	0.20	0.65	0.03	0.79	1.10	0.37	0.40	0.28	0.66	0.88	1.01	0.41	1.73	0.48	0.03
B10	0.25	0.73	0.18	1.33	1.01	0.60	0.47	0.33	0.26	0.34	1.21	0.82	0.45	1.35	0.46	1.77	0.10	0.54
B11	0.10	0.01	0.21	0.34	0.30	0.16	0.43	1.13	0.91	0.48	1.02	0.13	0.58	0.09	0.46	0.02	0.69	1.32
B12	0.88	0.03	0.21	0.23	0.07	0.86	0.08	1.39	1.67	0.86	1.00	0.16	0.49	0.24	0.49	0.00	0.64	1.63
B13	0.62	0.53	0.36	0.20	0.57	0.35	0.02	0.82	0.42	0.27	0.80	0.02	0.06	1.08	0.65	0.08	1.24	0.16
B14	0.66	1.72	0.27	1.32	0.24	1.09	0.73	0.49	0.10	0.62	0.61	0.45	1.18	0.20	0.19	0.08	1.02	0.82
B15	0.78	0.05	0.42	0.11	0.23	0.71	0.51	0.26	0.76	0.38	0.02	0.03	0.09	0.15	0.03	0.02	0.05	0.31
B16	0.62	0.15	0.67	0.40	0.80	0.55	0.40	0.14	0.16	0.34	0.14	0.21	0.35	0.19	0.21	0.37	0.46	0.86
B17	0.16	0.20	1.10	0.29	1.03	1.26	0.91	0.40	0.92	0.72	0.13	0.24	0.26	0.34	0.19	0.35	0.52	1.16
B18	0.47	0.67	0.20	0.38	0.27	0.02	0.23	0.48	1.23	0.84	0.47	0.28	0.20	0.67	0.00	0.13	0.58	1.47
B19	0.25	0.56	0.57	0.43	0.50	0.52	0.10	0.57	1.25	0.59	0.21	0.15	0.54	1.32	0.16	0.08	0.60	1.47
B20	0.32	0.47	1.30	0.09	1.30	1.27	1.14	0.08	0.31	0.12	0.35	0.04	0.06	0.33	0.19	0.47	0.06	0.31
B21	0.36	0.26	0.66	0.11	1.39	0.31	0.71	0.61	0.60	0.07	0.07	0.37	0.12	0.04	0.05	0.38	0.16	0.07
B22	0.10	0.36	0.53	0.14	0.53	0.74	0.81	0.16	0.32	0.13	0.08	0.10	0.28	0.98	0.02	0.27	0.09	0.30
B23	1.38	1.55	1.15	1.27	0.86	1.48	1.56	0.49	0.64	0.76	1.49	0.37	1.40	0.31	0.48	0.43	0.13	0.36
B24	0.09	0.32	0.42	0.05	0.09	0.42	0.84	1.19	0.45	0.58	0.35	0.50	0.13	0.30	0.25	0.08	0.58	0.09
B25	0.05	0.11	0.22	0.26	0.18	0.54	0.41	0.66	0.15	0.62	0.06	0.16	0.05	0.00	0.39	0.01	0.36	0.15
B26	0.26	0.10	0.13	0.26	0.86	0.43	0.10	0.45	0.28	0.20	0.15	0.47	0.16	0.95	0.03	0.12	0.24	0.23
B27	0.31	0.21	0.35	0.00	0.68	0.11	0.51	1.11	0.43	0.83	0.09	0.63	0.21	0.95	0.41	0.13	0.61	0.08
B28	0.97	1.40	0.28	1.12	0.36	0.63	1.26	0.78	0.11	0.06	1.50	0.17	1.33	0.34	0.04	0.04	0.39	0.58
F1	1.25	0.92	0.52	0.83	0.76	0.47	0.61	0.62	0.93	1.15	0.94	1.15	0.97	1.37	1.04	1.09	0.91	0.91
F10	0.75	0.99	0.37	0.79	0.51	0.64	0.67	0.85	0.35	0.69	0.94	0.72	1.05	0.78	0.41	1.12	0.77	0.42
F2	0.91	0.75	0.82	1.03	0.90	0.87	0.70	0.45	0.40	0.82	0.92	0.60	0.99	1.09	0.33	1.08	0.18	0.37
F3	0.75	1.00	0.57	1.16	0.55	0.55	0.84	0.47	0.83	0.88	1.00	0.48	1.00	0.38	0.17	0.10	0.47	1.03
F5	0.40	0.49	0.71	0.55	0.48	0.83	0.47	1.10	1.02	0.85	0.08	0.62	0.36	0.25	0.20	0.05	0.44	1.14
F6	0.47	0.52	0.94	0.65	0.83	0.92	0.80	0.88	0.83	0.70	0.26	0.49	0.18	0.33	0.22	0.25	0.54	0.87
F7	0.25	0.37	1.02	0.61	0.89	1.05	0.71	0.90	0.57	0.41	0.25	0.39	0.10	0.22	0.26	0.25	0.37	0.21
F8	0.45	0.57	0.36	0.25	0.57	0.43	0.51	0.90	0.57	0.90	0.62	0.81	0.61	0.70	0.44	1.09	0.59	0.70
T	0.79	0.73	0.78	0.59	0.74	0.81	0.77	0.83	0.76	0.76	0.75	0.78	0.72	0.72	0.65	0.58	0.78	0.75

Supplementary Table 4.2 - Species means for two physical (relative water content and specific leaf area) and 16 chemical (all others) leaf traits. All chemical traits are calculated based on oven-dry weight. Carbon fractions are calculated based on ash-free weight.

Species	Relative Water Content (%)	Specific Leaf Area (cm^2/g)	Soluble Cell Contents (%/mass)	Hemicellulose & Bound Proteins (%/mass)	Cellulose (%/mass)	Lignin (%/mass)	Carbon (%/mass)	Nitrogen (%/mass)
Acer negundo	71.7%	166.6	61.8%	16.3%	17.7%	17.2%	45.2%	1.5%
Acer rubrum	60.4%	178.2	67.2%	9.6%	15.8%	12.5%	57.3%	0.7%
Betula papyrifera	69.5%	225.1	57.5%	15.5%	14.4%	20.4%	49.8%	0.9%
Juniperus virginiana	63.6%	32.4	49.0%	15.6%	19.1%	25.8%	52.2%	1.7%
Pinus banksiana	62.2%	35.1	45.0%	13.2%	20.9%	24.0%	56.1%	0.6%
Pinus resinosa	51.4%	26.2	53.0%	13.9%	19.5%	16.4%	51.4%	0.4%
Pinus strobus	53.6%	65.3	32.3%	15.9%	25.7%	30.0%	59.8%	0.7%
Quercus alba	58.0%	156.7	56.7%	16.6%	17.9%	16.2%	49.3%	0.8%
Quercus ellipsoidalis	58.6%	116.7	44.7%	15.1%	17.3%	26.6%	53.2%	1.3%
Quercus macrocarpa	59.3%	94.4	48.8%	16.9%	18.4%	20.8%	57.0%	2.0%
Quercus rubra	54.9%	136.0	42.3%	16.9%	22.5%	22.0%	52.3%	0.9%
Tilia americana	72.9%	368.7	54.0%	24.7%	20.5%	13.9%	45.5%	1.2%

Species	Carbon / Nitrogen Ratio	Phosphorus (%/mass)	Calcium (%/mass)	Potassium (%/mass)	Magnesium (%/mass)	Manganese (%/mass)	Molybdenum (ppm)	Zinc (ppm)	Iron (%/mass)	Condened Tannins (%/mass)
Acer negundo	33.1	0.217%	2.608%	1.553%	0.350%	0.011%	1.34	21.15	0.05%	6.99%
Acer rubrum	93.2	0.193%	1.020%	0.748%	0.230%	0.038%	0.23	40.28	0.01%	4.69%
Betula papyrifera	59.8	0.311%	1.841%	1.510%	0.473%	0.096%	0.05	280.79	0.01%	5.42%
Juniperus virginiana	33.0	0.173%	3.169%	0.348%	0.284%	0.037%	0.52	35.79	0.04%	1.97%
Pinus banksiana	100.1	0.103%	0.913%	0.225%	0.134%	0.033%	0.19	32.71	0.02%	18.32%
Pinus resinosa	156.2	0.048%	0.947%	0.199%	0.157%	0.025%	0.17	36.33	0.03%	22.10%
Pinus strobus	88.0	0.152%	1.227%	0.421%	0.225%	0.042%	0.03	86.90	0.01%	7.71%
Quercus alba	65.3	0.170%	1.994%	0.456%	0.211%	0.060%	0.16	17.88	0.01%	3.86%
Quercus ellipsoidalis	43.7	0.163%	1.079%	0.763%	0.257%	0.044%	0.07	31.02	0.02%	6.83%
Quercus macrocarpa	32.3	0.253%	1.215%	0.909%	0.243%	0.044%	0.35	29.41	0.03%	5.01%
Quercus rubra	64.1	0.133%	1.403%	0.334%	0.298%	0.093%	0.05	47.90	0.01%	3.96%
Tilia americana	40.4	0.262%	4.525%	0.758%	0.590%	0.027%	0.38	23.92	0.01%	12.13%

Supplementary Table 4.3 - Breakdown by mixture of deviance from expected decomposition for mass loss and each carbon fraction. Mean DFP and confidence intervals (+/- 1 standard error) are given in units of years-1. When a given mixture's confidence interval does not include zero, its DFP is considered to be non-additive. Non-additive DFPs indicate either a lower (antagonistic) or a higher (synergistic) rater of decomposition than what is expected based on single-species bags. Mixtures that conform to expectations are considered to have decomposed additively.

Mixture	Mass Loss			Soluble Cell Contents		
	Mean DFP	DFP +/- 1 SE	Non-Additivity?	Mean DFP	DFP +/- 1 SE	Non-Additivity?
A. negundo, A. rubrum	0.076	(0.001, 0.151)	Synergistic	-0.208	(-0.447, 0.031)	Additive
B. papyrifera, T. americana	-0.036	(-0.076, 0.003)	Additive	0.004	(-0.149, 0.156)	Additive
J. virginiana, P. banksiana	-0.060	(-0.079, -0.04)	Antagonistic	-0.429	(-0.45, -0.407)	Antagonistic
J. virginiana, P. resinosa	-0.042	(-0.051, -0.033)	Antagonistic	-0.484	(-0.572, -0.396)	Antagonistic
J. virginiana, Q. rubra	0.047	(0.018, 0.076)	Synergistic	-0.124	(-0.206, -0.041)	Antagonistic
J. virginiana, T. macrocarpa	0.070	(-0.069, 0.209)	Additive	-0.027	(-0.395, 0.342)	Additive
P. banksiana, P. resinosa	0.011	(-0.013, 0.035)	Additive	-0.041	(-0.057, -0.026)	Antagonistic
P. banksiana, P. strobus	0.140	(0.111, 0.169)	Synergistic	0.125	(0.057, 0.193)	Synergistic
P. resinosa, P. strobus	0.038	(0.013, 0.062)	Synergistic	-0.059	(-0.115, -0.004)	Antagonistic
P. resinosa, Q. alba	-0.047	(-0.071, -0.022)	Antagonistic	-0.071	(-0.163, 0.022)	Additive
P. resinosa, Q. rubra	-0.082	(-0.118, -0.046)	Antagonistic	-0.080	(-0.141, -0.02)	Antagonistic
A. negundo, Q. alba	0.004	(-0.024, 0.033)	Additive	-0.832	(-0.956, -0.707)	Antagonistic
P. strobus, Q. alba	0.025	(-0.031, 0.081)	Additive	-0.037	(-0.14, 0.065)	Additive
P. strobus, Q. ellipsoidalis	0.038	(0.008, 0.067)	Synergistic	0.011	(-0.029, 0.051)	Additive
P. strobus, Q. rubra	0.013	(-0.033, 0.06)	Additive	0.066	(0.03, 0.101)	Synergistic
P. strobus, T. americana	0.000	(-0.076, 0.077)	Additive	-0.474	(-0.542, -0.406)	Antagonistic
Q. alba, Q. macrocarpa	0.061	(0.001, 0.121)	Synergistic	0.203	(-0.016, 0.422)	Additive
Q. ellipsoidalis, Q. macrocarpa	0.049	(0.035, 0.063)	Synergistic	0.063	(0.014, 0.113)	Synergistic
Q. ellipsoidalis, Q. rubra	0.024	(-0.002, 0.05)	Additive	0.280	(0.042, 0.517)	Synergistic
Q. macrocarpa, Q. rubra	0.040	(0.034, 0.047)	Synergistic	0.165	(0.156, 0.175)	Synergistic
Q. macrocarpa, T. americana	0.004	(-0.057, 0.065)	Additive	-0.368	(-0.431, -0.305)	Antagonistic
A. negundo, Q. ellipsoidalis	0.054	(0.027, 0.081)	Synergistic	-0.388	(-0.781, 0.005)	Additive
A. rubrum, J. virginiana	-0.050	(-0.069, -0.031)	Antagonistic	-0.401	(-0.486, -0.315)	Antagonistic
A. rubrum, P. banksiana	-0.015	(-0.05, 0.021)	Additive	-0.343	(-0.419, -0.266)	Antagonistic
A. rubrum, T. americana	-0.018	(-0.06, 0.024)	Additive	-0.411	(-0.795, -0.027)	Antagonistic
B. papyerifera, P. banksiana	0.060	(0.04, 0.08)	Synergistic	-0.175	(-0.238, -0.113)	Antagonistic
B. papyrifera, Q. ellipsoidalis	-0.016	(-0.063, 0.031)	Additive	-0.312	(-0.36, -0.265)	Antagonistic
B. papyrifera, Q. macrocarpa	0.013	(-0.028, 0.055)	Additive	-0.297	(-0.353, -0.24)	Antagonistic
A. negundo, B. papyrifera, P. resinoa, Q. rubra, T. americana	0.070	(0.063, 0.078)	Synergistic	-0.308	(-0.636, 0.019)	Additive
B. papyrifera, J. virginiana, Q. alba, Q. macrocarpa, T. americana	-0.083	(-0.107, -0.058)	Antagonistic	-0.408	(-0.479, -0.337)	Antagonistic
A. rubrum, B. payrifera, Q. ellipsoidalis, Q. rubra, T. americana	-0.061	(-0.085, -0.037)	Antagonistic	-0.292	(-0.447, -0.137)	Antagonistic
A. rubrum, P. banksiana, P. resinosa, Q. alba, T. americana	0.055	(0.012, 0.097)	Synergistic	-0.111	(-0.311, 0.088)	Additive
A. rubrum, P. banksiana, P. resinosa, Q. ellipsoidalis, Q. macrocarpa	0.062	(0.048, 0.077)	Synergistic	-0.061	(-0.098, -0.023)	Antagonistic
A. rubrum, P. resinosa, P. strobus, Q. alba, Q. macrocarpa	0.014	(-0.006, 0.035)	Additive	0.175	(0.039, 0.311)	Synergistic
A. rubrum, P. strobus, Q. alba, Q. ellipsoidalis, Q. macrocarpa	0.067	(0.042, 0.093)	Synergistic	-0.038	(-0.073, -0.003)	Antagonistic
B. papyrifera, J. virginiana, P. banksiana, Q. ellipsoidalis, Q. macrocarpa	0.062	(0.016, 0.108)	Synergistic	0.477	(0.173, 0.78)	Synergistic
All Twelve	-0.044	(-0.07, -0.018)	Antagonistic	-0.340	(-0.488, -0.191)	Antagonistic

Supplementary Table 4.3 (cont.)

Mixture	Hemicellulose and Bound Proteins			Cellulose			Lignin		
	Mean DFP	DFP +/- 1 SE	Non-Additivity?	Mean DFP	DFP +/- 1 SE	Non-Additivity?	Mean DFP	DFP +/- 1 SE	Non-Additivity?
A. negundo, A. rubrum	0.077	(-0.034, 0.188)	Additive	0.097	(0.021, 0.172)	Synergistic	0.014	(0, 0.028)	Additive
B. papyrifera, T. americana	-0.329	(-0.572, -0.087)	Antagonistic	-0.094	(-0.146, -0.043)	Antagonistic	-0.032	(-0.074, 0.009)	Additive
J. virginiana, P. banksiana	-0.115	(-0.147, -0.082)	Antagonistic	-0.036	(-0.081, 0.01)	Additive	-0.034	(-0.062, -0.006)	Antagonistic
J. virginiana, P. resinosa	-0.095	(-0.152, -0.037)	Antagonistic	-0.047	(-0.083, -0.011)	Antagonistic	0.005	(-0.044, 0.055)	Additive
J. virginiana, Q. rubra	0.100	(-0.051, 0.251)	Additive	0.090	(0.03, 0.151)	Synergistic	0.014	(-0.066, 0.095)	Additive
J. virginiana, T. macrocarpa	0.113	(-0.468, 0.694)	Additive	0.137	(-0.038, 0.312)	Additive	0.056	(-0.051, 0.164)	Additive
P. banksiana, P. resinosa	-0.136	(-0.19, -0.083)	Antagonistic	-0.035	(-0.069, -0.002)	Antagonistic	0.002	(-0.022, 0.026)	Additive
P. banksiana, P. strobus	0.209	(0.168, 0.25)	Synergistic	0.159	(0.136, 0.182)	Synergistic	0.211	(0.194, 0.229)	Synergistic
P. resinosa, P. strobus	0.021	(-0.036, 0.078)	Additive	0.005	(-0.042, 0.052)	Additive	0.070	(0.019, 0.12)	Synergistic
P. resinosa, Q. alba	-0.121	(-0.188, -0.053)	Antagonistic	-0.042	(-0.076, -0.007)	Antagonistic	0.018	(0.001, 0.034)	Synergistic
P. resinosa, Q. rubra	-0.191	(-0.257, -0.125)	Antagonistic	-0.090	(-0.113, -0.066)	Antagonistic	-0.021	(-0.021, -0.021)	Antagonistic
A. negundo, Q. alba	-0.168	(-0.237, -0.1)	Antagonistic	-0.022	(-0.041, -0.004)	Antagonistic	0.004	(0, 0.008)	Additive
P. strobus, Q. alba	0.007	(-0.078, 0.092)	Additive	0.049	(-0.018, 0.115)	Additive	0.121	(0.046, 0.196)	Synergistic
P. strobus, Q. ellipsoidalis	0.008	(-0.023, 0.038)	Additive	0.107	(0.06, 0.154)	Synergistic	0.090	(0.025, 0.155)	Synergistic
P. strobus, Q. rubra	-0.022	(-0.104, 0.059)	Additive	-0.097	(-0.15, -0.043)	Antagonistic	0.023	(-0.024, 0.069)	Additive
P. strobus, T. americana	0.241	(-0.411, 0.894)	Additive	0.023	(-0.039, 0.084)	Additive	0.065	(-0.014, 0.144)	Additive
Q. alba, Q. macrocarpa	0.244	(0.063, 0.424)	Synergistic	0.003	(-0.045, 0.05)	Additive	0.000	(0, 0)	Additive
Q. ellipsoidalis, Q. macrocarpa	0.138	(0.061, 0.215)	Synergistic	0.064	(0.041, 0.086)	Synergistic	0.036	(0.007, 0.064)	Synergistic
Q. ellipsoidalis, Q. rubra	0.348	(0.032, 0.663)	Synergistic	-0.022	(-0.106, 0.061)	Additive	-0.002	(-0.032, 0.028)	Additive
Q. macrocarpa, Q. rubra	0.146	(0.084, 0.207)	Synergistic	0.027	(-0.022, 0.076)	Additive	-0.017	(-0.017, -0.017)	Antagonistic
Q. macrocarpa, T. americana	0.010	(-0.312, 0.333)	Additive	0.068	(-0.024, 0.159)	Additive	0.008	(-0.04, 0.056)	Additive
A. negundo, Q. ellipsoidalis	0.103	(0, 0.206)	Synergistic	0.039	(-0.038, 0.116)	Additive	0.008	(-0.003, 0.02)	Additive
A. rubrum, J. virginiana	-0.062	(-0.083, -0.041)	Antagonistic	-0.059	(-0.074, -0.045)	Antagonistic	-0.095	(-0.095, -0.095)	Antagonistic
A. rubrum, P. banksiana	-0.014	(-0.04, 0.013)	Additive	-0.018	(-0.063, 0.027)	Additive	-0.024	(-0.024, -0.024)	Antagonistic
A. rubrum, T. americana	-0.390	(-0.478, -0.302)	Antagonistic	-0.024	(-0.086, 0.038)	Additive	-0.040	(-0.04, -0.04)	Antagonistic
B. papyerifera, P. banksiana	-0.094	(-0.23, 0.041)	Additive	0.061	(0.026, 0.096)	Synergistic	-0.002	(-0.036, 0.031)	Additive
B. papyrifera, Q. ellipsoidalis	-0.145	(-0.225, -0.064)	Antagonistic	-0.113	(-0.173, -0.052)	Antagonistic	0.032	(-0.018, 0.081)	Additive
B. papyrifera, Q. macrocarpa	-0.217	(-0.345, -0.088)	Antagonistic	0.052	(0.032, 0.071)	Synergistic	0.072	(0.02, 0.124)	Synergistic
A. negundo, B. papyrifera, P. resinoa, Q. rubra, T. americana	-0.133	(-0.248, -0.019)	Antagonistic	0.096	(0.065, 0.127)	Synergistic	0.064	(0.041, 0.087)	Synergistic
B. papyrifera, J. virginiana, Q. alba, Q. macrocarpa, T. americana	-0.668	(-0.691, -0.646)	Antagonistic	-0.153	(-0.18, -0.126)	Antagonistic	-0.028	(-0.048, -0.008)	Antagonistic
A. rubrum, B. payrifera, Q. ellipsoidalis, Q. rubra, T. americana	-0.651	(-0.736, -0.566)	Antagonistic	-0.146	(-0.204, -0.088)	Antagonistic	-0.042	(-0.042, -0.042)	Antagonistic
A. rubrum, P. banksiana, P. resinosa, Q. alba, T. americana	-0.320	(-0.346, -0.294)	Antagonistic	0.102	(0.064, 0.14)	Synergistic	0.011	(-0.017, 0.038)	Additive
A. rubrum, P. banksiana, P. resinosa, Q. ellipsoidalis, Q. macrocarpa	0.107	(0.011, 0.202)	Synergistic	0.054	(0.03, 0.078)	Synergistic	-0.009	(-0.013, -0.005)	Antagonistic
A. rubrum, P. resinosa, P. strobus, Q. alba, Q. macrocarpa	0.201	(0.089, 0.314)	Synergistic	0.040	(0.023, 0.058)	Synergistic	0.029	(0.007, 0.051)	Synergistic
A. rubrum, P. strobus, Q. alba, Q. ellipsoidalis, Q. macrocarpa	0.186	(0.132, 0.24)	Synergistic	0.056	(0.029, 0.083)	Synergistic	0.039	(-0.008, 0.086)	Additive
B. papyrifera, J. virginiana, P. banksiana, Q. ellipsoidalis, Q. macrocarpa	-0.079	(-0.214, 0.056)	Additive	-0.012	(-0.051, 0.026)	Additive	-0.020	(-0.067, 0.026)	Additive
All Twelve	-0.126	(-0.257, 0.004)	Additive	-0.074	(-0.127, -0.02)	Antagonistic	-0.006	(-0.032, 0.02)	Additive

Supplementary Table 4.4 - Best models of deviance from predicted (DFP) decomposition based on trait identity and univariate trait diversity (as determined through forward selection; A-C) and on random predictors only (when multdimensional functional dispersion did not predict DFP; D-F). Model are presented for mass loss (A,D), cellulose (B,E), and lignin decomposition (C,F); corresponding models for soluble cell contents and hemicellulose and bound proteins decomposition are given in Table 4.4. Litter composition type, nested within block, is included as a random predictor. All estimates for fixed predictors (A-C) are standardized.

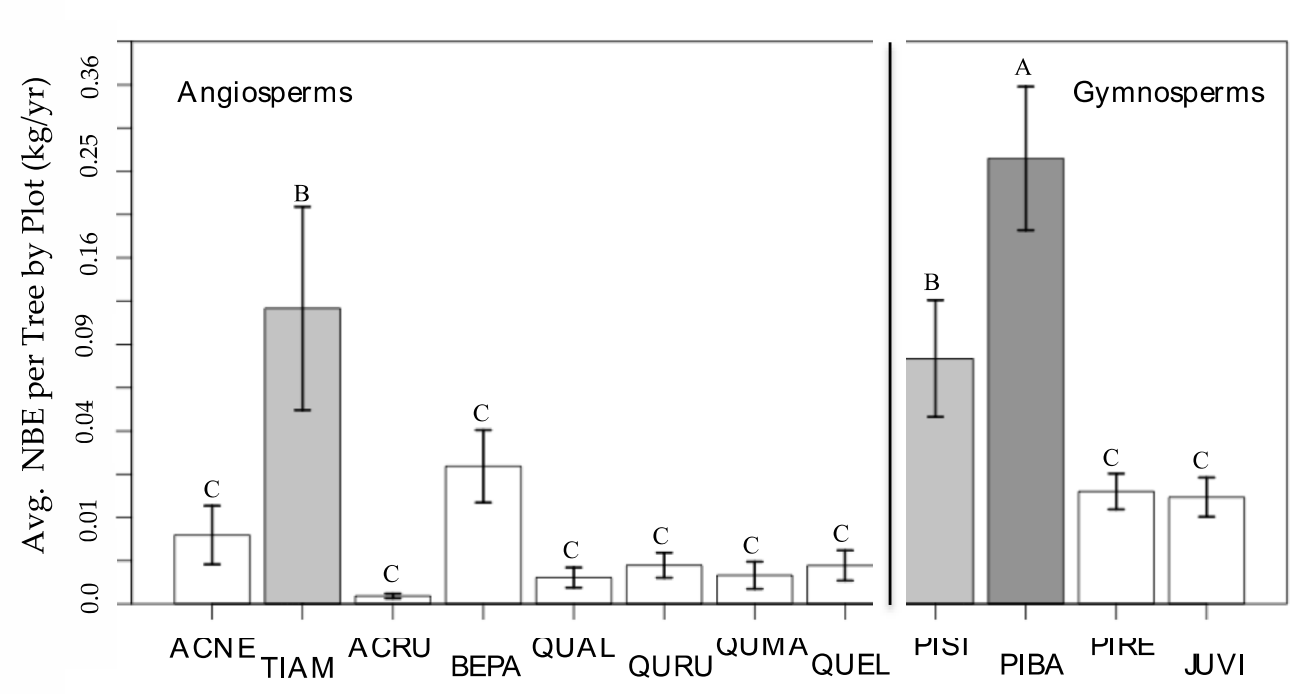
	Fixed Terms	Estimate	t	Random Terms	St. Dev.	Levels
A. Mass Loss - DFP - CWMs and univariate trait diversity						
	Calcium functional dispersion	-0.311	-3.17	Number of Obs.	NA	114
	Carbon functional dispersion	0.236	2.41	Block/Composition	0.004	111
	Marginal R^2 = 0.092					
	Conditional R^2 = 0.692					
B. Cellulose - DFP - CWMs and univariate trait diversity						
	Manganese functional dispersion	-0.228	-2.50	Number of Obs.	NA	114
	Iron functional dispersion	0.154	1.68	Block/Composition	0.105	111
	Marginal R^2 = 0.071					
	Conditional R^2 = 0.938					
C. Lignin - DFP - CWMs and univariate trait diversity						
	Soluble Cell Contents CWM	-0.325	-3.77	Number of Obs.	NA	114
	Relative Water Content functional dispersion	0.326	3.13	Block/Composition	0.059	111
	Calcium functional dispersion	-0.248	-2.32			
	Marginal R^2 = 0.196					
	Conditional R^2 = 0.748					

Supplementary Table 4.4 (cont.)

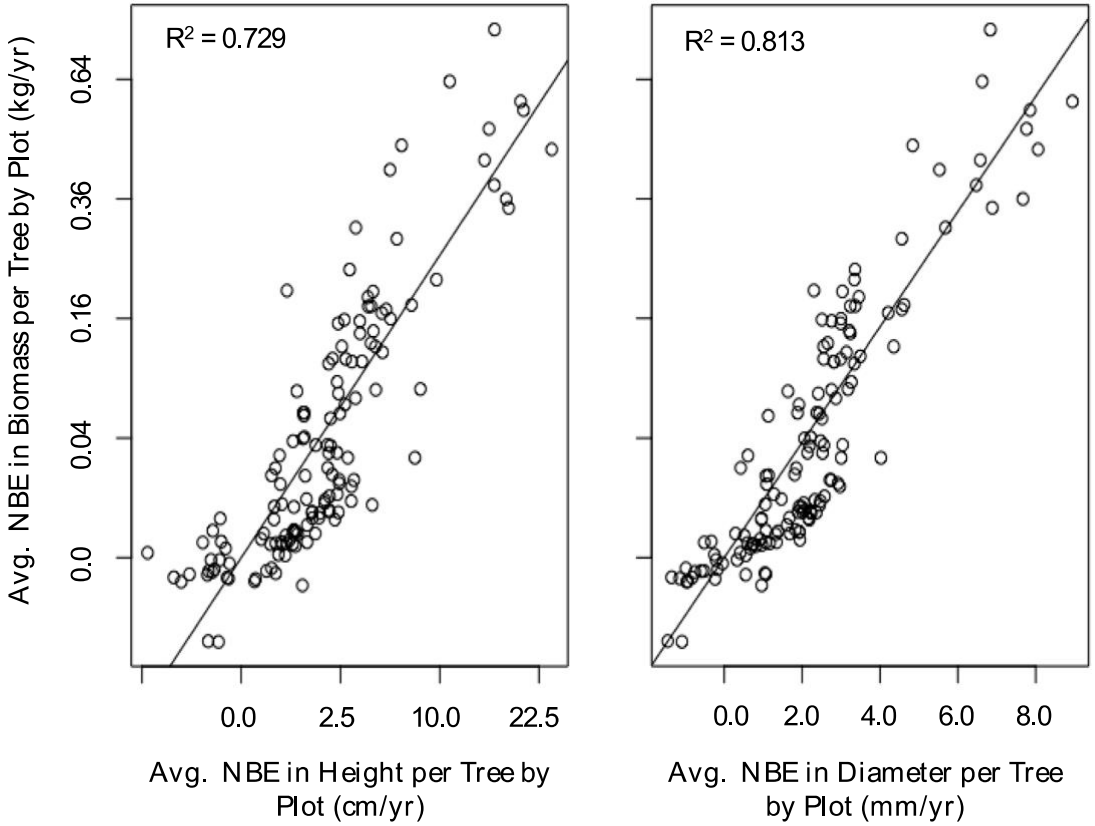
D. Mass Loss - DFP - fixed intercept and random effects					
Intercept	0.015	1.93	Number of Obs.	NA	114
			Block/Composition	0.067	111
Marginal R^2 = 0					
Conditional R^2 = 0.689					
E. Cellulose - DFP - fixed intercept and random effects					
Intercept	0.007	0.618	Number of Obs.	NA	114
			Block/Composition	0.108	111
Marginal R^2 = 0					
Conditional R^2 = 0.936					
F. Lignin - DFP - fixed intercept and random effects					
Intercept	0.017	2.23	Number of Obs.	NA	114
			Block/Composition	0.067	111
Marginal R^2 = 0					
Conditional R^2 = 0.732					

Appendix S5: Supplementary Figures

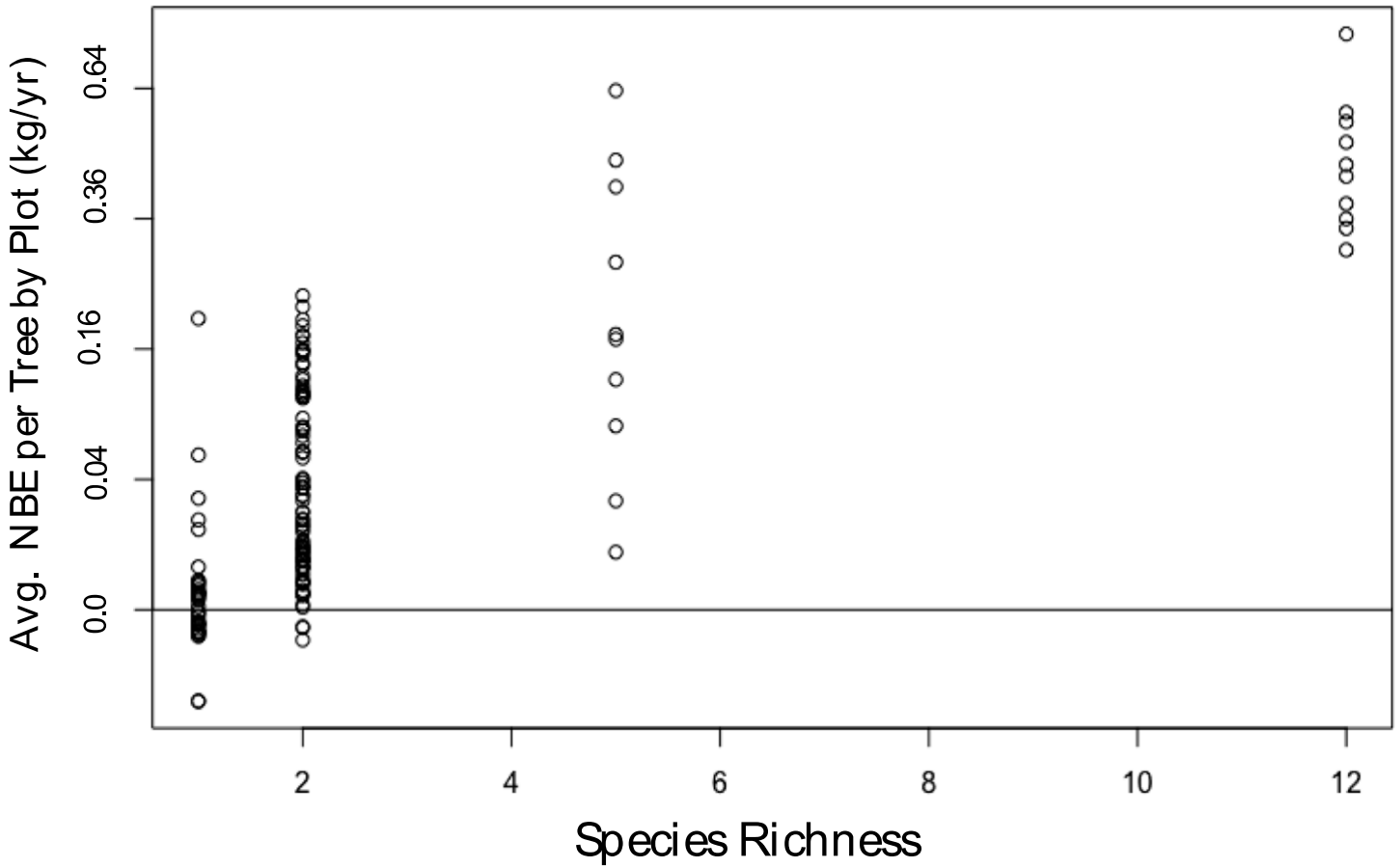
Supplementary Figure 1.1 - Square root of mean aboveground annual increase in stem biomass (kg/year) per tree in monocultures by species; error bars are one standard error. Species are ordered from lowest leaf mass per unit area (box elder/ACNE, 1.57 g/m2) on the left to highest LMA (eastern red cedar/JUVI, 2.52 g/m2) on the right. Post-hoc testing by species (Tukey's HSD; $\alpha = 0.05$) indicates that jack pine (PIBA; white column; "A") grew significantly faster than all other species, followed by white pine (PIST) and basswood (TIAM) in a second group (gray columns; "B") and then all other species in a third, slow-growing group (white columns "C").



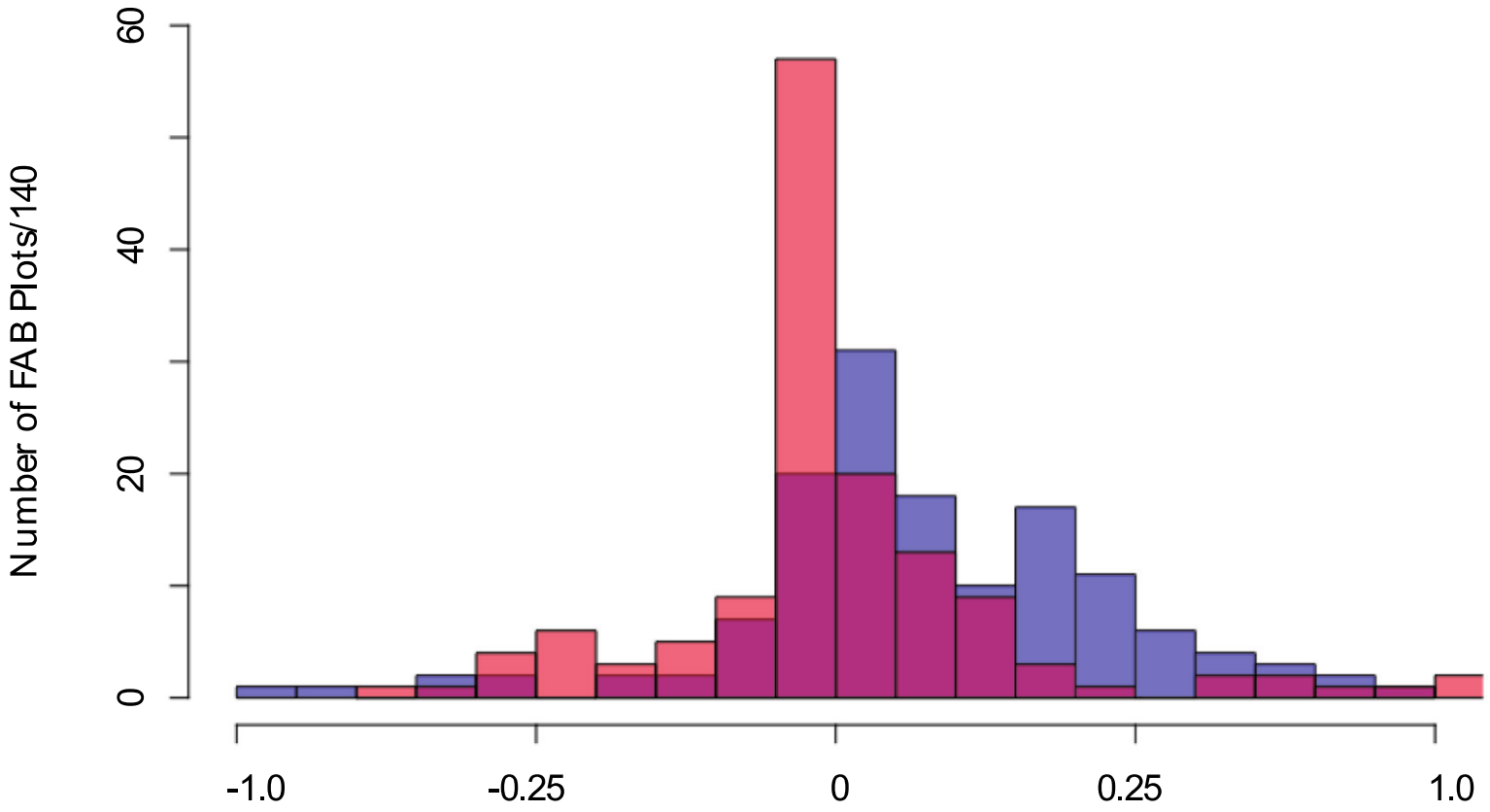
Supplementary Figure 1.2 - Net biodiversity effects (NBE) in biomass (kg/yr) were correlated with NBE for height (left; cm/yr) and diameter (right; mm/yr); qualitative patterns in the response of growth to diversity were similar for all three dimensions of stem size. Data for 2014-2015 are shown and all responses are square-root transformed.



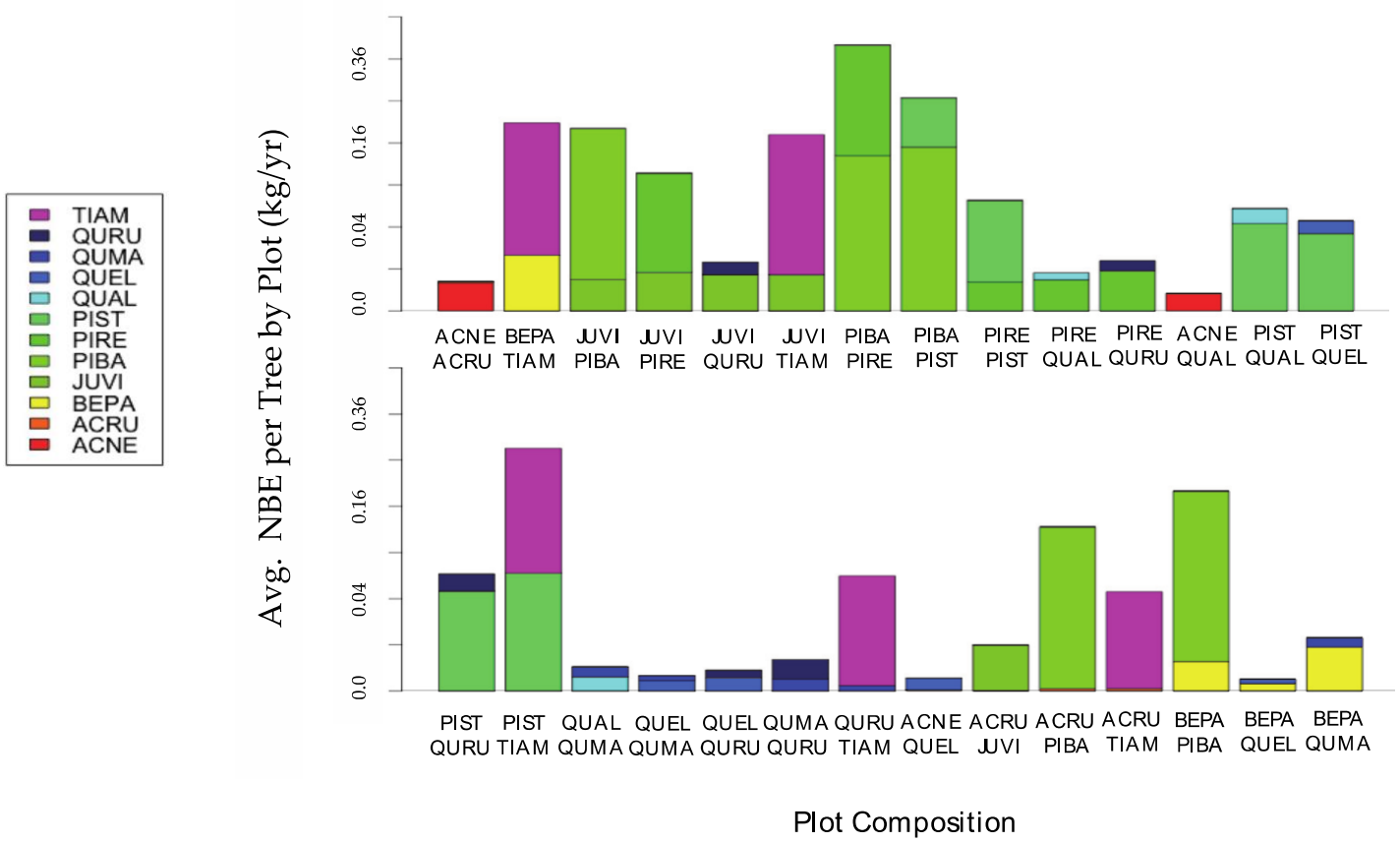
Supplementary Figure 1.3 - Overyielding in biomass (kg/yr; square root-transformed with sign retained) in 2014-2015 by Species Richness, demonstrating significant trasngressive overyielding at all levels of SR. Data from 2013-2014 display a similar trend.



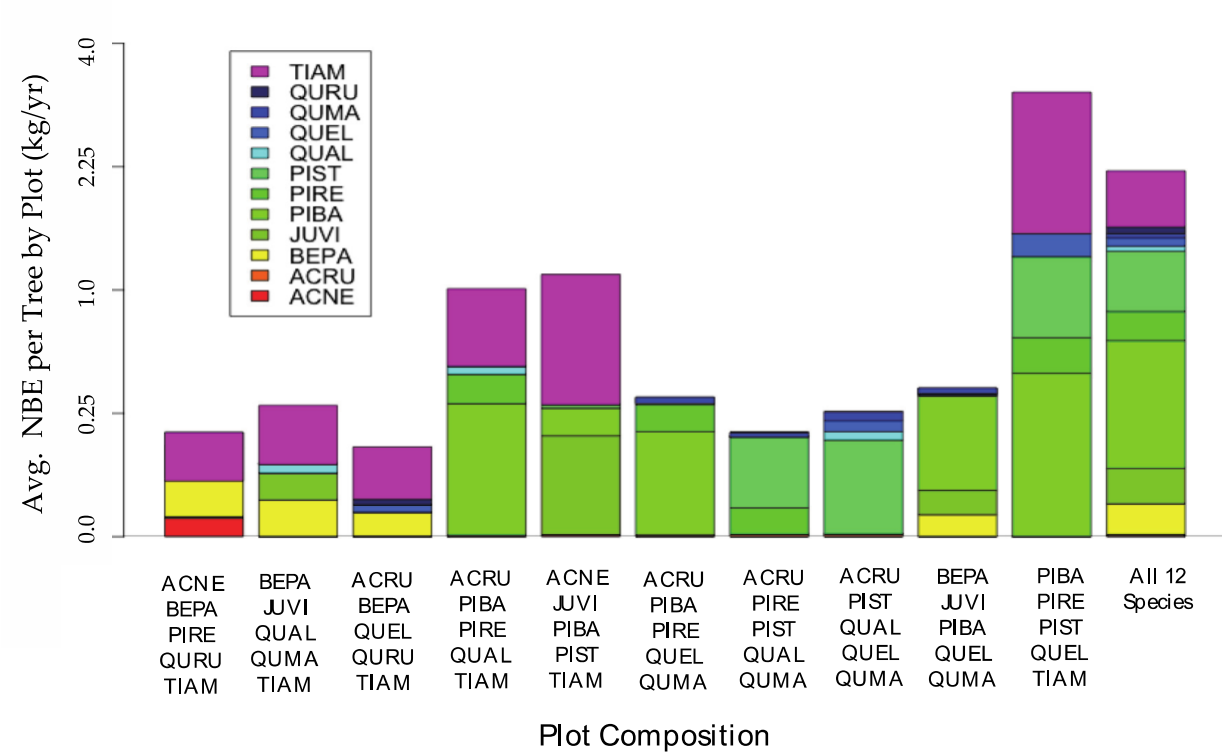
Supplementary Figure 1.4 - Histogram showing Complementarity Effects (blue) and Selection Effects (red; both are given in kg/yr). The two components of overyielding add to give NBE for a particular plot. Bar heights shown the number of plots within a binned range of complementarity effects or selection effects. Data from 2013-2014 display a similar trend.



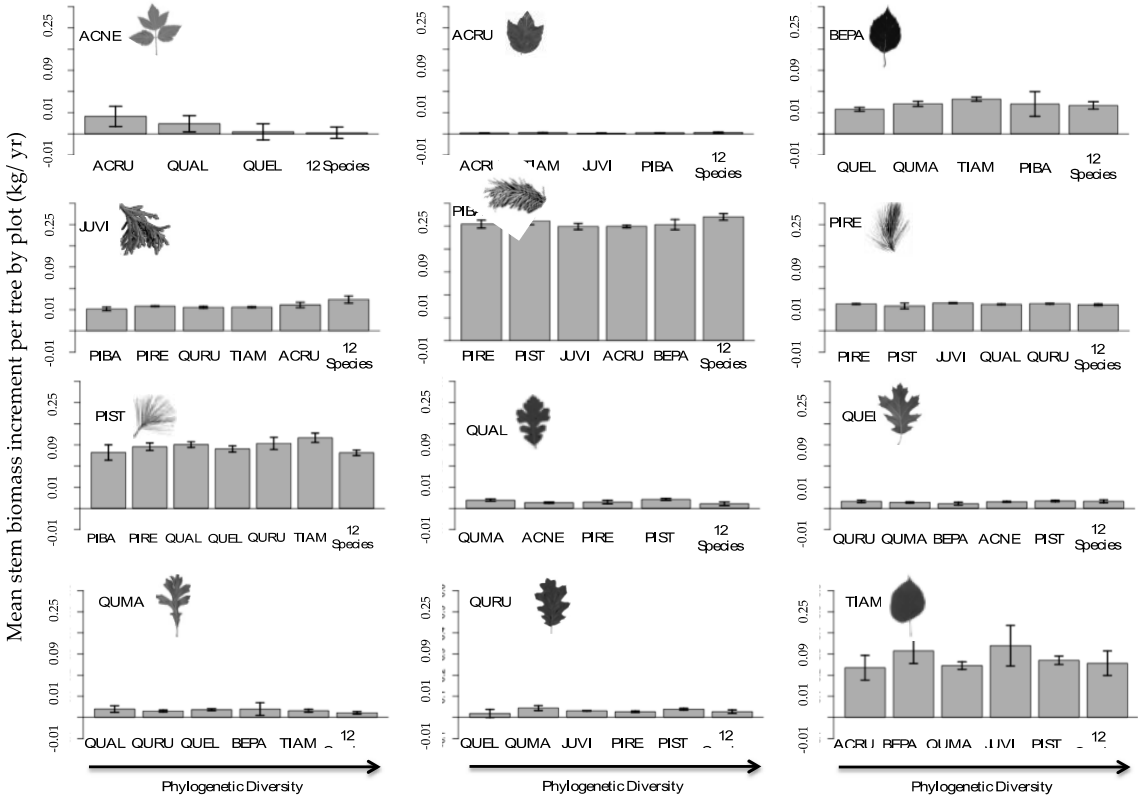
Supplementary Figure 1.5 - Square root of mean per-capita aboveground change in stem biomass from 2014-15 (kg/year) by bicultural composition.
The height of each bar gives the total of all species average per-capita growth, so higher bars indicate that species overyielded more. Each bar is split to indicate constituent species' contribution to overyielding, with each colored bar segment giving the per-capita overyielding value for a given species. Species are color-coded, and the first species listed below the x-axis corresponds to the bar segment closer to the x-axis.



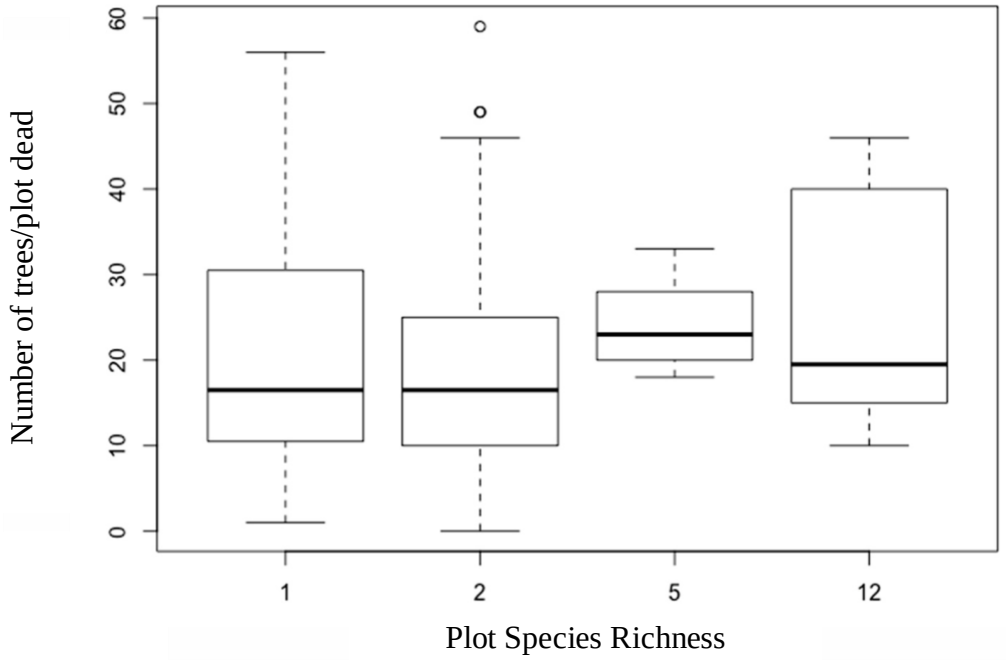
Supplementary Figure 1.6 - Square root of mean per-capita aboveground change in stem biomass from 2014-15 (kg/year) by five-species or 12-species polycultural composition. The height of each bar gives the total of all species average per-capita growth, so higher bars indicate that species overyielded more. Each bar is split to indicate constituent species' contribution to overyielding, with each colored bar segment giving the per-capita overyielding value for a given species. Species are color-coded as in Supplementary Figure 1.1. Additionally, the first species listed below the x-axis corresponds to the bar segment closer to the x-axis, and the last species listed below the axis corresponds to the bar segment farthest from the axis.



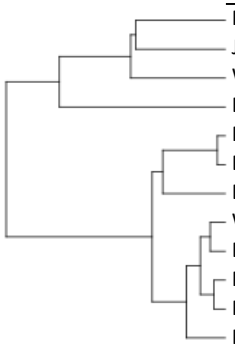
Supplementary Figure 1.7 - Square root of mean aboveground increase in stem biomass (kg/year) per tree for the 2014-15 growing season in all biculture and twelve-species plots. Error bars are standard errors. Five-species plots were not compositionally replicated, and so are not included. Each panel displays information for a focal species, the code of which is displayed in the upper left corner of the panel. The height of each column displays the focal species' per-capita growth rate when grown with the species whose name is given at the base of the column. Error bars give one standard error, with plots serving as replicates. A value of zero indicates no growth. Columns are ordered by Faith's Phylogenetic Diversity (FPD) as in Fig. 1.4.



Supplementary Figure 1.8 - Number of trees per plot of 64 trees that died from Fall 2014 –Fall 2015 vs. Species Richness of each plot. Trees were replanted each spring. Tree mortality here includes trees that died in summer and winter 2014 and were replanted in May 2015.

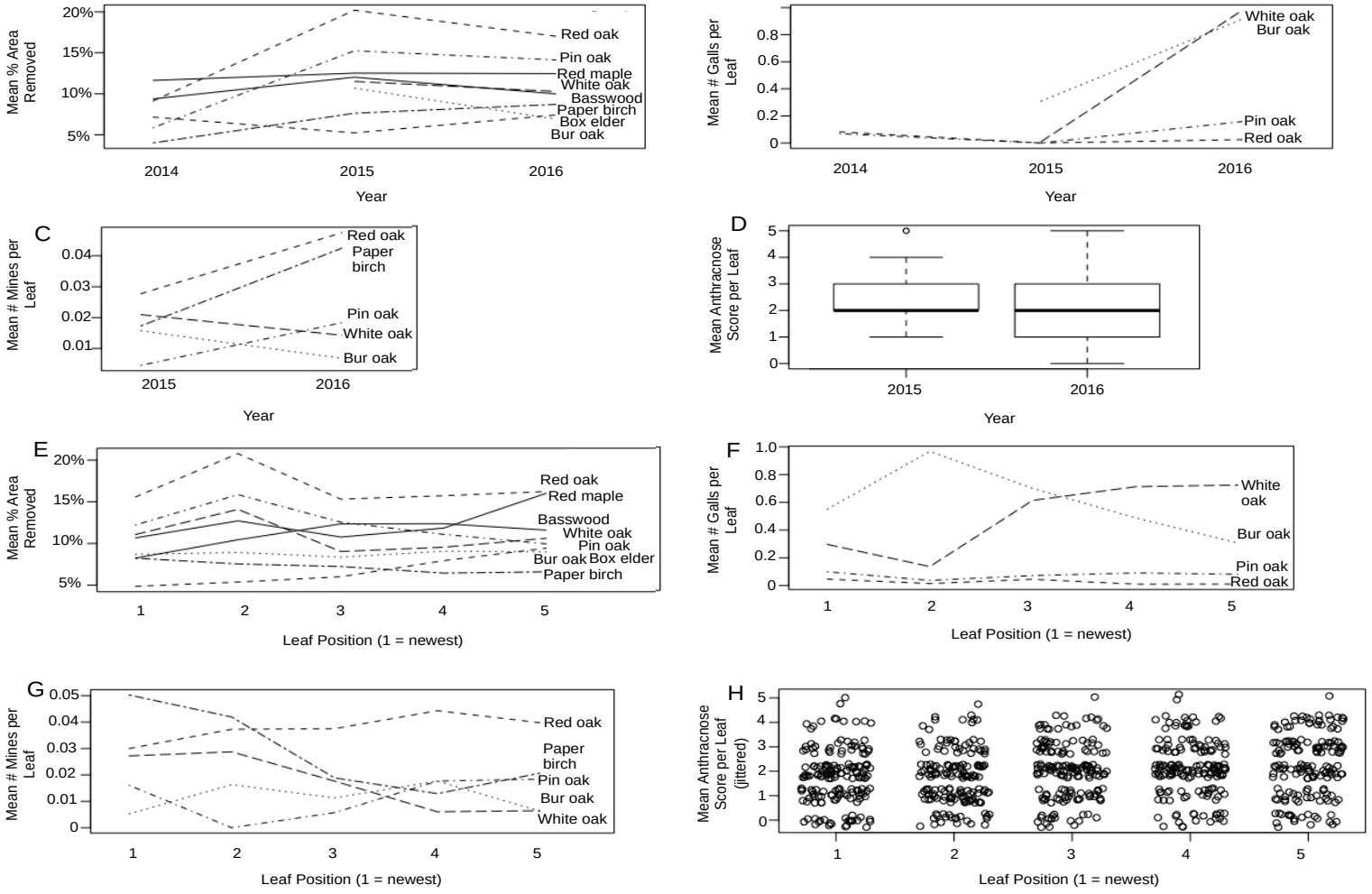


Supplementary Figure 2.1 – Species-level means of trait values for all FAB species. Trait measurements were collected from mature trees in and adjacent to the FAB experiment in eastern Minnesota, USA. Phylogeny adapted from Zanne et al. (2014).



Species	Specific Leaf Area (cm^2/g)	Relative Water Content (% wet mass)	Leaf Lignin (% dry mass)	Leaf Nitrogen (% dry mass)	Leaf Phosphorus (% dry mass)	Condensed Tannins (% dry mass)
Red pine (*Pinus resinosa*)	26.2	51.4%	16.4%	0.35%	0.04%	22.1%
Jack pine (*Pinus banksiana*)	35.1	62.2%	24.0%	0.60%	0.07%	18.3%
White pine (*Pinus strobus*)	65.3	53.6%	30.0%	0.74%	0.19%	7.7%
Eastern red cedar (*Juniperus virginiana*)	32.4	63.6%	25.8%	1.69%	0.18%	2.0%
Red maple (*Acer rubrum*)	178.2	60.4%	12.5%	0.67%	0.15%	4.7%
Box elder (*Acer negundo*)	166.6	71.7%	17.2%	1.47%	0.23%	7.0%
Basswood (*Tilia americana*)	368.7	72.9%	13.9%	1.21%	0.28%	12.1%
White oak (*Quercus alba*)	156.7	58.0%	16.2%	0.81%	0.17%	3.9%
Bur oak (*Quercus macrocarpa*)	94.4	59.3%	20.8%	1.96%	0.28%	5.0%
Pin oak (*Quercus ellipsoidalis*)	116.7	58.6%	26.6%	1.32%	0.20%	6.8%
Red oak (*Quercus rubra*)	136.0	54.9%	22.0%	0.90%	0.12%	4.0%
Paper birch (*Betula papyrifera*)	225.1	69.5%	20.4%	0.90%	0.26%	5.4%

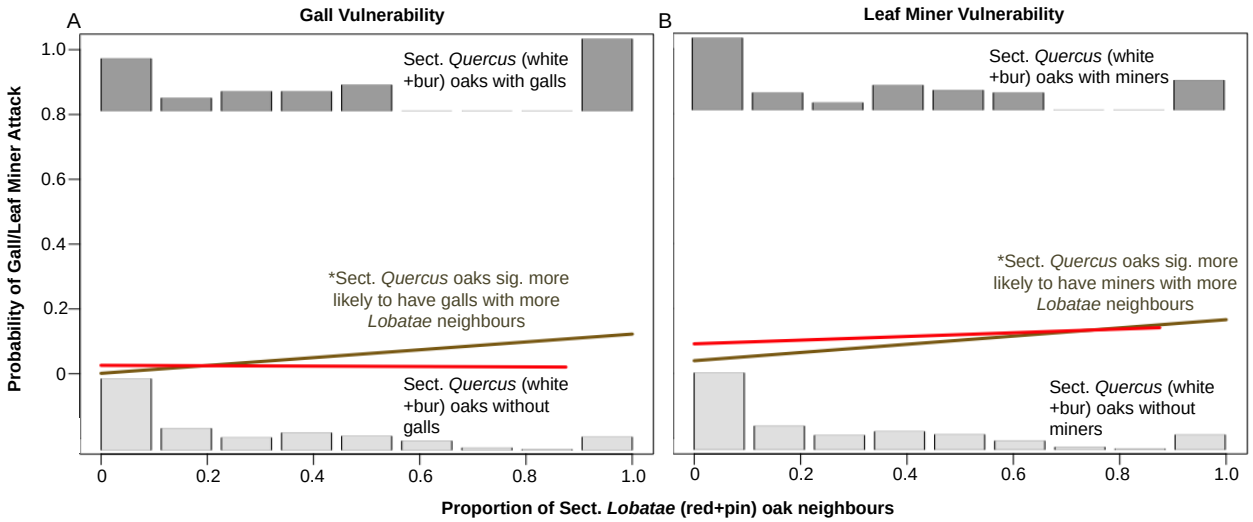
Supplementary Figure 2.2 – Effects of study year (A-D) and leaf position (E-H; with "1" indicating the newest fully expanded leaf and "5" indicating the fifth newest) on leaf removal (A, E), oak galling (B, F), oak and birch leaf mining (C, G), and red maple anthracnose infection (D, H). The



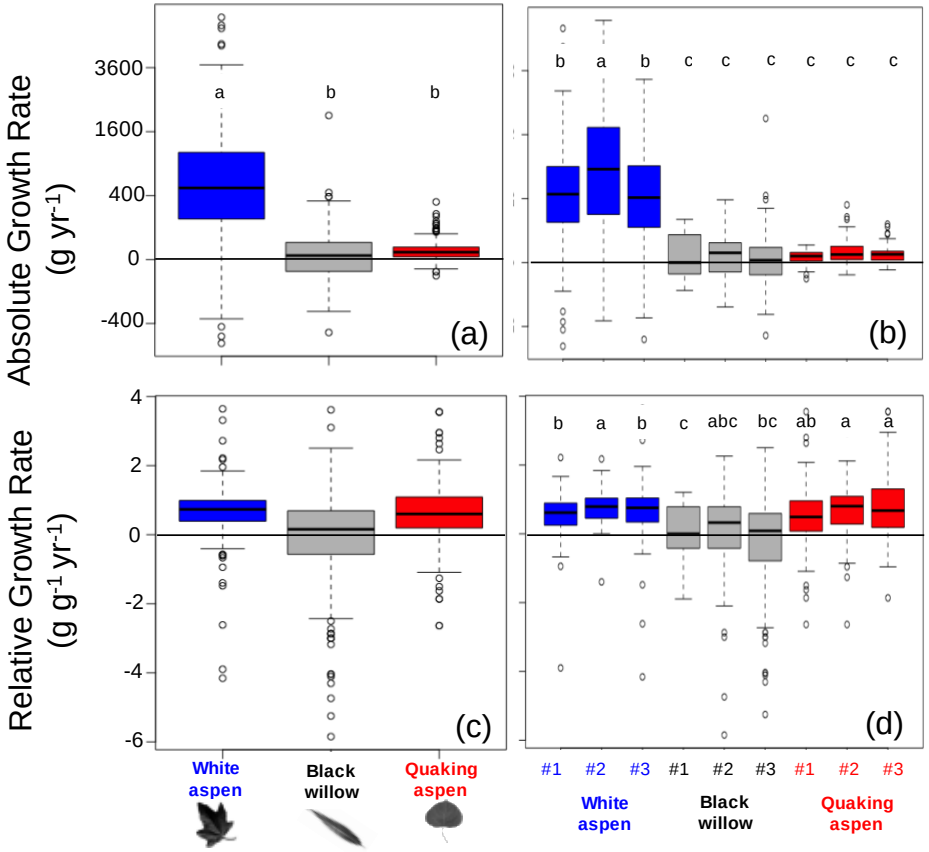
Supplementary Figure 2.2 (cont.)

relationship between damage from natural enemies and year or leaf position is significant and interacts with species for all plots shown except that of leaf miner damage vs. year (C); differences in leaf miner damage by year were not significant, but species differences were.

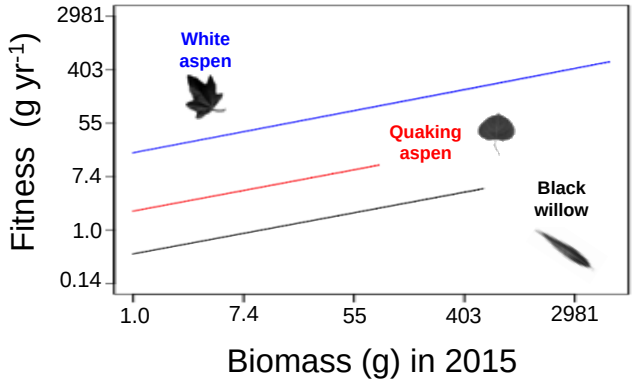
Supplementary Figure 2.3 – Trees in the white oak clade (*Quercus* Sect. *Quercus*; white and bur oak) were significantly more likely to experience galling than trees in the red oak clade (*Quercus* Section *Lobatae*; red and pin oak). Additionally, oaks in the white/*Quercus* clade were more vulnerable to both galling (A) and leaf mining (B) when they had additional neighbours in the red/*Lobatae* clade. The reverse was not true nor was having neighbours from the same clade associated with differences in galling or mining. We speculate that the associational susceptibility of white oaks in the presence of red oak neighbours to specialist herbivores may be due to host dilution (Otway et al. 2005). White oak specialists may congregate on available white oak hosts, increasing in density in the presence of many non-host red oaks.



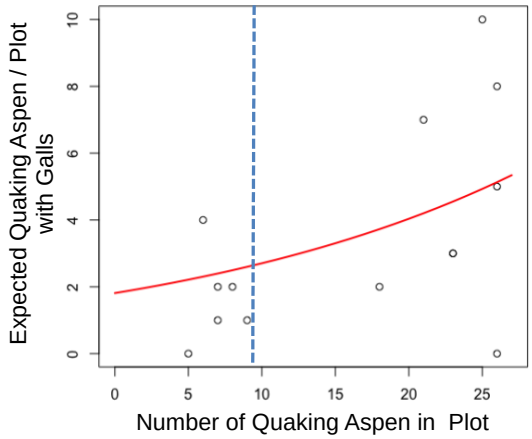
Supplementary Figure 3.1 – Effect of species (a,c) and genotype (b,d) identity on absolute (a,b; g yr^{-1}) and relative (d,d; g g^{-1} yr^{-1}) growth rate, 2015-2016. Groups of trees with different means (by Tukey post-hoc test, $\alpha = 0.05$) are indicated by letters above bars. Panels without letters present data with statistically indistinguishable means. The central horizontal bar in each boxplot displays the median growth rate.



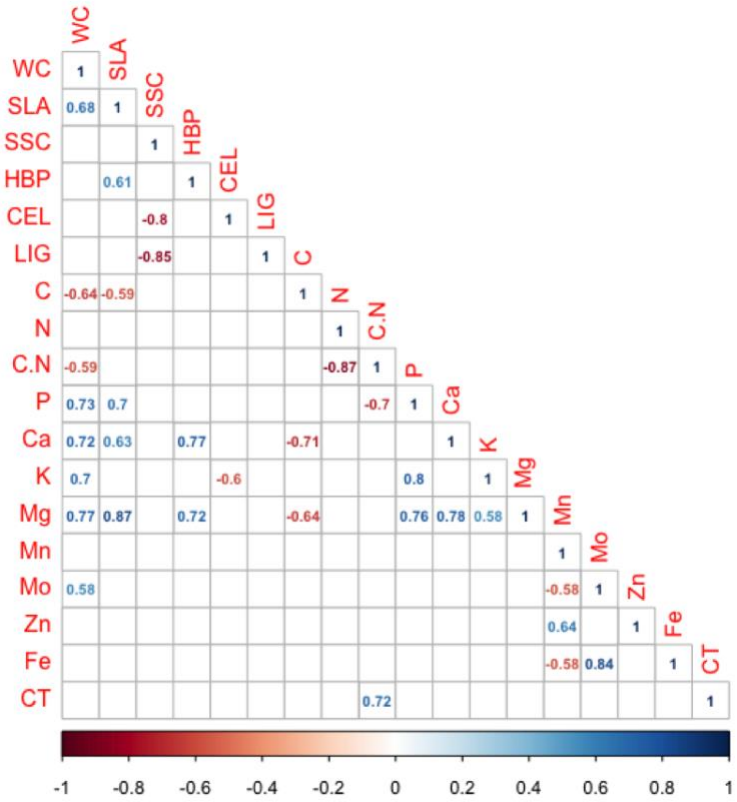
Supplementary Figure 3.2 – Species varied in fitness (g yr^{-1}), as determined by conditional aster models (Table 3.2). Plant size was log-transformed for analysis so that all species could be included in the same aster model. Predicted fitness for individuals for each species is displayed across the range of sizes documented in the experiment.



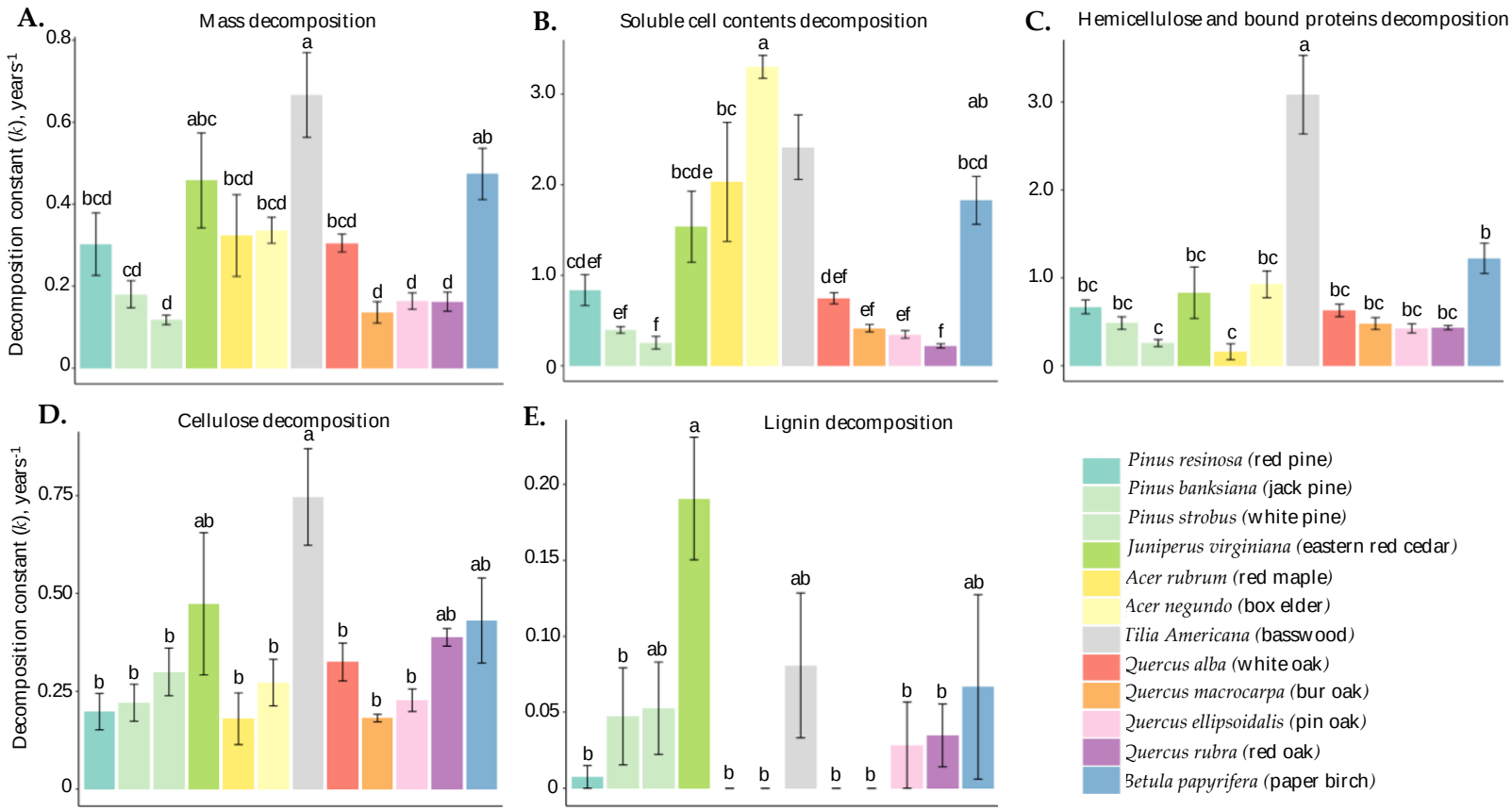
Supplementary Figure 3.3 – Rarefaction curve (red) showing expected number of quaking aspens with galls versus number of quaking aspens in a given plot. Predictions are based on gall counts in 1S1G, 1S3G, and 3S3G plots. Rarefaction indicates that in a 3S9G plot with nine quaking aspens (blue line), roughly two trees ought to have galls. In contrast, we did not find any galled quaking aspens in 3S9G plots.



Supplementary Figure 4.1 – Crlations of leaf litter functional traits across the 12 species included in litterbags. Significant correlations at $\alpha = 0.10$ are printed below in blue (positive correlation coefficients) and red (negative correlation coefficients). Traits are listed as in Supplementary Table 4.2 and abbreviated using standard chemical abbreviations or as WC (relative water content), SLA (specific leaf area), SSC (solube cell contents), HBP (hemicellulose and bound proteins), CEL (cellulose), LIG (acid unhydrolyzables; lignin), C.N. (carbon to nitrogen ratio), and CT (condensed tannins).



Supplementary Figure 4.2 – Species-level decomposition constants (*k*; years^{-1}) for mass (A), and all carbon fractions (B-E). Letters above columns indicate the results of Tukey post-hoc testing at the 0.10 level; values of *k* for species that share a letter are not significantly different. Error bars indicate standard error.



Supplementary Figure 4.3. Species-level changes in the percentage of initial litter A) mass, B) soluble cell contents, C) hemicellulose and bound proteins, D) cellulose, and E) lignin remaining at four points over two years of decomposition. Error bars indicate standard error based on three replicate sets of bags with the same composition. Species differed in decomposition of mass and all carbon fractions. Total mass, soluble cell contents, hemicellulose and bound proteins, and cellulose in litter of each species degraded over two years. Lignin did not substantially degrade for any species except *Juniperus virginiana* (eastern red cedar; yellow-green). Lignin mass remaining values in excess of 100% may reflect the presence of microbially produced lignin-like compounds or of allocthonous lignin that migrated into litter during decomposition.