12-2014

Plant functional traits mediate above- and belowground species interactions in ecological communities

Courtney E. Gorman
University of Tennessee - Knoxville, cgorman5@vols.utk.edu

Recommended Citation

Gorman, Courtney E., "Plant functional traits mediate above- and belowground species interactions in ecological communities. " Master's Thesis, University of Tennessee, 2014.
https://trace.tennessee.edu/utk_gradthes/3150

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I am submitting herewith a thesis written by Courtney E. Gorman entitled "Plant functional traits mediate above- and belowground species interactions in ecological communities." I have examined the final electronic copy of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

Joseph K. Bailey, Major Professor

We have read this thesis and recommend its acceptance:

Daniel Simberloff, Charlie Kwit

Accepted for the Council:
Carolyn R. Hodges

Vice Provost and Dean of the Graduate School

(Original signatures are on file with official student records.)

Plant functional traits mediate above- and belowground species interactions in ecological communities

A Thesis Presented for the

Master of Science

Degree

The University of Tennessee, Knoxville

Courtney E. Gorman

December 2014

ACKNOWLEDGEMENTS

I would like to acknowledge Joe Bailey, Jen Schweitzer, and Mark Genung for their support and guidance. I thank my graduate committee members, Dan Simberloff and Charlie Kwit, for their support and frequent helpful comments. I would also like to acknowledge the CRC for Forestry and Forestry Tasmania for supporting the trial establishment and providing the trial site used for the research presented in Chapter I. Additionally I would like to acknowledge my classmates in Field Ecology who contributed greatly to the research presented in Chapter II, and the Tennessee Valley Authority for establishing and providing information about the monoculture plots that we used.

ABSTRACT

Functional plant traits provide a means whereby species identity can influence above- and belowground community interactions. To examine the role of plant functional traits in shaping ecological communities, Chapter I examines how the evolution of functional differences between closely related groups of endemic and non-endemic species influence associated species interactions, and Chapter II examines how plant functional traits can influence associated community composition.

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INTRODUCTION

Biodiversity has profound consequences on community interactions and ecosystem processes. To determine the significance of biodiversity, many studies have examined the role of species richness (i.e. the number of species represented in an ecological community) in community and ecosystem processes (Naeem et al. (1994, 1995, 1996), Tilman *et al.* 1996, Hector *et al.* 1999, Tilman *et al.* 2001). For example, one early study examined the impacts of plant diversity (number of species) on primary productivity in European grassland communities, and found that average aboveground biomass declined with the reduction of species (Hector *et al.* 1999). Additionally, several other studies have reported negative effects of species loss on community productivity (Schläpfer and Schmid 1999, Schwartz et al. 2000). However, it is important to note that many additional studies have failed to find consistent effects, resulting in a heated debate in the literature (Hodgson et al. 1998, Huston et al. 2000). Regardless, studies such as these have undeniably improved our understanding of the effects of biodiversity on ecosystem function. Furthermore, they have substantially influenced how conservation efforts are prioritized. For example, it has been suggested that the conservation of biodiversity hotspots (hotspot being defined as an area harboring at least 1500 endemic plant species and having lost 70% of its primary vegetation) is the “silver bullet strategy” for conservation efforts (Myers et al. 2000). This hotspot approach to conservation gained popularity and effectively influenced the channeling of conservation spending to areas with unusually high species richness and many endemic species (Dalton 2000, Kareiva & Marvier 2003, Halpern et al. 2006). It is now a popular scientific paradigm that areas with high species richness and large concentrations of rare and/or endemic species have high biological value, and should therefore warrant the primary focus of conservation efforts. However, within this idea lies a simple question that has rarely been considered: Are these species different, ecologically?

To fully comprehend the ecological effects of biodiversity, examining the consequences of diversity that extend beyond traditional taxonomic classification is necessary (Diaz & Cabido 2001, Cornelissen *et al.* 2003). It is now accepted that other factors such as number and composition of genotypes, species, and functional groups in an ecological system are critical aspects of biodiversity, with functional diversity being of particular importance (Diaz & Cabido 2001). The functional diversity (i.e. range and value of plant functional traits) of species is an especially important component of biodiversity, as it strongly predicts ecosystem functioning (Diaz & Cabido 2001, Hooper et al. 2005). Given that plant functional traits are those that delimit species in their ecological roles (i.e. how they interact with other species and the environment), they inherently influence ecosystem properties (Diaz & Cabido 2001, Hooper et al. 2005). For example, leaf traits such as toughness**,** nutrient concentration, and photosynthetic capacity can mediate ecosystem processes such as carbon assimilation and mineral nutrient cycling (e.g. nitrogen and phosphorus) (De Deyn et al. 2008). Moreover, leaf traits such as chemical defenses, toughness, and lifespan have the potential to influence associated species interactions, such as herbivory (Westoby and Wright 2006). These properties, coupled with the fact that many functional traits are fairly easy and inexpensive to measure for large numbers of individuals, make them particularly valuable in addressing ecological questions at the levels of communities or ecosystems (Cornelissen *et al.* 2003). Although plant functional traits clearly play a substantial role in community and ecosystem processes, we are far from having a robust understanding of the interplay among taxonomic richness, functional diversity, and community structure (Hooper et al. 2005).

Functional plant traits provide a conduit whereby species identity can influence community interactions and ultimately ecosystem processes. To further elucidate the ecological relationships between taxonomic diversity, functional diversity, and community structure, I examine how the evolution of functional differences between closely related endemic and non-endemic species influences associated species interactions (Chapter I), and then examine the role of plant functional traits as linkages between above- and belowground communities, and their impacts on community composition (Chapter II).

CHAPTER I

SHIFTS IN SPECIES INTERACTIONS DUE TO THE EVOLUTION OF FUNCTIONAL DIFFERENCES BETWEEN ENDEMICS AND NON-ENDEMICS

A version of this chapter has been published in *PLOS ONE* by Courtney E. Gorman, Brad M. Potts, Jennifer A. Schweitzer, and Joseph K. Bailey.

Abstract

Species ranges have been shifting since the Pleistocene, whereby fragmentation, isolation, and the subsequent reduction in gene flow have resulted in local adaptation of novel genotypes and the repeated evolution of endemic species. While there is a wide body of literature focused on understanding endemic species, very few studies empirically test whether or not the evolution of endemics results in unique function or ecological differences relative to their widespread congeners; in particular while controlling for environmental variation. Using a common garden composed of 15 *Eucalyptus* species within the subgenus *Symphyomyrtus* (9 endemic to Tasmania, 6 non-endemic), here we hypothesize and show that endemic species are functionally and ecologically different from non-endemics. Compared to non-endemics, endemic *Eucalyptus* species have a unique suite of functional plant traits that have extended effects on herbivores. We found that while endemics occupy many diverse habitats, they share similar functional traits potentially resulting in an endemic syndrome of traits. This study provides one of the first empirical datasets analyzing the functional differences between endemics and non-endemics in a common garden setting, and establishes a foundation for additional studies of endemic/non-endemic dynamics that will be essential for understanding global biodiversity in the midst of rapid species extinctions and range shifts as a consequence of global change.

Introduction

Species ranges have been shifting since the Pleistocene (Davis & Shaw 2001), whereby fragmentation, isolation, and the subsequent reduction in gene flow have resulted in local adaptation of novel genotypes and the repeated evolution of endemic species. Endemic species have long been valued for their novelty by both the general and scientific communities, which has resulted in a vast body of evolutionary and natural history research (Kruckeberg & Rabinowitz 1985, Kunin & Gaston 1993, Ferreira & Boldrini 2011). However, in the midst of a biodiversity crisis where species extinction rates are 100 to 1000 times greater than the background geological rate (Pimm & Russell 1995), understanding the biology of endemic species has become a priority rather than a pursuit of novelty, as these species are often the ones most at risk (Cowling 2000). Studies have investigated the causes and consequences of endemism (Kruckeberg & Rabinowitz 1985, Kunin & Gaston 1993, Ferreira & Boldrini 2011), the geography, risks, and prospects of endemic species (Myers *et al.* 2000, Dirzo & Raven 2003, Kier *et al.* 2009, Caujapé-Castells *et al.* 2010), as well as the genetic differences between endemic (or rare/narrowly distributed) vs. widespread species (Karron 1987, Gitzendanner & Soltis 2000, Cole 2003). The literature is generally lacking, however, in studies that attempt to investigate the ecological significance of endemic species. Because the formation of relict populations and the evolution of endemic species is thought to be a major consequence of species range shifts due to climate change (Hampe & Petit 2005), identifying whether endemics are functionally different and support unique species interactions may place even greater conservation value on these populations and species.

Linking evolutionary history to contemporary ecological interactions is a burgeoning field that is bringing with it many new insights into the relationship between biodiversity, species interactions, and ecosystem function (Cadotte *et al.* 2010). Despite studies on their evolutionary novelty, few studies have experimentally investigated the ecological differences between endemic species and their non-endemic congeners or how endemicity may influence species interactions; particularly while controlling for environmental variation. A 2003 study measured net photosynthesis, leaf nitrogen content, and specific leaf area of 78 crop, endemic, and non-endemic plant species (Gulias *et al.* 2003). They noted variation between endemic and non-endemic species, however did not find statistical significance for the observed differences between any of the measured parameters in the field. Additionally, a recent study compared traits of 20 congeneric pairs of endemic and widespread plant species and while they found that endemics were smaller and produced fewer flowers, they found no differences in traits related to resource acquisition, resource conservation, and patterns of herbivory (Lavergne *et al.* 2004). While these studies provide a valuable basis for understanding the ecological differences between endemic and non-endemic species, they are limited in the inferences that they can make, since traits were measured *in situ* rather than in an experimental common garden and are thus influenced by a range of environmental variables. Common garden experiments provide an opportunity to more accurately partition genetic and environmental components of trait variation when attempting to characterize the ecology of a set of species (Reich *et al.* 2005) and provide a powerful tool for linking evolutionary history to contemporary ecological interactions.

Endemic species have frequently been characterized based on generalizations of their perceived commonalities, such as low genetic diversity (Stebbins 1942), (Karron 1987, Gitzendanner & Soltis 2000, Cole 2003) and limited reproduction and dispersal abilities (Gottlieb 1979, Cowling 2000). For example, a 2000 study summarized the generalizations that are often made regarding the reproductive biology of endemic species as an increased tendency for self-compatibility, lower investment in reproduction, poorer dispersal abilities, and shorter generation times in comparison to common species (Cowling 2000). Although attempts have been made to characterize endemic species based on their shared traits, the extent of this convergence on an endemic syndrome of traits remains unclear, along with how these shared differences may influence species interactions differently than those of common species. Here we hypothesize that endemic species are a homogenous group that can be characterized based on commonalities that result from isolation and lead to an 'endemic syndrome'.

The genus *Eucalyptus* in Tasmania provides an ideal natural system for examining an endemic syndrome among congeners, as the island has 29 native eucalypts from two subgenera, 17 of which are endemic to the island of Tasmania, while the others also occur on the Australian mainland (Williams & Potts 1996). We used a common garden with 15 *Eucalyptus* species (9 endemic, 6 non-endemic) to test the hypothesis that functional plant traits and associated patterns of herbivory of endemic species differ from those traits in closely related non-endemic species. To our knowledge this is the first endemic/non-endemic comparative study to use an experimental common garden design to separate differential environmental conditions as explanatory variables. Here we show that endemic plant species are ecologically different than non-endemics. We show that these differences include functional plant traits with extended effects across trophic levels. Furthermore, we found that while endemics occupy many diverse habitats (from loamy sites near sea-level to alpine scrub), they share similar functional traits potentially resulting in an endemic syndrome of traits.

Material and Methods

Common Garden

In order to test whether endemic species are ecologically different than non-endemics without the constraints of environmental/habitat variation, we used a common garden experiment. The common garden was part of a forestry trial established by The Cooperative Research Centre for Forestry (CRC). This experimental forest trial was established in 2009 with 15 species of closely related Eucalypts native to Tasmania that occur in the subgenus *Symphyomyrtus* (Williams & Potts 1996). Nine of these species are endemic to Tasmania, while the other 6 are native non-endemics that also occur on the Australian mainland. Both groups of species exhibit a widespread distribution within Tasmania and co-occur throughout the state. Non-endemic species included in the trial were *E. dalrympleana, E. rubida*, and *E. viminalis, E. brookeriana*, and *E. ovata* and *E. perriniana*. Endemic species included in the trial were *E. johnstonii*, *E. subcrenulata*, and *E. vernicosa*, *E. archeri, E. cordata, E. gunnii, E. morrisbyi*, and *E. barberi* and *E. rodwayi*. The endemic species included in the trial occupy a diverse variety of habitats ranging from loamy sites near sea-level (*E. cordata* and *E. morrisbyi*), poorly drained montane forest (*E. johnstonii*), well-drained subalpine rainforest (*E. subcrenulata*), and alpine scrub (*E. vernicosa*) (Williams & Potts 1996). Each species was represented by an average of four open-pollinated families collected from native trees in Tasmania with between 1 and 17 plants per family. Individuals were planted in rows that were 36 trees long. Plant positions within a row were allocated randomly, and the total sample size was 412 trees. Both mammalian and insect herbivores had unrestricted access to the garden. No specific permissions were required to carry out this study and field studies did not involve endangered or protected species.

Plant Measurements

To quantify differences between endemics and their closely related non-endemic species, common plant functional traits (height, internode length, leaf thickness, and specific leaf area (SLA)) and herbivory were measured in 2011 on 4 year-old plants. Total tree height was measured to the nearest cm. Two random shoots and two fully expanded leaves were collected from the terminal stems of each tree (juvenile foliage) for measurements of shoot and leaf functional traits. Internode lengths (in mm) were measured on these shoots as the length between the first two fully expanded leaves; typically the 4th and 5th plastochron. Leaf thickness (in mm) was measured with digital calipers. Leaf length, width and area were estimated from the leaf samples using the imaging program ImageJ. Leaves were oven-dried at 70° C for 48 h. Specific leaf area (SLA) was calculated as the leaf area/average dry weight (cm^2/g) for each leaf.

To understand how potential functional differences between the endemic and non-endemic species might influence the response of interacting species, we quantified herbivory by common mammals and arthropods. Herbivory was estimated in three ways: total insect folivory on the whole tree, insect folivory on the most damaged branch, and total mammal browsing damage. Total insect folivory was visually surveyed and characterized as percent foliar tissue removed from 1-100 percent (i.e., 0, 1, 2, 3, 5, 10, 20, continuing in 10% increments). Because herbivory is often not uniform across an individual tree, a second survey was conducted on the most damaged branch of each tree using the same methodology. Characteristic shoot clipping by mammal browsing (O'Reilly-Wapstra *et al.* 2002), typically by *Trichosurus vulpecula* (common brushtail possum) and *Thylogale billardierii* (red-bellied pademelon), was estimated on each tree as a total damage score. Scores were characterized as the percentage of shoot tips clipped from each tree (using the same scale as insect survey's described above).

Statistical Analyses

The data were analyzed using mixed effect models and Restricted Maximum Likelihood (REML) using the statistical program JMP 10. We tested for quantitative differences in several plant functional traits (height, internode length, leaf thickness, and specific leaf area (SLA)), as well as herbivory between endemic species and non-endemics. We used a conservative approach and constructed a mixed model that included seed family nested within tree species and row as random effects to account for variance explained by these factors that would otherwise contribute to differences between endemics and non-endemics. Endemism/non-endemism and tree species nested within endemism were included as fixed effects. Additionally, to account for multiple comparisons of traits between endemic and non-endemic species, we used the function 'p.adjust' in R (2.15.3) (R Core Team 2013) to apply a Holm-Bonferroni correction to estimates of significance.

Because the divergence of *Eucalyptus* species in the subgenus *Symphyomyrtus* has been relatively recent, resolution of phylogenetic relationships at the species level has not been possible with standard DNA sequence markers (Steane 1999, Steane *et al.* 2002, McKinnon *et al.* 2008). This makes it impossible to use advanced comparative methods such as phylogenetically independent contrasts (PIC) to account for phylogenetic dependency of our data. In an attempt to account for phylogenetic dependency, we took a conservative approach and constructed a mixed model identical to the one above but that also included clade as a fixed effect. Clade was defined by taxonomic series (Ovatae or Viminales; (Williams & Potts 1996). Species included in the series Ovatae were *E. brookeriana, E. barberi, E. ovata,* and *E. rodwayi*, and species included in the series Viminales were *E. archeri, E. cordata, E. dalrympleana, E. gunnii, E. johnstonii, E. morrisbyi, E. perriniana, E. rubida, E. subcrenulata, E. vernicosa,* and *E. viminalis.*

Additionally, regression analyses were used to examine the relationships between plant functional traits (height, internode length, leaf thickness, and SLA) and percent foliar herbivory. Because variation in functional traits can reflect niche differentiation, we compared suites of functional traits that differed between endemic and non-endemic species using a two-dimensional ordination of multivariate data using Nonmetric Multidimensional Scaling (NMDS) (R 2.15.3, vegan package) (Oksanen *et al.* 2013). A distance matrix was constructed using Euclidean distances based on the values of functional plant traits and patterns of herbivory, which were standardized by maximum resemblance for all individuals in the study. Differences were quantified using ANOSIM (analysis of similarity) (R 2.15.3, vegan package) (Oksanen *et al.* 2013), a non-parametric method for determining if there is significant variation between groups of samples based on a Euclidean distance (Clarke 1993).

Results

The endemic species differed from non-endemic species in functional plant traits. Height, internode length, leaf thickness, and specific leaf area varied significantly between endemic and non-endemic *Eucalyptus* species (**Table 1**, **Figure 1**). The endemic species had 22% thicker leaves (Figure 1E) and 9% lower average SLA (Figure 1F) than the non-endemic congeners. The endemics also had 23% shorter internodes (Figure 1D) and were 18% shorter in height (Figure 1C) than their non-endemic congeners (Table 1). The Holm corrected estimates of significance generally supported our inferences from uncorrected p-values (Table 1). When the functional traits were combined in a multivariate framework, there were significant differences between the endemic and non-endemic species (**Figure 2**, ANOSIM: R= 0.119, p<0.001) providing evidence of an endemic syndrome of traits. Endemic species also exhibited less herbivory than non-endemic species. The endemic species had 40% less total insect folivory (Figure 1A) and 44% less herbivory on the most damaged branch (Figure 1B) than the non-endemics (Table 1). Additionally, the response of insect herbivores was correlated with plant functional traits (height, internode length, leaf thickness, and specific leaf area) (**Table 2**). Significant differences in mammal browsing were not detected (p=0.502); all trees experienced ~10.5% of mammal damage.

It is also possible that shared evolutionary history could influence the differences between endemic and non-endemic species in functional traits. When evolutionary history was accounted for in the mixed model, the levels of significance of endemism as a fixed effect did not change (**Table 3**), suggesting that shared evolutionary history was not driving the differences in functional traits or patterns of herbivory.

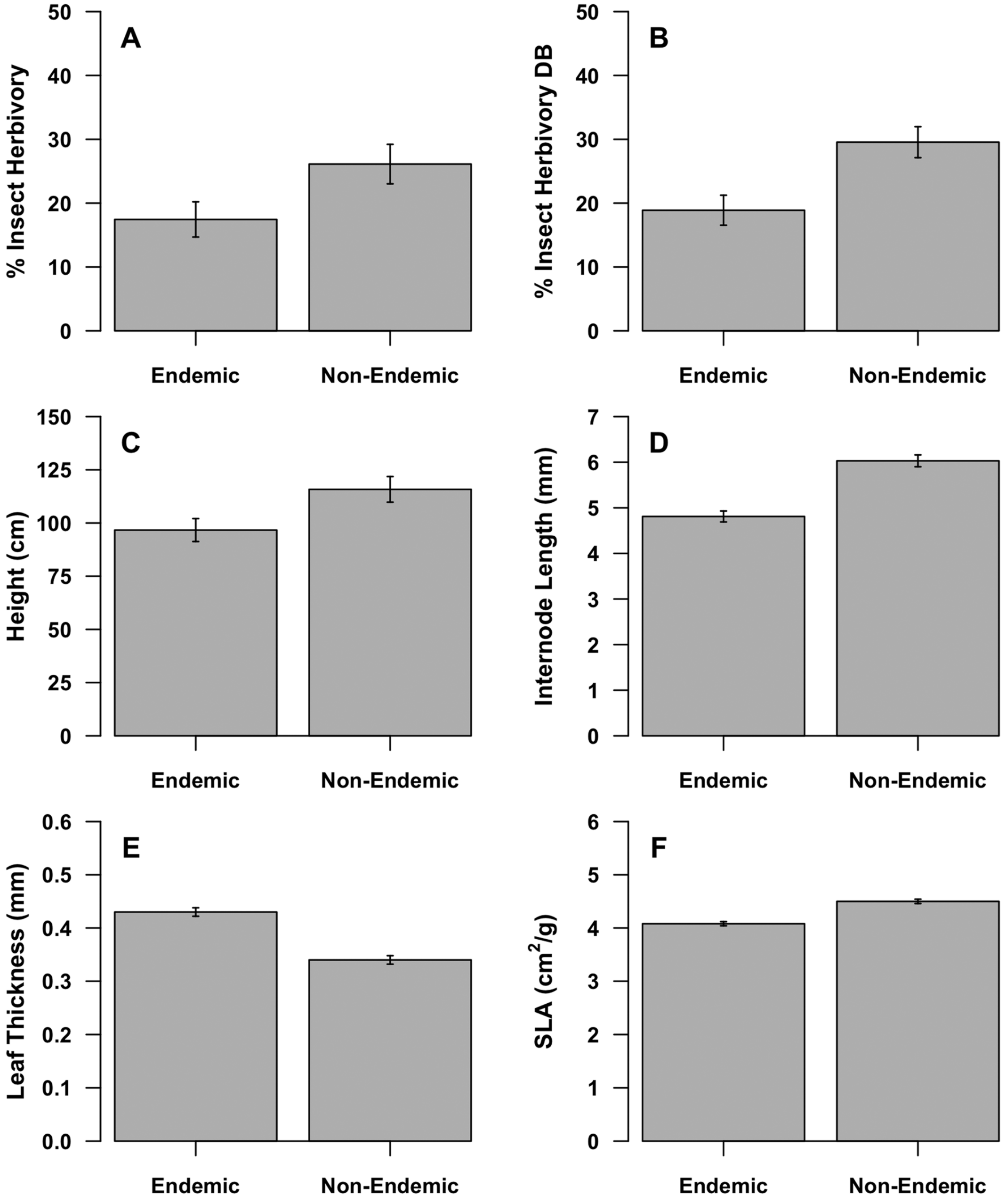

Figure 1. Functional traits and herbivory differ between endemic and non-endemic *Eucalyptus* species. Variation in plant functional traits and insect herbivory: A) total foliar herbivory (B) foliar herbivory on the most damaged branch (DB), (C) height, (D) internode length, (E) leaf thickness, (F) specific leaf area (SLA). Total sample size was 412 trees. Error bars represent the standard error

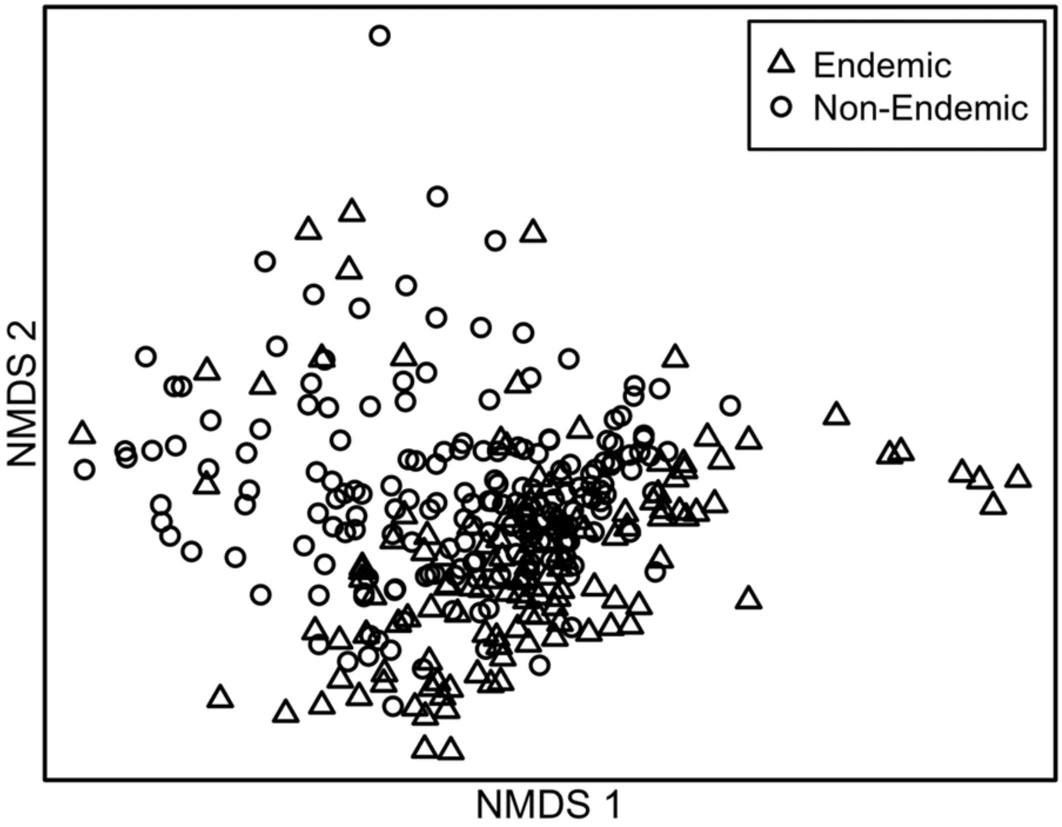

Figure 2. Endemic *Eucalyptus* species contribute a unique suite of functional traits to the landscape. Non-metric multidimensional scaling (NMDS) plot using functional trait and herbivory data showing separation between suites of functional traits and patterns of herbivory of endemic species versus non-endemics. Open circle symbols represent non-endemic species and open triangle symbols represent endemic species.

Table 1. Mixed model analysis of plant functional traits**.** Summary of mixed model analysis using Restricted Maximum Likelihood (REML) of the differences between samples of endemic (*n*=9) and non-endemic (*n*=6) eucalypt species of the subgenus *Symphyomyrtus* growing on the island of Tasmania. Holm- Bonferroni corrected *p*-values are given in parentheses.

Response Variable	$F_{1,13}$	p
% Insect Herbivory	4.446	0.039* (0.078)
% Insect Herbivory (damaged branch)	9.932	0.002* (0.008*)
% Mammal Herbivory	0.454	0.502 (0.502)
Specific Leaf Area (cm^2/g)	41.919	<0.001* (0.001*)
Height (cm)	5.588	0.021* (0.063)
Internode Length (mm)	45.066	<0.001* (0.001*)
Leaf Thickness (mm)	49.318	<0.001* (0.001*)

Table 2. Multiple regression model results for leaf traits on herbivore response. Summary of regression analysis of the correlation between plant functional traits and total foliar herbivory (*n*=412).

	Coefficient	Standard Error	*p*	R^2
Height (cm)	0.211	2.779	<0.001*	0.152
Internode Length (mm)	4.195	1.041	<0.001*	0.048
Leaf Thickness (mm)	-62.654	13.018	<0.001*	0.067
SLA (cm^2/g)	7.610	3.222	0.018*	0.017

Table 3. Mixed model analysis of functional trait measures including clade as a fixed effect. Summary of mixed model analysis using Restricted Maximum Likelihood (REML) for the difference between samples of endemic (*n*=9) and non-endemic (*n*=6) eucalypt species of the subgenus *Symphyomyrtus* growing on the island of Tasmania when evolutionary history is accounted for.

	Endemism		Clade	
Response Variable	$F_{1,13}$	p	$F_{1,13}$	p
% Insect Herbivory	1.572	0.232	0.987	0.337
% Insect Herbivory DB	2.768	0.121	0.016	0.901
Height (cm)	1.518	0.248	0.741	0.411
Internode Length (mm)	5.671	0.038*	0.065	0.805
Leaf Thickness (mm)	7.633	0.017*	0.904	0.361
Specific Leaf Area (cm^2/g)	11.794	0.005*	1.267	0.282

Discussion

This study demonstrates that despite having evolved from sea-level to tree-line, and under a broad range of selective pressures, endemic *Eucalyptus* species are functionally different from closely related non-endemic congeners. These results support a general hypothesis of convergence on an endemic syndrome of traits. Specifically, we found that endemics have more stress tolerant resource acquisition traits, such as lower SLA, thicker leaves, shorter internodes, and slower growth than widespread, non-endemic species. Although studies involving more species are required to fully understand the driving forces behind these differences, we believe that convergent evolution in response to an environmental gradient (such as elevation or harsh soil conditions) is likely playing a substantial role in the differences in functional traits that we found. Regardless of the environmental conditions driving this convergence, such functional differences in plant traits between endemics and non-endemics reflect differences in nutritional quality and palatability of these species, which in turn likely impacted the response of insect herbivores.

In general, the functional plant traits associated with the endemic species reflect a poorer quality resource for herbivores. For example, we found endemics to have lower SLA than non-endemics, a trait correlated with water use, leaf life span, and leaf nitrogen content (McIntyre & Lavorel 1999). We also found that the endemic species experienced less insect herbivory than non-endemics. This is consistent with the resource availability hypothesis (Coley *et al.* 1985) that suggests that the local environment heavily influences anti-herbivore defenses, and that plants with traits such as slow growth rates and long leaf lifespans generally invest more in anti-herbivore defense. Additionally, the response of herbivores was correlated with internode length, leaf thickness, and SLA. While this result suggests that endemics represent a poorer quality resource for herbivores than non-endemics, the alternate hypothesis, that the herbivores specialized for the endemic or non-endemic species were absent from the common garden, cannot be dismissed. Additionally, significant differences in mammal browsing were not detected. However, this result is inconsistent with those from a 2002 study of eucalypt susceptibility to marsupial damage that found that the endemic species *E. gunnii* and *E. morrisbyi* are significantly more susceptible to possum browsing than the two non-endemic species used in the study (*E. globulus* and *E. ovata*) (Dungey & Potts 2001). More studies should examine both insect and mammalian herbivory to determine if there are general differences between endemic and non-endemic species in this ecologically important interaction.

Endemic species are highly valued from a biodiversity standpoint, as the scientific community has made preventing extinctions an urgent priority (Ricketts *et al.* 2005). Our research shows that endemic *Eucalyptus* species contribute a novel syndrome of traits, with extended consequences across trophic levels (i.e., endemic species experienced less herbivore damage). These results contribute to a growing body of research that suggests genetically based plant traits can have direct and indirect effects on communities (Whitham *et al.* 2003, Wimp *et al.* 2004, Johnson & Agrawal 2005), that can in turn influence ecosystem processes (Schweitzer *et al.* 2004, Bailey *et al.* 2006). For example, a recent study showed that variation in species interactions has major consequences for community composition and ecosystem processes, such as energy flow, that increase across levels of organization (Bailey *et al.* 2006). This has important implications for the conservation of biodiversity, as the loss of endemics as a group might also represents the loss of novel ecological interactions.

Endemic plant species generally evolve in response to a broad range of environmental conditions, including edaphic factors, altitude, geographic isolation, and several other ecological conditions. In the context of climate change where species ranges have been shifting since the Pleistocene (Davis & Shaw 2001), fragmentation, isolation, and the subsequent reduction in gene flow have resulted in local adaptation of novel genotypes and the evolution of endemics (Dynesius & Jansson 2000, Jansson & Dynesius 2002, Jansson 2003, Jump & Peñuelas 2005). It remains to be seen if endemics across gradients are commonly different from closely related non-endemics, but our results provide a testable hypothesis for endemic syndromes that is worthy of future attention across plant systems. Much more research is needed to elucidate the causes and consequences of the evolution of endemism and to understand whether the conservation of endemics also preserves a unique suite of species interactions.

CHAPTER II

SPECIES IDENTITY INFLUENCES BELOWGROUND ARTHROPOD ASSEMBLAGES VIA FUNCTIONAL TRAITS

A version of this chapter has been published in *Annals of Botany PLANTS* by Courtney E. Gorman, Quentin Read, Michael Van Nuland, Jessica Bryant, Jessica Welch, Joseph Altobelli, Morgan Douglas, Mark Genung, Elliot Haag, Devin Jones, Hannah Long, Adam Wilburn, Jennifer Schweitzer, and Joseph Bailey.

Abstract

Plant species influence belowground communities in a variety of ways, ultimately impacting nutrient cycling. Functional plant traits provide a means whereby species identity can influence belowground community interactions, but little work has examined whether species identity influences belowground community processes when correcting for evolutionary history. Specifically, we hypothesized that closely related species would exhibit (i) more similar leaf and root functional traits than more distantly related species, and (ii) more similar associated soil arthropod communities. We found that after correcting for evolutionary history, tree species identity influenced belowground arthropod communities through plant functional traits. These data suggest that plant species structure may be an important predictor in shaping associated soil arthropod communities and further suggest the importance of better understanding the extended consequences of evolutionary history on ecological processes, as similarity in traits may not always reflect similar ecology.

Introduction

Global biodiversity loss is occurring at unprecedented rates (Pimm *et al.* 1995, Sala *et al.* 2000) in response to a variety of human alterations to the environment (Vitousek 1994, Vitousek *et al.* 1997, Chapin *et al.* 2000), making understanding the consequences of such loss on community and ecosystem function a top priority. Much attention has been given to understanding the effects of biodiversity aboveground, with particular emphasis on the relationship between species diversity and primary productivity (Tilman *et al.* 1996, Hooper and Vitousek 1997, Hector *et al.* 1999, Tilman *et al.* 2001). While these studies have undeniably improved our understanding of the effects of biodiversity, it is equally important to consider how aboveground biodiversity affects the diversity and function of belowground communities, and to understand how above- and belowground communities interact to influence community and ecosystem processes. Interest in the effects of plant species diversity on belowground soil organisms and the soil food web is growing (Kowalchuk *et al.* 2002, Wardle *et al.* 2003, De Deyn *et al.* 2004, Eisenhauer *et al.* 2010), however, the interactions among plant species identity and diversity and belowground communities are not well understood (Wardle 2002, Hooper *et al.* 2005). Plant species influence belowground communities in a variety of ways including the amount of organic matter returned to the soil, and the chemical composition of litter (Wardle 2002, Wardle *et al*. 2004), ultimately impacting nutrient cycling. Further understanding of the relationships between species identity and diversity aboveground and community properties and processes belowground is needed to fully understand the consequences of biodiversity loss and to identify the mechanisms of diversity effects.

Functional plant traits provide a means whereby aboveground processes can influence belowground interactions. For example, species level differences in leaf and root functional traits strongly influence the quality of plant litter inputs to the belowground subsystem, which subsequently impacts microbial communities and associated food web dynamics (Wardle and Lavelle 1997). Using a plant removal design in a grassland system, Wardle *et al.* (1999) found that while larger soil decomposing animals (i.e., earthworms) were not affected by plant community composition, there were significant responses to the removal treatments at finer taxonomic levels. These organisms were presumably responding to shifts in functional traits rather than species composition, per se. Additionally, tree species in species-rich temperate and tropical forests may possess distinct soil faunal communities (Kaneko *et al.* 2005, Donoso *et al.* 2010, Novotny *et al.* 2010), despite the homogenizing effect of decomposition processes on the soil and litter environment. For example, Donoso *et al.* (2010) found that 12.5-33.3% of focal species were specialists on certain tree species, presumably due to variation in the ability of tree species to modify leaf litter through differences in functional traits. Thus, aboveground-belowground connections are common, however the relationships among plant functional traits, plant species identity, and soil biota remains unclear.

Using long-term common gardens planted with a variety of eastern North American tree species, our study aims to determine if tree species identity has ecological consequences for associated belowground communities when correcting for evolutionary history, and to identify the role of plant functional traits as a mechanism for driving soil community differences. Specifically, we hypothesized that after correcting for evolutionary history, closely related species would exhibit (i) more similar leaf and root functional traits than more distantly related species, (ii) more similar associated soil arthropod communities. We measured plant functional traits above- and belowground, and characterized soil arthropod communities of five tree species that are widespread across the eastern United States. Our results indicate that when correcting for evolutionary history, species identity influences belowground arthropod communities via functional similarity. We speculate that phylogenetic conservatism of functional traits may be playing a role in determining belowground arthropod community assemblages.

Material and Methods

Study Site and Field Sampling

To determine if tree species identity governs functional traits and associated belowground community composition, we studied monocultures of five tree species located at Norris Dam State Park, Tennessee, USA (36.23960°N 84.10944°W). On a floodplain adjoining the Clinch River, the Tennessee Valley Authority (TVA) previously established experimental forestry plots of several native trees for a hardwood tree improvement program in the 1960's (specific details unknown by TVA). The plots consisted of approximately 25-50 trees per species with trees spaced equally every 3 m; additional woody species were not present in the plots. Plots are underlain by cherty silt loam (NRCS Web Soil Survey) and are arranged randomly along the adjacent riparian area (approximately 45 m from river). The tree species we sampled included *Quercus alba* (white oak), *Quercus prinus* (chestnut oak), *Juglans nigra* (black walnut), *Ilex opaca* (American holly), and *Liriodendron tulipifera* (tulip-poplar). These species represent three plant orders (Magnoliales, Fagales, Aquifoliales) and four families (Aquifoliaceae, Fagaceae, Juglandaceae, Magnoliaceae) with varying degrees of relatedness.

Plant Functional Traits & Soil Communities and Processes

To examine the hypothesis that after correcting for evolutionary history, more closely related tree species had similar functional traits and soil communities, five randomly chosen individual trees were sampled from each plot. Three randomly selected and fully expanded leaves from terminal shoots at the mid-canopy level were collected with pole pruners, and approximately 25 cm of root within a 50 cm radius around each tree were collected and stored at 4°C until analysis. We measured two different functional traits: specific leaf area (SLA), and specific root area (SRA). Specific leaf area is an indicator of potential relative growth rate, gives an indication of investment in leaf structural defense, and typically correlates positively with resource availability (Cornelissen *et al.* 2003). Specific root area is strongly correlated with absorptive activity by the root biomass (Cornelissen *et al.* 2003). To determine SLA (foliar area:mass ratio), leaf area was measured via WinFOLIA (Regent Instruments, Toronto, Canada) and leaves were oven-dried at 70°F for 48 h and the oven-dried leaf mass was recorded. To determine SRA, roots were rinsed with deionized water and then scanned for root surface area and root volume via WinFOLIA software (Regent Instruments, Toronto, Canada). To account for differences in root size between species, we calculated the specific root area (SRA) by dividing the root surface area by root volume.

To characterize soil communities, we collected two 5 cm diameter soil core samples from the organic layer (unconsolidated organic matter mixed with mineral soil). Soil cores (to a depth of 10 cm) were taken from two opposite sides of the tree approximately one meter from the base of each focal tree. Soil pH (measured in de-ionized water with a Denver Instruments model 220 pH meter) and soil temperature (soil thermometer at 15 cm depth) were also recorded, however temperature did not vary among species plots (15.5° C). The collected soil was stored in a cooler during transport and at 4°C until analysis. Soils were then sieved (4 mm mesh). The soil from one core was used to determine extracellular enzyme activity and total C while the other was used to analyze soil arthropod communities. Arthropods were extracted from soil over 72 h using the Berlese funnel method (Macfadyen 1961). We used a dissection microscope to classify arthropods to order.

We measured potential extracellular enzyme activity of C-degrading enzymes in soil to assess soil quality and microbial activity within the belowground communities. Approximately 1 g of soil, sieved to 2 mm, was analyzed for potential activity of α-glucosidase (EC 3.2.1.20) and β-glucosidase (EC 3.2.1.21); 1.0 g of soil was extracted with 50 mmol/L sodium acetate buffer, pH of 6. Both extracellular enzymes are secreted by soil microbes, and can be used as indicators of soil quality; α-glucosidase degrades starch and β-glucosidase oxidizes cellulose. We used Methyl-umbelliferone (MUB) as a fluorometric substrate in eight analytical replicates that incubated for 2 h each; activity was measured on a Synergy HT microplate reader (Sinsabaugh 1994, BioTek Instruments, Inc., Winooski, VT). Potential α-glucosidase enzyme activity levels greater than 100 nmol g-1 h-1 were discarded, as they were extreme outliers.

Organic matter was removed by the loss-on-ignition technique (Ball 1964) by ashing in a muffle furnace at 550°C for at least 6 h. Organic matter is measured as the difference in mass before and after combustion in the muffle furnace. Soil organic carbon (SOC) was calculated as 28.4% of organic matter (Donkin 1991). A sub-sample of each soil was also oven-dried at 105 °C for 48 h to determine soil water content; all final data are reported on an oven-dried mass basis.

Statistical Analyses

We used a phylogeny with branch lengths based on a neutral molecular clock for the five tree species (J. Beaulieu, unpubl. data) to create a pairwise phylogenetic distance matrix (R 2.14.1, ape package). We generated a pairwise distance matrix of the species means of SLA and SRA of the trees. We also generated a pairwise dissimilarity matrix for the soil arthropod community associated with each tree species in monoculture by aggregating the arthropod communities by host tree species, doubly standardizing the aggregated values using Wisconsin standardization, then calculating the Bray-Curtis dissimilarity between each pair of communities (R 2.14.1, vegan package). Finally, we calculated the pairwise distance between the means of each of the soil properties of each tree species (α-glucosidase, β-glucosidase, total SOC, pH).

We ran Mantel autocorrelation tests with 9999 permutations (R 2.14.1, ade4 package) to determine if closely related species shared more similar functional trait values than expected by chance and to determine whether pairwise phylogenetic distances between tree species were correlated with either arthropod community similarity or soil properties. In addition, we calculated the Mantel correlation between all pairs of soil property and functional trait distance matrices, including soil pH, SOC, SLA and SRA.

To infer potential mechanisms for the effect of host tree phylogeny on soil arthropod communities, we employed a structural equation modelling approach (Grace 2006, Fox 2006). We used Mantel correlations between pairwise matrices of host tree phylogenetic distances, pairwise root and leaf trait distances, and soil arthropod community Bray-Curtis dissimilarities to create a correlation matrix, which we used to estimate the parameters of the structural equation models that we specified, following the procedure of Leduc *et al.* (1992) and Meneses *et al.* (2012). We selected the models with the lowest Akaike's corrected (AICc) and Bayesian (BIC) information criteria. Modeling was done in R 2.14.1 (sem package).

Results

Specific leaf area varied roughly threefold across the five tree species; *I. opaca* had the thickest, densest leaves, while *L. tulipifera* had the thinnest (**Table 4**). Specific root area varied slightly less than twofold across the sampled species. Again, *I. opaca* and *L. tulipifera* represented the extremes of the continuum, but with *I. opaca* having the most root area (Table 4). Consistent with the expectation that closely related species tend to be more similar functionally, both SLA (r = 0.63, $p = 0.09$) and SRA (r = 0.71, $p = 0.06$) were conserved across the tree phylogeny, although neither trend was significant at the $\alpha = 0.05$ level.

Effects of tree species identity on belowground arthropod communities: Six orders of arthropods were identified among all soil samples. As would be expected if trait conservatism from associated plants persists in the soil, tree species that had similar functional traits tended to have more similarly structured soil arthropod communities (r = 0.58, $p = 0.03$, **Figure 3**, **Table 5**). The two oaks, *Q. alba* and *Q. prinus*, and the walnut *J. nigra* were associated with relatively even soil communities with roughly equal numbers of mites and collembolans. The soil communities underneath *I. opaca* and *L. tulipifera* were both dominated by mites, but *L. tulipifera* hosted a more species-poor community with only two orders represented. Soil pH (range = 0.9) and SOC (range = 0.8%) were somewhat variable among tree species.

Table 4. Mean values for specific leaf area (SLA), specific root area (SRA), soil pH, soil organic carbon (SOC), α-glucosidase potential activity (α-GLUC), and β-glucosidase potential activity (β-GLUC) with standard deviations in parentheses.

Species	**SLA (cm^2 g^{-1})**	**SRA (cm^2 cm^{-3})**	**Soil pH**	**SOC**	**α-GLUC**	**β-GLUC**
I. opaca	65.8 (1.1)	54.6 (12.6)	5.6 (0.2)	2.2 (0.3)	-0.2 (1.3)	48.5 (26.8)
Q. alba	154.1 (11.2)	38.9 (6.6)	6.5 (0.2)	2.4 (0.3)	2.7 (2.4)	398.4 (162.4)
Q. prinus	126.6 (28.7)	44.1 (8.9)	6.1 (0.4)	2.8 (0.3)	145.3 (230.5)	278.4 (117.3)
J. nigra	146.6 (23.8)	37.5 (7.4)	6.5 (0.2)	2.8 (0.5)	116.1 (267.3)	636.8 (160.3)
L. tulipifera	177.7 (18.9)	28.6 (7.3)	6.5 (0.2)	2.9 (0.5)	3.4 (1.5)	335.7 (96.3)

Table 5. Observed Mantel correlations between tree phylogenetic distance (PD), soil invertebrate community composition (IC), and soil (soil pH and soil organic C) and plant properties (specific leaf area (SLA) and specific root area (SRA). Bold type indicates a correlation significant at α = 0.10, and bold italic type indicates a correlation significant at α = 0.05.

	IC	**Soil pH**	**Soil C**	**SLA**	**SRA**
PD	***0.584***	0.299	0.289	**0.629**	**0.709**
IC		**0.538**	***0.624***	**0.691**	***0.807***
Soil pH			0.601	***0.884***	***0.754***
Soil C				**0.717**	**0.588**
SLA					***0.925***

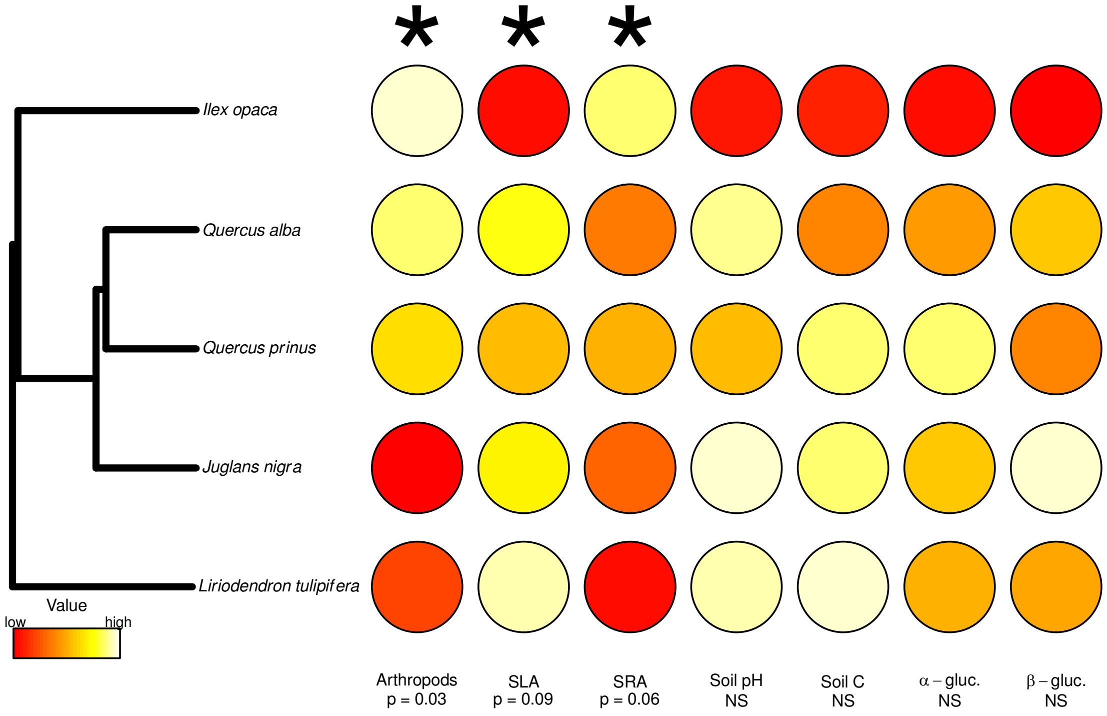

Figure 3. Phylogenetic tree of focal species. Phylogeny of the five focal tree species, with circles shaded by the Z-scores for soil arthropod community composition NMDS axis 1, host tree specific leaf area and specific root area, soil pH, soil organic carbon, and potential α-glucosidase and β- glucosidase activity. The gradient of colors represents the relative magnitude of differences in mean values for measured traits. Significance (p-values) for Mantel tests between the phylogenetic distance matrix and each trait or soil property distance matrix are given below the figure, with correlations significant at α = 0.10 indicated with asterisks.

Although host tree phylogenetic distance did not predict similarity in pH or SOC in the soil surrounding the trees ($p > 0.10$ in both cases), soils with more similar arthropod communities tended to have more similar pH ($r = 0.54$, $p = 0.10$) and SOC ($r = 0.62$, $p = 0.05$). While potential C-degrading enzyme activity differed widely among soils associated with different tree species, neither α-glucosidase ($r = 0.30$, $p = 0.36$) nor β-glucosidase potential activity ($r = 0.10$, $p = 0.52$) were significantly conserved by host tree species. This is an indication that the effect of tree species identity may become too diffuse to detect at higher levels of organization, and is consistent with our expectations and previous work across levels of organization (Bailey *et al.* 2009).

Structural equation modelling suggested that the significant effect of host tree species on soil arthropod communities is mediated by SRA, but not SLA (arthropod community $R^2 = 0.39$, **Figure 4**). The best model identified by both AICc and BIC [see Supporting Information] did not include any significant residual (i.e., not trait-mediated) effect of host tree phylogeny on arthropod community composition. However, it should be noted that only two significantly correlated traits were used in the model, and it is possible that an unmeasured but correlated trait or set of traits may be driving the observed patterns.

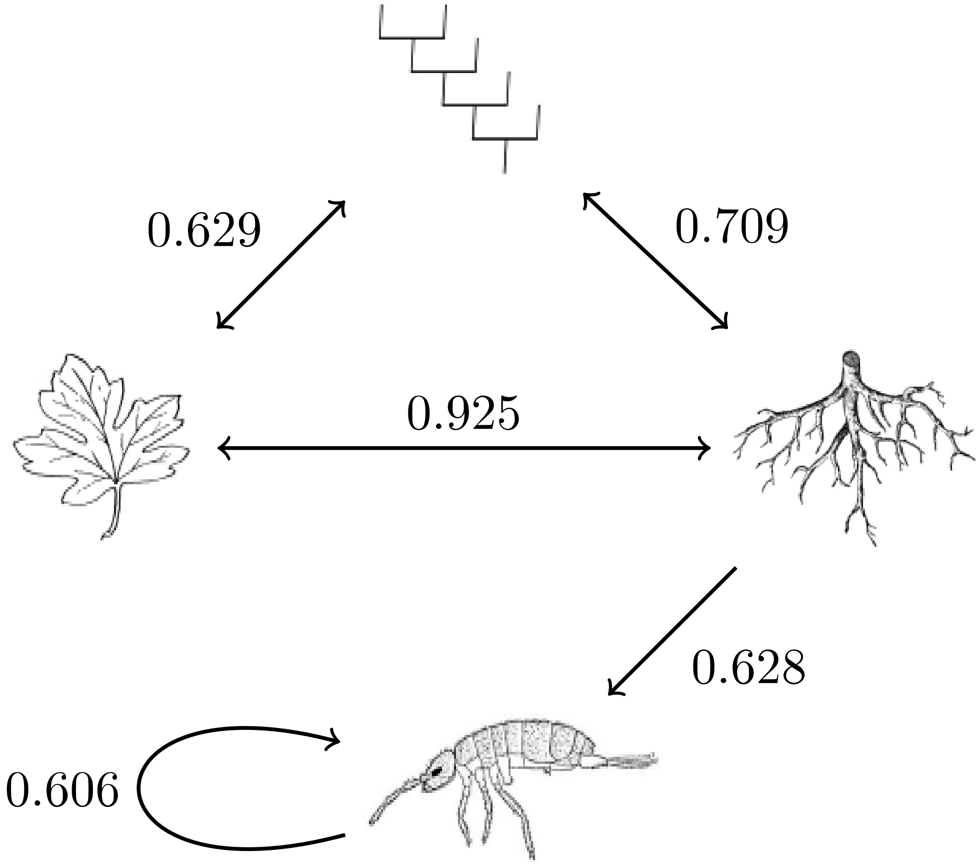

Figure 4. Path diagram of the best structural equation model with bidirectional arrows indicating covariance among host tree phylogeny (branched tree), specific leaf area (leaf), and specific root area (root). Unidirectional arrows indicate estimated effect of tree specific root area on soil arthropod community composition (springtail), and looped path indicating error variance of community composition. Arrows are labelled with the appropriate path coefficient.

Discussion

Our results demonstrate that after evolutionary history is accounted for, individual tree species support similar communities through conservatism of functional traits. We show that closely related tree species trend toward more similar leaf and root functional traits and soil arthropod communities in comparison to more distantly related species. While previous studies have shown that soil moisture and plot location can affect soil arthropod communities (Luptacik *et al.* 2012), our study controlled these two variables through the use of monoculture plots randomly positioned along a common riparian area with similar soil type and consistent temperature. Our study is the first to our knowledge to examine the effect of host tree identity on soil arthropod community composition, with evolutionary history accounted for; however, similar positive relationships exist for canopy arthropod communities (Novotny *et al.* 2006).

Bottom-up forces exert strong control on soil communities through altering resource availability. Detritivores consume dead plant matter and mobilize nutrients, making resources available to the living plant (Setälä 2005). The quantity and quality of organic matter entering the soil subsystem is the primary driver of belowground community structure and function, with fast-growing, short-lived plant tissue promoting bacteria and macroinvertebrates such as earthworms, and slow-growing, long-lived plant tissue promoting fungi and microarthropods such as mites (Wardle *et al.* 2004, Bardgett and Wardle 2010). Because SLA and SRA, traits that are correlated with plant growth rate and patterns of C allocation (Díaz *et al.* 2004), were conserved across species, after accounting for evolutionary history, we expected to see soil properties associated with detrital C processing vary in response to species. Although we found correlations between plant species and the soil community, those effects did not impact soil properties, which could result from the dilution of the effect of litter identity by arthropod processing. Before leaves and other detritus are processed by microbes they are broken down by soil arthropods into smaller fragments to harvest energy and nutrients, causing properties of organic matter originating from different plant species to converge in size and chemistry after it is processed by arthropods (Preston *et al.* 2009, Moore *et al.* 2011). Thus, processing reduces the effect of litter identity, which may be why we found no correlation between C dynamics and tree relatedness. In addition, the lack of observed trait conservatism may be because soil arthropod community composition was analyzed at a coarse taxonomic resolution (order), and few tree species were sampled, relative to previous studies (Pokon *et al.* 2005, Novotny *et al.* 2006).

Plants link above- and belowground subsystems, and their phylogenetic relationships may leave a “fingerprint” on belowground communities. With biodiversity rapidly declining (Pimm et al. 1995), it is important to fully understand how species identity aboveground may influence the properties and processes of the belowground system to be able to predict how the loss of diversity will affect the functioning of communities and ecosystems. Future studies should particularly focus on functional traits that are conserved across phylogenies. Experimental studies that manipulate tree species identity, with multiple levels of phylogenetic composition or diversity, and measure the response of the soil arthropod community would be especially useful. A mechanistic approach grounded in functional traits and phylogenetic relationships will improve our ability to understand and predict the cascading effects of species loss aboveground on belowground communities and processes. While a small study, the data reported here suggest important above- /belowground linkages among functional traits and associated communities reflecting past evolutionary history. Studies such as this are critical to bolstering our understanding of the genetic linkages among species and the consequences for community assembly and ecosystem processes.

CONCLUSION

Functional diversity plays a substantial role in determining community interactions and ecosystem processes. The interplay among taxonomic richness, functional diversity, and community structure should be investigated further (Hooper et al. 2005). Our results help to elucidate these relationships, as we show that the functional identity of a species has important consequences for associated species and community interactions. We found that in comparison to their widespread congeners, endemic species contribute a unique suite of functional traits to the landscape, and that these functional differences have extended effects on herbivores. Specifically, we found that endemics have more stress tolerant resource acquisition traits, such as lower SLA, thicker leaves, shorter internodes, and slower growth, as well as less herbivory than non-endemic species. The functional differences that we found likely reflect the nutritional quality and palatability of these species, which in turn probably impacted the response of herbivores. Because endemic species support unique species interactions, the ecological value of endemic species extends beyond their taxonomic significance.

Furthermore, we elucidate the role of plant functional traits as links between above- and belowground subsystems. We found that after evolutionary history is accounted for, individual tree species support similar communities through conservatism of functional traits. We show that closely related tree species trend toward more similar functional traits and soil arthropod communities, in comparison to more distantly related species. These results demonstrate important above- and belowground linkages among functional traits and associated communities. Additionally, these results contribute to current knowledge of the relationships between species identity and diversity aboveground and community properties and processes belowground.

These studies contribute to a growing body of research that suggests genetically based plant functional traits can have direct and indirect effects on communities (Whitham et al. 2003, Wimp et al. 2004, Johnson & Agrawal 2005) that can in turn influence ecosystem processes (Schweitzer et al. 2004). For example, a recent meta-analysis showed that variation in species interactions has major consequences for community composition and ecosystem processes, such as energy flow, that increase across levels of organization (Bailey et al. 2009). Studies such as these, on the importance of functional diversity, are critical to bolstering our understanding of how biodiversity affects community assembly and ecosystem processes.

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VITA

Courtney E. Gorman was born in Clarksville, TN. In August 2006 she started working towards an undergraduate degree at Austin Peay State University in Clarksville, TN. At Austin Peay State University she attained a Bachelor of Science in Biology in 2010 and a Master of Science in Biology in 2012. In August 2012 she entered the Ecology and Evolutionary Biology graduate program at The University of Tennessee at Knoxville.