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ASSOCIATED WITH WHITE OAK (*Quercus alba* L.)

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B.S., Biology, University of Missouri-St. Louis, 2008

A thesis submitted to the Graduate School of the University of Missouri - St. Louis in

partial Fulfillment of the Requirements for the degree of

Master of Science in Biology

August, 2011

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THESIS ABSTRACT

I investigated how ecosystem engineering by leaftying caterpillars and foliage quality affect the arthropod community associated with white oak (*Quercus alba* L.). In Chapter 1, I review the literature on ecosystem engineering, shelter building caterpillars, and foliage quality. I examine the origins of the concept of ecosystem engineering, the controversies surrounding it, and the current framework. I review previous studies on shelter building caterpillars, with a special emphasis on those studies performed on oaks. In addition, I review the components of foliage quality in oaks and how these components can influence arthropods, including ecosystem engineers. In Chapter 2, I present the results of a study designed to determine the impact of leaftying caterpillars as ecosystem engineers and foliage quality on the arthropod community associated with white oak. I found that the presence of leaftying caterpillars significantly impacted arthropod communities by altering community structure and increasing arthropod diversity. In addition, I found that the impact of leaftying caterpillars on the arthropod community varied between host plants of different quality, suggesting that environmental context can have an influence on the community impacts of ecosystem engineering.

KEYWORDS: Ecosystem engineering, leaf quality, bottom-up, arthropod, herbivore, community structure, diversity, oaks, Missouri, Lepidoptera

ACKNOWLEDGMENTS

I owe many thanks to my advisor, Dr. Robert Marquis, for his constant advice, encouragement, and financial support. Bob's example and guidance has taught me the importance of patience and independent thinking to scientific research. I would also like to thank my committee members, Dr. Zuleyma Tang-Martinez and Dr. Peter Stevens, who provided thoughtful comments and constructive criticism on this thesis.

All of the members of the Marquis lab have been incredibly helpful in giving thoughtful feedback, help in the field and in the lab, and statistical advice. I am going to miss the Marquis lab meetings (even those at 8:30am). Special thanks to Beto, Diego, Nick, Galen, Daniel, Christina, and Marina. I especially wish to thank my good friend Kirk for his unending help in the field and in the lab, and for sharing my sense of humor.

Thanks to the Missouri Department of Natural Resources and Bruce Schuette for access to the field site at Cuivre River State Park, and the University of Missouri-St. Louis Department of Biology for logistical support and supplying vehicles to get to the field site. This work was supported by grants from the National Science Foundation (DEB-0614397) and the Whitney R. Harris World Ecology Center at the University of Missouri-St. Louis.

I am also extremely thankful to my friends and family. My parents supported my decision to continue with my studies, and have always been there when I needed them. Finally, I owe more to my wife, Tabitha, than to anyone else. She deserves an award for her encouragement and patience.

CHAPTER 1.

Ecosystem Engineering, Shelter Building Caterpillars, and Foliage Quality: a Review of the Literature

INTRODUCTION

Ecological communities are shaped by the interactions among species. The arthropod communities associated with Missouri oaks (*Quercus* spp.) are no different. The diversity of these communities is influenced by traditional trophic interactions, such as predation, parasitism, competition, and mutualisms (Feeny 1970; Lawton and Strong 1981; Strong *et al.* 1984). More recently, it has been recognized that nontrophic interactions can also play a role in structuring arthropod communities on plants (Ohgushi 2008; Olff *et al.* 2009). One such nontrophic interaction is the construction of leaf shelters by lepidopteran caterpillars. By constructing leaf shelters, these caterpillars are acting as ecosystem engineers (Fukui 2001; Jones *et al.* 1994, 1997; Lill and Marquis 2003).

Ecosystem engineering is a type of nontrophic interaction first formally introduced by Jones *et al.* in 1994, and expanded upon in 1997. In this literature review, I discuss (1) ecosystem engineering, by explaining the origin of the concept, the controversies that have surrounded it, the current framework, and the implications of environmental context for ecosystem engineering. (2) The arthropod community associated with Missouri oaks is presented here as a unique case study of the effects of ecosystem engineering, and I discuss previous work and results in the system. (3) Foliage quality is a potentially important element of environmental context for ecosystem engineering, and I briefly discuss the components of oak foliage quality, past work

demonstrating how oak foliage quality affects arthropod communities in general,

leaftying caterpillars in particular, and what implications environmental context might

have for engineering effects.

ECOSYSTEM ENGINEERING

Ecology is the study of how organisms interact with each other, and has

traditionally focused on trophic interactions, such as competition (intra- and inter-

specific), predation, parasitism, mutualism, and commensalism (Olff *et al.* 2009). These

interactions are key in determining the diversity and abundance of species in ecological

communities, and have been extensively studied using interaction webs (e.g., Polis and

Winemiller 1996). Unfortunately, this focus on direct trophic interactions has meant that

indirect, nontrophic interactions have been largely ignored. Recently, there has been a

growing recognition of the significance of these nontrophic interactions for the

understanding of community dynamics (Bruno *et al.* 2003; Ohgushi 2008; Pressier *et al.*

2005). Community ecologists have begun to include nontrophic interactions such as

facilitation and indirect responses in their construction of community models and

interaction webs (Ohgushi 2005; Jordano et al 2006).

One type of nontrophic interaction that has been gaining attention is ecosystem

engineering. Jones *et al.* introduced the ecosystem engineering concept in a 1994 paper,

in which they defined ecosystem engineers as organisms that can influence resource

availability, directly or indirectly, to other organisms by causing 'physical state changes

in biotic or abiotic materials'. By causing these physical changes, ecosystem engineers

modify, create, or maintain habitats (Jones *et al.* 1994). Under this definition, a broad

range of organisms could be considered ecosystem engineers; beavers creating dams, gophers that move soil, termites that build mounds, and trees that create shade and moderate temperature (Jones *et al.* 1994, 1997). Because the concept covers such a broad array of organisms, Jones *et al.* (1994) separated ecosystem engineers into two main categories: autogenic engineers and allogenic engineers.

Autogenic ecosystem engineers modify their physical environment via their own physical structures. One of the most straightforward examples of an autogenic ecosystem engineer is a tree. Trees modify their physical environment by changing the hydrology, nutrient cycles, soil stability, and the overall microclimate of the surrounding habitat (Holling 1992; Jones et al 1994). It is important to clarify that the production of living tissue such as leaves or flowers is not what constitutes ecosystem engineering by the tree; it is the changes in the physical environment (i.e., the creation and maintenance of new habitats) as a result of the tree's growth that constitutes ecosystem engineering (Jones *et al.* 1994, 1997). Autogenic ecosystem engineering also includes examples such as *Sphagnum* bog moss changing hydrology and pH, and corals creating large underwater structures that change wave dynamics of the surrounding water (Anderson 1992, Jones *et al.* 1994, 1997).

Allogenic ecosystem engineers modify the physical environment by mechanically changing biotic or abiotic material from one state to another. Beavers are often used as the archetypical example of an allogenic ecosystem engineer. Beavers take trees and mechanically transform them into beaver dams, changing the state of the physical environment upstream from the dam (Jones *et al.* 1994; Wright *et al.* 2002). By creating a dam in a stream, the beavers create a pond, which has a significant impact on the

ecological community by strongly influencing resource availability and creating a new habitat (Wright *et al.* 2002). The species assemblages present in a habitat with a beaver pond are significantly different from that of an ordinary stream (Wright *et al.* 2002). Other important examples of allogenic ecosystem engineers include alligators, which maintain wallows that retain water in droughts, and prairie dogs, which dig burrows that are then occupied by other organisms (e.g., burrowing owls and arthropods) (Butts and Lewis 1982; Campbell and Mazzotti 2004; Jones *et al.* 1994).

A Useless Concept?

Since the concept of ecosystem engineering was first outlined by Jones *et al.* (1994, 1997), it has generated a large amount of attention as well as controversy. All plants and animals influence their physical environment in some way, simply by virtue of existing. Because of this, some ecologists argue that the concept of ecosystem engineering is useless, while others argue that only species that cause relatively large changes in the physical environment should be classified as ecosystem engineers (Reichman and Seabloom 2002a, 2002b). Other questions arise when attempting to restrict use of the term to organisms that have large magnitude effects: how do we define what 'large magnitude' is? Is magnitude measured spatially, temporally, or otherwise? Hastings *et al.* (2007) argue that consideration of both spatial and temporal scales are important when considering organisms as ecosystem engineers. Conversely, Wilby (2002) asserts that if we study only the most obvious (the most 'important' species with 'large magnitude' effects) scenarios of ecosystem engineering, this damages our efforts to understand the ecological importance of ecosystem engineering in general.

Despite such controversies, either conceptual or semantic, a resolution seems to have been reached that even if the label of 'ecosystem engineer' is not particularly useful *per se*, the process of ecosystem engineering itself is quite important (Hastings *et al.* 2007; Reichman and Seabloom 2002b; Stinchcombe and Schmitt 2006; Wilby 2002; Wright and Jones 2006). With this in mind, it becomes important to establish a framework by which we can determine the key causes and effects of ecosystem engineering.

Models and Framework for the Study of Ecosystem Engineering

Early conceptual models of ecosystem engineering were divided between autogenic and allogenic engineering, and split into several 'cases' (Fig. 1) (Jones *et al.* 1994). These cases were sufficient for classifying many obvious examples of ecosystem engineering, but they were not exclusive (i.e., some examples of ecosystem engineering could fit into multiple cases), and they did not provide any framework by which engineering effects could be predicted or estimated (Jones *et al.* 1994, 2010). Jones *et al.* (1997) later expanded upon the concept, and suggested that ecosystem engineering can have both positive and negative effects on species richness and abundance at local and patch scales, but the net effect of engineering on communities at the landscape scale is likely positive.

Consideration of the effects of ecosystem engineers at the landscape level (as opposed to the patch level) has led ecologists to a modified intermediate disturbance hypothesis. Wright (2009) suggests that there are two "endpoints" on the scale of habitat diversity with respect to ecosystem engineering: landscapes where there are no modified

(engineered) habitats, and landscapes where there are no unmodified (original) habitats. Between these endpoints, ecological theory suggests that diversity will be maximized (Connell 1978; Marquis and Lill 2006). However, this prediction is complicated by several factors: possible overlap in species assemblages between the modified and unmodified habitats, temporal variation in the ratio of modified to unmodified habitat, and environmental context (Crain and Bertness 2006; Wright 2009).

Recently, several ecologists have proposed models of ecosystem engineering which attempt to build an integrated framework for predicting and understanding the dynamics of ecosystem engineering, and to define when ecosystem engineering is important for understanding how ecological communities are structured (Cuddington *et al.* 2009; Jones *et al.* 2010). Cuddington *et al.* (2009) suggest that ecosystem engineering is especially important when it alters population dynamics. They then use a general modeling framework to identify the conditions under which these changes in population dynamics would occur. In addition, Cuddington *et al.* (2009) make new a distinction between obligate engineers, which cannot survive without the engineering effect, and non-obligate engineers, which are not dependent on engineering.

More recently, Jones *et al.* (2010) have attempted to construct a framework that could help ecologists explain and predict the effects of ecosystem engineering (Fig. 2). In their paper, a graphical presentation of ecosystem engineering is accompanied by explanatory parameters and equations for the four main relationships in ecosystem engineering: (1) engineers causing structural change, (2) structural change causing abiotic change, (3) structural and abiotic changes causing biotic changes, and (4) feedbacks to the engineers themselves (Jones *et al.* 2010). This framework is the most recent attempt

to simplify and explain the causes and effects of ecosystem engineering, and updates the concepts introduced by Jones *et al.* over a decade ago (1994, 1997) with more recent work (Cuddington *et al.* 2009; Hastings *et al.* 2007).

Environmental Context

Though often left out of the ecosystem engineering framework, the context of the physical and biotic environment can have important implications for the effects of engineering. Ecosystem engineers interact with their associated communities by modifying the environment; if the context of the physical environment changes (i.e., increasing or decreasing environmental stress, competition, or predation levels), it has been suggested that the engineering effect could also change in either magnitude or direction (Crain and Bertness 2006). This seems reasonable, especially since the ways that engineering may affect ecological communities include habitat amelioration and refuge from predators (Crain and Bertness 2006; Hastings *et al.* 2007).

Crain and Bertness (2006) predicted that as environmental stress increases, the importance of certain types of engineering effects will change (Table 1). At high levels of environmental stress, Crain and Bertness (2006) suggest that engineers who ameliorate environmental stress will be most important, whereas engineers that offer refuge from predation or competitors would be more important in intermediate- to low-stress environments (Crain and Bertness 2005; Menge and Sutherland 1987). These changes in the importance of different engineering effects are likely to impact the overall strength of engineering effects on ecological communities (Badano *et al.* 2010; Crain and Bertness 2006).

SHELTER BUILDING CATERPILLARS

Many species of Lepidoptera construct shelters on plants using leaves, branches, and silk web (Berenbaum 1999; Fukui 2001). Shelter building caterpillars are able to produce silk using modified exocrine glands, and they apply this silk to leaves or branches using spinnerets (Berenbaum 1999). Constructed shelters benefit the caterpillar by serving as protection from predators or weather, acting as a food source, modifying the quality of that food source, or creating a favorable internal microclimate (Fukui 2001). This habit seems to be especially prevalent in microlepidoptera (Wilson 1974; Carroll 1977).

Shelter building by caterpillars can take several forms, such as leaf rolling, leaf folding, leaf webbing, and leaf tying. Leaf tying microlepidopteran caterpillars (i.e., those species of shelter builders that construct "leaf sandwiches" using silk to tie leaves together) in particular have been extensively studied on oaks (*Quercus*) (e.g., Carroll and Kearby 1978; Carroll *et al.* 1979; Lill 2004; Lill and Marquis 2003; Lill *et al.* 2007; Marquis *et al.* 2002; Forkner *et al.* 2004; Marquis and Lill 2007, 2010). Leaftying microlepidoptera associated with *Quercus* represent several families, including: Gelechiidae, Hesperiidae, Noctuidae, Oecophoridae, Pyralidae, and Tortricidae (Carroll 1977; Forkner *et al.* 2004; Lill and Marquis 2003).

Leaftying caterpillars generally feed on the internal leaf surfaces of the shelter, once completed (Carroll and Kearby 1978). Only a few larger species construct multiple shelters (due to exhaustion of food resources) in order to complete their development (Carroll and Kearby 1978). Most leaftying caterpillar species complete larval

development inside the shelter, and fall to the forest floor during the pupal stage (Lill and Marquis 2004).

On oaks, the number of leaves tied by leaftying caterpillars can be as high as 10% of total leaves, but the mean number of tied leaves varies by species (Marquis and Lill 2010). One species that shows an especially high level of leaftier attack is white oak (*Quercus alba*), with a mean of 5% of total leaves tied during a season (Marquis and Lill 2010). Within-species differences in leaftier attack have been associated with varying levels of host plant quality (i.e., foliage quality and plant architecture) (Marquis *et al.* 2002; Marquis and Lill 2010). It has also been shown that different species of leaftying caterpillars show different host preferences, and that leaftier diversity can vary among host species as a result (Marquis and Lill 2010).

Leaftying Caterpillars as Ecosystem Engineers

Leaftying caterpillars and their associated arthropod community offer a unique system in which to study the effects of ecosystem engineering. Ties constructed by these caterpillars often last for an entire season, until leaf abscission in autumn (Carroll and Kearby 1978). Leafties have been shown to be colonized by other species of insect herbivores and non-herbivore arthropods, either concurrently or after the leaftier has left (Carroll and Kearby 1978; Carroll *et al.* 1979; Lill and Marquis 2003). This suggests that leaftying caterpillars can have an influence on arthropod communities.

Lill and Marquis (2003) conducted an experiment to assess how early season leaftying caterpillars impact insect herbivores on *Quercus alba* (white oak) saplings. They found that leafties significantly increased insect herbivore species richness. Engineering by early season leaftying caterpillars had the largest impact on (late season)

leaftying caterpillars, beetles, and sawflies, all of which are commonly found inside

leafties (Lill and Marquis 2003). Further study demonstrated that certain arthropod

guilds (e.g., leaf-chewing herbivores, free feeding caterpillars) had strong oviposition

preferences for tied leaves over non tied leaves (Lill and Marquis 2004). These results

suggest that leaftying caterpillars, as ecosystem engineers, are an important factor in

determining the diversity and structure of insect herbivore communities.

FOLIAGE QUALITY

Components of leaf quality in Quercus *spp.*

Foliage quality has been demonstrated to have significant impacts on *Quercus*

arthropod communities, including leaftying caterpillars. "Foliage quality" is a broad term

that encompasses several physical and chemical traits. Some of the most commonly

measured traits in oaks are: leaf toughness, leaf hair density, water content, nitrogen

content, and defensive chemical concentrations (Feeny 1970, 1976; Forkner *et al.* 2004;

Lill and Marquis 2001; Marquis and Lill 2010). While high water and nitrogen content

are generally associated with high quality foliage due to nutritional value, leaf toughness,

hair density, and high levels of defensive chemistry are generally associated with low

quality leaves.

Foliar water content in *Quercus* spp. generally ranges between 50-60%, and

exhibits a slight decline in concentration over the course of a season (Marquis and Lill

2010). The percent dry weight nitrogen can vary between 1.7 and 2.3%, depending on

the species and time of year (Forkner *et al.* 2004; Marquis and Lill 2010). Leaf

toughness and the density of leaf hairs vary greatly by species, and some species, such as

Q. alba, completely lack hairs on fully-developed leaves (RJM and JRR *pers. obs.*).

The defensive chemistry of *Quercus* spp. consists of a variety of phenolic

compounds, including tannins (Feeny 1970; Forkner *et al.* 2004). Tannins as a whole are

a group of water soluble polymers made up of phenolic constituents that have the ability

to bind proteins (Bate-Smith and Swain 1962). Tannins are categorized into two main

groups: hydrolysable and condensed tannins. Hydrolysable tannins are composed of

galloyl esters attached to glucose; they are named as such because they can be hydrolyzed

by acids or enzymes to produce phenolic acids (Barbehenn *et al.* 2006; Haslam 1981).

There are two subgroups of hydrolysable tannins: gallotannins, which range from the

simplest hydrolysable tannins to high-molecular-weight tannins, and ellagitannins, which

are formed from multiple galloyl groups by oxidative coupling (Barbehenn *et al.* 2006).

Condensed tannins (also known as proanthocyanidins) are a smaller subgroup of tannins

composed of flavon-3,4-diols, and cannot be cleaved by hydrolysis (Barbehenn *et al.*

2006; Okuda *et al.* 2000). Tannins are structurally diverse, and can be quite abundant in

the foliage of some species (Barbehenn *et al.* 2006; Salminen *et al.* 2004). In *Q. alba* in

particular, tannins as a whole can comprise up to 25% of leaf dry weight (Forkner *et al.*

2004; JRR *unpubl. data*).

Impacts of leaf quality on arthropod communities

In *Quercus* spp., leaf quality has been demonstrated to have significant impacts on

insect communities. Feeny (1970) showed that tannin concentrations in leaves of

Quercus robur (English oak) showed a pattern of seasonal increase, and found that insect

abundance declined along with this increase. It was suggested that the decline in insect abundance was due to the decreased leaf quality caused by higher levels of defensive chemistry (Feeny 1970). Feeny (1970) went on to argue that this pattern of seasonally increasing tannin concentrations was responsible for the fact that the majority of insect herbivory is concentrated in the spring. The seasonal accumulation described by Feeny (1970) may be the result of chemical induction. Wold and Marquis (1997) found that the chemical defenses of *Q. alba* can be induced through herbivore damage, and that insect herbivores were much less likely to be associated with leaves that were damaged, and those damaged leaves had higher concentrations of phenolics.

More recent studies have shown that total phenolics and hydrolysable tannin concentrations are negatively associated with pupal mass in a common insect herbivore, *Psilocorsis quercicella* feeding on *Q. alba* (Lill and Marquis 2001). Additionally, Forkner *et al.* (2004) re-examined the findings of Feeny (1970), and demonstrated that insect herbivore abundance and species richness on *Q. alba* and *Q. velutina* (black oak) were negatively correlated with condensed tannin concentrations in both early and late season. In these studies, condensed tannins increased over the course of the season, while hydrolysable tannins showed a steady decline (Forkner *et al.* 2004; Lill and Marquis 2001). The results from these studies suggest that both condensed and hydrolysable tannin concentrations may play an important role in structuring insect herbivore communities on the plants studied.

Leaf quality and leaftying caterpillars

Leaftying caterpillars, as part of the arthropod community, can also be impacted by foliage quality. Lill and Marquis (2001) performed an experiment to determine how leaf quality affected the survivorship, development time, and pupal mass of *Psilocorsis quercicella*, a common leaftying caterpillar found on *Q. alba*. Their results revealed that low leaf quality significantly reduced survivorship for early season caterpillars, but not those of the second generation (Lill and Marquis 2001). Total phenolic and hydrolysable tannin concentrations had a significant negative association with pupal mass, but there were no tannin effects on the development time of caterpillars (Lill and Marquis 2001).

Recent work has suggested that foliar nitrogen content is the most important aspect of leaf quality for predicting attack by leaftying caterpillars (Marquis and Lill 2010). Across five *Quercus* spp., nitrogen concentration was shown to be positively correlated with caterpillar pupal weight (Marquis and Lill 2010). Additionally, nitrogen content and protein binding capacity (a method of measuring phenolic concentrations) were both associated with differences in leaftier colonization rates among four species of *Quercus* (Marquis and Lill 2010).

It may seem obvious that if insect herbivores in general are affected by the quality of their food, that leaftying caterpillars, being insect herbivores, would also be affected. However, it should be noted that leaftying caterpillars are especially important to arthropod communities due to the impacts they have as ecosystem engineers (e.g., Lill and Marquis 2003, 2004). The fact that leaftying caterpillars, in particular of all insect herbivores, are influenced by leaf quality is especially significant because any changes in leaftier survival or colonization rates could have significant impacts on the ecosystem

engineering effects of the caterpillars, and ultimately impact the arthropod community as a whole.

DISCUSSION

Ecosystem engineering is relatively new as a formal concept in community ecology, but it is quickly becoming a popular topic of study. Several models have been put forward to help researchers study ecosystem engineering in a variety of systems (e.g., Cuddington *et al.* 2009; Hastings *et al.* 2007; Jones *et al.* 1994, 1997, 2010; Wright and Jones 2006). Additionally, there has been extensive research on individual examples of ecosystem engineering in various communities (e.g., Badano *et al.* 2006; Castilla *et al.* 2004; Fukui 2001; Lill and Marquis 2003; Reichman and Seabloom 2002; Wright *et al.* 2002). These studies have solidified the importance of the ecosystem engineering *concept* in ecology, even if some do not consider the *label* of 'ecosystem engineer' to be very useful, or misleading.

Recently, an important focus in ecosystem engineering research has been the role of environmental context in predicting the variation (in magnitude or direction) of engineering effects (Badano *et al.* 2010; Wright and Jones 2006). The arthropod community associated with Missouri oaks offers a unique system in which to study the interaction between environmental conditions and ecosystem engineering. Leaftying caterpillars on oaks have been extensively studied as ecosystem engineers (e.g., Carroll and Kearby 1978; Carroll *et al.* 1979; Lill 2004; Lill and Marquis 2003; Lill *et al.* 2007; Marquis *et al.* 2002; Marquis and Lill 2007, 2010), and foliage quality represents an environmental condition with strong impacts on the arthropod community as a whole

(e.g., Feeny 1970; Forkner *et al.* 2004; Wold and Marquis 1997), and leaftying

caterpillars in particular (Lill and Marquis 2001; Marquis and Lill 2010).

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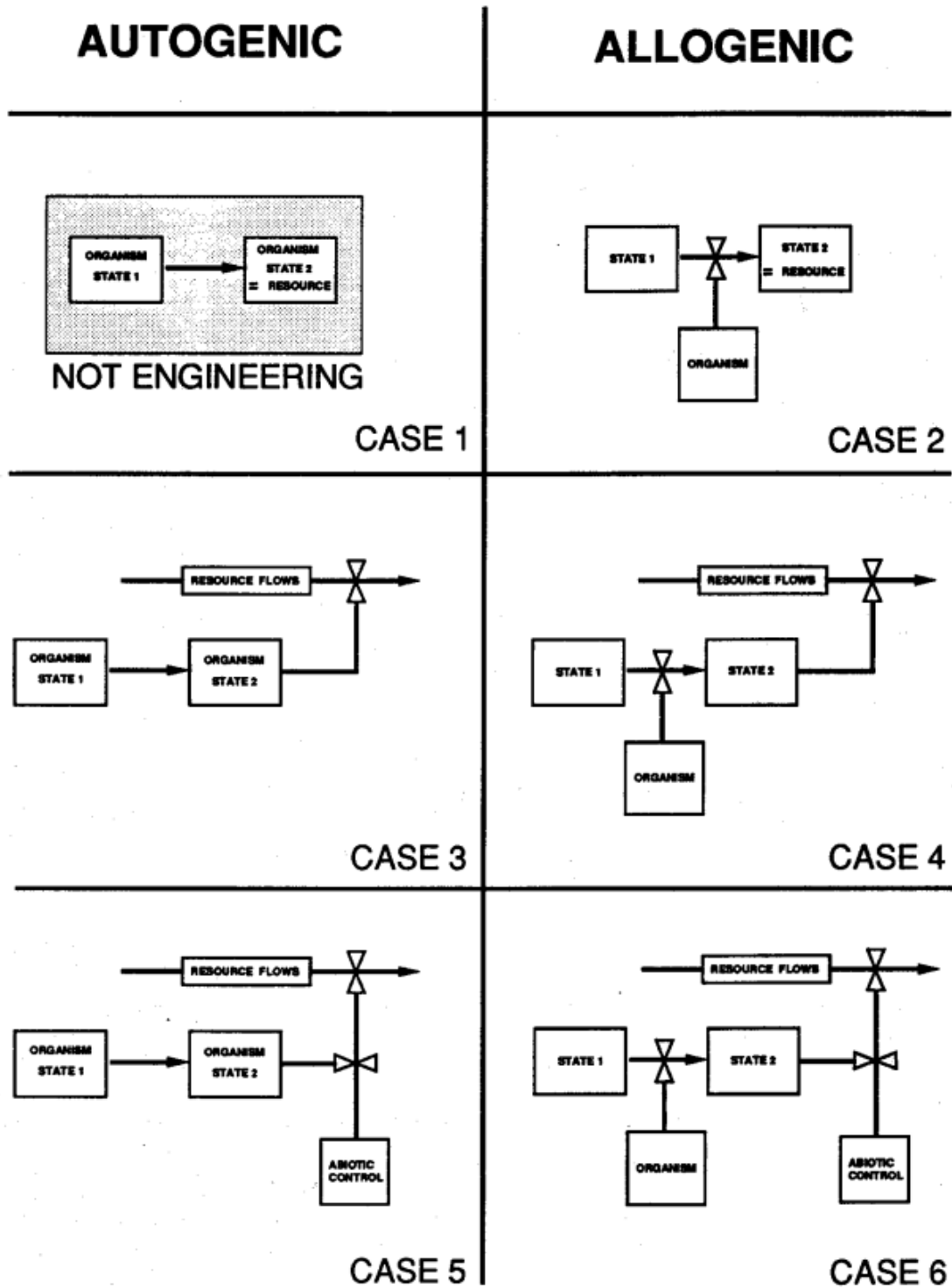
TABLES AND FIGURES

Figure 1. Early conceptual models of ecosystem engineering. Adapted from Jones *et al.* 1994.
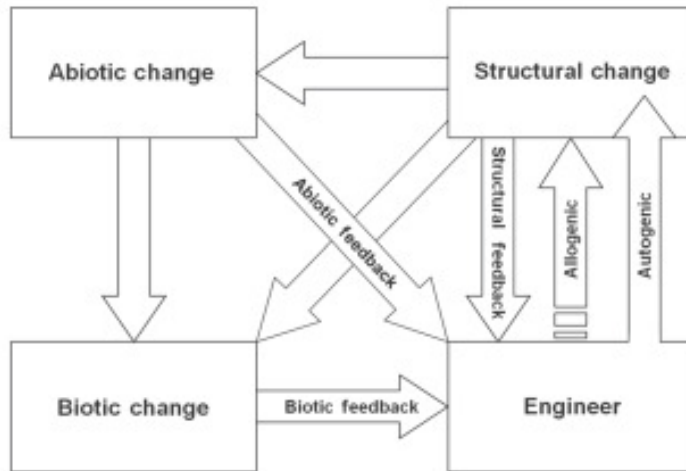
Figure 2. Illustration of the general framework of physical ecosystem engineering. Adapted from Jones *et al.* 2010.

Table 1. Predicted mechanisms of important ecosystem engineers in environments under varying levels of stress. Adapted from Crain and Bertness (2006).

Environmental stress	Important engineering mechanisms	Engineering impact	Importance of engineer
Extreme	Stress amelioration	Increased abundance, diversity, and ecosystem functioning	Essential
Intermediate	Competition refuge	Increased diversity and ecosystem functioning	Improves and stabilizes ecosystem function
Benign	Predation refuge	Increased diversity and ecosystem functioning	Improves and stabilizes ecosystem function

CHAPTER 2. Ecosystem engineering and leaf quality affect arthropod community structure and diversity on white oak (*Quercus alba* L.)

ABSTRACT

Shelter-building caterpillars act as ecosystem engineers by creating and maintaining leaf shelters which are then colonized by other arthropods. Environmental factors, such as foliage quality, have been shown to influence colonization by shelter-building caterpillars. In this study, I examined how leaftying caterpillars, as ecosystem engineers, impact arthropod communities on *Quercus alba* (white oak), and how these engineering effects may be affected by foliage quality. For an entire season (June-September), I removed all leaftying caterpillars and leafties on 35 *Q. alba* saplings. Paired with these leaftie removal trees were control trees, where all leaftying caterpillars and leafties were left intact. Removal of these ecosystem engineers had no impact on the overall species richness or abundance of arthropods, but significantly affected the species diversity, similarity, and structure of the arthropod community as the season progressed. This suggests that trees with and without leaftying caterpillars had different arthropod species assemblages. Additionally, trees with higher foliage quality had a much higher ecosystem engineering effect size on species diversity than those with low foliage quality, suggesting that the quality of the host plant can influence how ecosystem engineering affects the overall arthropod community.

INTRODUCTION

Studies of ecological communities focus on interactions between and within species, and the influence of these interactions on the diversity and abundance of organisms in a community. Traditionally, most of these studies have focused on trophic interactions, such as competition, mutualisms, and predation (Ohgushi 2008; Olff et al. 2009). Recently, however, it has been suggested that nontrophic interactions can occur just as often, and have effects just as large as trophic interactions (Pressier *et al.* 2005; Schmitz *et al.* 2004). One non-trophic interaction that can influence ecological communities is ecosystem engineering. Ecosystem engineers alter their physical environment in such a way that habitats are created, modified, or destroyed (Jones *et al.* 1994, 1997).

While it could be argued that all organisms modify their physical environment in some way, ecosystem engineers modify their environments so that the population dynamics of associated species are altered (Cuddington *et al.* 2009). This occurs because the habitat is changed in such a way that certain species assemblages become associated with, or avoid, the engineered habitat. This is because the change in resource availability and/or predation pressure associated with the change in habitat has the potential to have significant effects (positive or negative) on birth and death rates of the associated species. As a result, species assemblages in engineered habitats may differ from those in original, unmodified habitats (Wright *et al.* 2006).

Ecosystem engineering also differs from trophic interactions on a temporal scale. The modifications made to the physical environment by ecosystem engineers often outlast the engineers themselves, creating a legacy effect; this contrasts with trophic

interactions, which most often occur on short term timescales (Hastings *et al.* 2007). The duration of the legacy of engineered habitats depends on (1) the tendency of the environment to revert to its original state, and (2) the ability of the engineer to perform maintenance (Cuddington *et al.* 2009; Hastings *et al.* 2007). Examples of this legacy effect include beaver meadows, which can persist for over seventy years, and termite mounds, some of which can last for thousands of years (Moore and Picker 1991; Wright *et al.* 2003).

Recently, interest has grown in the effects of ecosystem engineers at the landscape scale, particularly, in predicting and quantifying the impacts of ecosystem engineers in communities composed of both modified and unmodified habitats (Castilla *et al.* 2004; Crain and Bertness 2006; Lill and Marquis 2003; Wright *et al.* 2002). Wright (2009) suggests that there are two "endpoints" on the scale of habitat diversity with respect to ecosystem engineering: landscapes where there are no modified (engineered) habitats, and landscapes where there are no unmodified (original) habitats. Between these endpoints, ecological theory suggests that diversity will be maximized (Connell 1978; Marquis and Lill 2006). However, this prediction is complicated by several factors: possible overlap in species assemblages between the modified and unmodified habitats, temporal variation in the ratio of modified to unmodified habitat, and environmental context (Crain and Bertness 2006; Wright 2009).

Ecosystem engineering and its effects may depend on environmental conditions (Bandano *et al.* 2010; Wright and Jones 2004). Thus, Crain and Bertness (2006) have suggested that the role of ecosystem engineering, as well as trophic interactions, may change across an environmental stress gradient. In arthropod communities, one

important aspect of environmental stress, from the arthropod's point of view, is plant leaf quality (Forkner *et al.* 2004). Leaf quality can directly influence levels of attack by insect herbivores (Forkner *et al.* 2004). Additionally, by influencing colonization of plants by ecosystem engineers, leaf quality may indirectly impact the arthropod community (Marquis and Lill 2010).

Shelter-building caterpillars and their associated arthropod community offer a unique system in which to study the effects of ecosystem engineering. These caterpillars act as ecosystem engineers by constructing leaf shelters (e.g., leafties, rolls, folds, tents). Leaftying caterpillars in particular (i.e., those species of shelter builders that construct "leaf sandwiches" using silk to tie leaves together) are among the most common shelter building caterpillars, and among the most well-studied (e.g., Carroll and Kearby 1978; Carroll *et al.* 1979; Lill *et al.* 2007; Lill and Marquis 2004; Marquis and Lill 2010). The shelters constructed by these caterpillars often last for the duration of the season, until leaf abscission in autumn (Carroll and Kearby 1978). Leafties are often colonized by other species of arthropods, either concurrently or after the caterpillar has left (Carroll and Kearby 1978; Carroll *et al.* 1979; Lill and Marquis 2003). It follows, then, that the ecosystem engineering effects of these caterpillars can alter the community dynamics of arthropods (e.g., Fukui 2001; Lill and Marquis 2003).

Previous studies of leaftying caterpillars on white oak (*Quercus alba* L.) have shown that leafties are significant colonization sites for arthropods, and that removal of leaftiers for a three-week period in early summer can have significant effects on insect herbivores in particular (Lill and Marquis 2003, 2004). Additional studies in this system (and other *Quercus* species) have shown that leaf quality can influence attack by insect

herbivores and leaftying caterpillars (Forkner *et al.* 2004; Lill and Marquis 2001; Marquis and Lill 2010). No studies have yet examined the season-long arthropod community level impacts of leaftying caterpillars in conjunction with leaf quality.

I conducted a study of the potential community level impacts of leaftying caterpillars as ecosystem engineers at the whole-plant level by completely removing leaftying caterpillars from a set of *Q. alba* saplings for the duration of the season. Specifically, I was interested in (1) the effects of ecosystem engineering as a whole on non-leaftying arthropod community structure, species richness, species diversity and similarity, and abundance, (2) how the quality of foliage affects the arthropod community as a whole, and (3) whether the effects of ecosystem engineering differed among plants with different levels of foliage quality.

I hypothesized that (1) based on previous studies of insect herbivores, ecosystem engineering by leaftying caterpillars should have a significant effect on the non-leaftying arthropod community structure. (2) Previous studies suggest that foliage quality will have significant impacts on the arthropod community, including leaftying caterpillars. (3) Based on previous studies of the influence of leaf quality on insect herbivore and leaftier attack, I predicted that plant quality would positively influence the arthropod community (i.e., higher quality plants would have more diverse communities), directly as it affects food quality, and indirectly as it affects the abundance of leafties.

METHODS

Study Site and System

Field experiments were conducted at Cuivre River State Park (CRSP), located in

Lincoln County, Missouri. The Park is approximately 25.9 km^2 and consists mainly of

forest and native prairie. The Park contains a second-growth mixed oak-hickory forest

with an understory composed mostly of flowering dogwood (*Cornus florida*), sassafras

(*Sassafras albidum*), sugar maple (*Acer saccharum*), eastern redbud (*Cercis canadensis*),

and an assortment of saplings, including many oaks (*Quercus* spp.). The canopy is

dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.).

Quercus alba (white oak), the focal plant of this study, is one of the most

common species of oak at CRSP. *Quercus alba* saplings can be found in various

understory locations around the Park, especially on the north end. There are generally

two generations of leaftying caterpillars that attack *Q. alba*; one that begins to emerge in

early to mid June and one generally in mid- to late August (the phenology of the second

generation can vary, see Lill 2004). Leaftying caterpillars (leaftiers) present in Missouri

oak communities represent several families, including: Gelechiidae, Hesperiidae,

Noctuidae, Oecophoridae, Pyralidae, and Tortricidae (Forkner *et al.* 2004; Lill and

Marquis 2003). The most common leaftiers found on *Q. alba* in Missouri are *Psilocorsis*

quercicella, Psilocorsis cryptolechiella, *Psilocorsis reflexa* (Oecophoridae), and

Pseudotelphusa sp. (Gelechiidae) (Forkner *et al.* 2004; Lill and Marquis 2003). Of these,

Pseudotelphusa sp. is the most common leaftier, and it appears that it has the most impact

on the insect herbivore community (Lill and Marquis 2003). The arthropod community

associated with white oaks is composed of individuals from several different orders, and

dozens of families. The most abundant arthropods are Lepidoptera and Psocoptera (Lill and Marquis 2004). Coleoptera and Aranae are also fairly abundant, but to a lesser extent (JRR *pers. obs.*).

Experimental Design

In early June 2009, seventy white oak saplings at the study site were marked and their leaves counted. The experiment used a randomized block design, with thirty-five pairs of treatment (leaftier removal) and control (leaftiers intact) trees. Trees were 1-4 m tall, with leaf counts ranging between 300 and 900. From mid-June to mid-September, all leaftying caterpillars were removed from all treatment trees on a weekly basis. Any leafties constructed were recorded and disassembled. The identity and quantity of all leaftiers removed were recorded. As a procedural control, the control tree in each pair was visited and handled at the same time as the treatment tree.

I conducted censuses in late June/early July, August, and September for the abundance and identity of arthropods. Each tree was carefully searched and arthropod species were counted and identified to morphospecies. I also recorded the location of the arthropods, whether inside a leaftie or not. Arthropods were collected only if they were unidentifiable to the morphospecies in the field; they were taken to the laboratory for identification, and reared to maturity if necessary. Small metal clips were placed on any leafties that were opened on control trees, to keep the leaftie intact. These clips were removed on the next visit, 4-7 days later.

Leaf quality data were collected from all study trees: leaf toughness, water content, percent dry weight carbon and nitrogen, and concentration of condensed tannins, hydrolysable tannins, and total phenolics. Five leaves for analysis were collected at the beginning and end of the experiment to determine how leaf quality changed over the course of the season. Collected leaves were kept on ice, returned to the laboratory and freeze-dried, ground into powder, and stored in a -80ºC freezer. Leaf toughness was measured at the time of collection using a leaf penetrometer (Force Dial FDK 32, Wagner Instruments, Greenwich, CT). Water content was measured by subtracting the dry weight from the weight at collection. Percent dry weight carbon and nitrogen were measured using a CHNS/O analyzer, which uses microcombustion to break down and estimate the elemental composition of organic samples (Perkin-Elmer Series II CHNS/O Analyzer 2400). Condensed tannin concentrations were determined using the acid-butanol technique (Rossiter *et al.* 1988). Hydrolysable tannin concentrations were estimated using the potassium-iodate assay (Schultz and Baldwin 1982). Total phenolic concentrations were estimated using the Folin-Denis assay (Waterman and Mole 1994). For the phenolic assays, a single bulk standard containing leaf tissue for each tree was prepared and purified by washing the leaf powder multiple times with 95% ethanol, followed by extraction using 70% acetone with Sephadex LH-20 in a Büchner funnel. Acetone was removed using rotary evaporation, leaving pure oak tannin in aqueous solution. The aqueous solution was freeze-dried, leaving only purified oak tannin powder. Individual aqueous extracted samples were obtained by purifying with multiple 95% ethanol washes followed by extraction with 70% acetone. Individual samples were compared with the bulk standard for each assay, and colorimetrically quantified using a

microplate reader (Versamax Microplate Reader, Molecular Devices Corporation, Sunnyvale, CA).

Statistical analyses

To determine the effects of leaftier removal on total arthropod species richness, sample-based rarefaction curves were constructed for both treatments for all non-leaftying arthropods, as well as herbivores and non-herbivores separately. Rarefaction curves were constructed by computing the expected richness function along with its 95% confidence intervals. To compare data in terms of species richness instead of species density, the computed sample-based curves and confidence intervals were re-scaled by number of individuals (Gotelli and Colwell 2001). Significant differences in species richness between treatments were distinguished using 95% confidence intervals (Colwell *et al.* 2004). Rarefaction curves were constructed using EstimateS 8.20 (Colwell 2009).

Treatment effects on arthropod species diversity were compared by calculating Simpson's reciprocal indices (1/D) for each tree during each census period. Repeated-measures analysis of variance (ANOVA) was used to compare the Simpson's reciprocal index values across censuses, with treatment as a between-subjects factor. To further investigate treatment effects on the arthropod community, the Morisita-Horn similarity index was calculated to estimate community similarities for all possible paired samples (*n* = 2415). I used repeated-measures ANOVA to compare the Morisita-Horn indices across censuses and between treatments (i.e., to compare within-treatment similarity to between-treatment similarity). To assess how the treatments affected overall arthropod abundance, I compared the number of arthropods on every tree during each census using

repeated measures ANOVA, with treatment as a between-subjects factor. Because of differences in sample tree size, arthropod abundances from each census were divided by the number of leaves$^{1/3}$.

I used discriminant analysis to compare the arthropod community structure between treatments. Numbers of non-leaftying arthropod species were pooled across all censuses for eight guilds: free-feeding caterpillars, non-leaftying shelter-building caterpillars (e.g., leaf rollers), leaf miners, (non-lepidopteran) chewing herbivores, sucking herbivores, detritivores, insect predators, and arachnids. Guilds were used as the predictor variables in the discriminant function. Species per leaf was used as the response variable, and species richness data were $\log_{10}(x+1)$ transformed in order to meet the assumption of multivariate normality. The discriminant function structure matrix was analyzed to determine which arthropod guilds were important predictors of treatment. Classification and cross validation tables were constructed to assess the ability of the calculated function to discriminate between treatments based on guild richness. The discriminant analysis was performed using SPSS Statistics 17.0 (SPSS Inc., 2008).

Seasonal variation in the number of leafties was assessed by comparing the percentage of leaves tied on control trees across censuses using repeated measures ANOVA. To determine how the proportion of modified habitat to unmodified habitat (i.e., leaftie density) might affect arthropod communities, linear regression was used to compare the percentage of tied leaves on control trees versus (1) arthropod species richness (species per leaf) and (2) abundance (individuals per leaf) during each census period.

Repeated measures ANOVA was used to determine seasonal differences in all of the measured leaf quality traits: water content, toughness, concentrations of condensed tannins, hydrolysable tannins, and total phenolics, and percent dry weight carbon and nitrogen. In order to normalize the residuals, toughness was $\log_{10}(x+1)$ transformed, and water content, condensed tannins, hydrolysable tannins, total phenolics, and percent dry weight carbon and nitrogen were arcsine square root transformed.

To assess the effects of leaf quality on the arthropod community, the number of leaf quality variables had to be reduced using principal components analysis (PCA). The transformed leaf quality data (mentioned above) were used in order to maintain linear relationships. Total phenolic concentrations were left out of the analysis due to high correlation with hydrolysable tannins. Two separate PCAs were performed, one for July data, and one for September. Analyses were performed using the correlation matrix.

To determine the effects of leaf quality on leaftying caterpillar colonization throughout the season, leaf quality principal components (PCs) were correlated with the number of leafties and leaftying caterpillar species per leaf on control trees in July and September. Leaf quality effects on non-leaftying arthropod richness and abundance on both control and removal trees were assessed using multivariate analysis of covariance (MANCOVA). Separate MANCOVAs were run for July and September. Leaf quality PCs were used as covariates, and leaftier treatment was used as a fixed factor, allowing me to test the interaction effects of treatment x leaf quality. If the overall MANCOVA model (corrected model) was at least marginally significant (i.e., $P \leq 0.1$), the test was followed up with univariate ANCOVAs. PCAs and MANCOVAs were completed using SPSS 17.0 (SPSS Inc., 2008).

To determine whether leaf quality impacts how ecosystem engineers influence community dynamics, plants were divided into two categories: low and high quality. Categories were created by comparing the variable loadings of leaf quality PCs for both July and September, and ranking them based on their association with high nitrogen and low tannin concentrations. Groups were formed by splitting plants at the 50th percentile rank for both control and treatment, yielding equal sample sizes. Separate two-way repeated measures ANOVAs were used to determine how treatment effects on arthropod species richness, diversity, and abundance differed between quality levels over the season. Treatment and leaf quality group were used as between-subjects factors.

RESULTS

Species richness, species diversity, and abundance

A total of 11,696 individuals from 111 morphospecies of arthropods were recorded across all trees and treatments. The second generation of leaftying caterpillars emerged in mid to late August, just after the second census. The percentage of leaves in ties found on control trees ranged from a low of 1.89% ($\pm$ 0.24) in August, to highs of 3.70% ($\pm$ 0.50) and 4.00% ($\pm$ 0.45) in September and July, respectively.

All sample-based rarefaction curves approached an asymptote near the maximum sample number, suggesting that my sampling effort was sufficient to estimate species richness (Fig. 1a-c). Control trees had higher mean species richness when comparing treatments for non-herbivore arthropods, and all arthropods; there were no differences between treatments for herbivorous arthropods, however.

The leaftier treatment had significant effects on the species diversity of the arthropod community, as measured by the Simpson's Reciprocal Index. The census × treatment interaction was not significant (Table 1). During each census period, control trees had higher species diversity than removal trees; differences between leaftier removal and control trees were greatest in September (Fig. 2). These results are consistent with the hypothesis that ecosystem engineering increased arthropod community diversity.

Overall arthropod abundance had significant seasonal variation, but there was no significant difference between leaftier treatments (Table 2). August arthropod abundances were significantly higher than either in July or September, due entirely to the high number of plant lice (Psocoptera) present during the August census. Arthropod abundance was highest in August, and lowest in September (Fig. 3).

Community composition and structure

Repeated measures ANOVA indicated significant census, treatment, and interaction effects on arthropod community similarity (Table 3). Community similarity, as measured by the Morisita-Horn Index, was much lower between treatments in September than within either treatment (Fig. 4). This result is consistent with the conclusion the leaftying caterpillars altered community composition, especially in September.

Discriminant analysis suggested that arthropod community structure differed between treatments. Box's M indicated that the assumption of equality of covariance

matrices was violated ($P = 0.0108$), but examination of the log determinants and visual inspection of the covariance matrices, in addition to the large sample size used, indicated that this was not a problem. Wilks' lambda was significant ($\lambda = 0.733$, $\chi^2 = 19.844$, $P = 0.0109$), suggesting that the discriminant function was able to successfully discriminate between treatments. Analysis of the discriminant function structure matrix revealed that non-lepidopteran chewing herbivores and free-feeding caterpillars were the only significant predictors of treatment (Table 4). Classification results show that 74.3% of trees were correctly classified by treatment; cross-validation showed that 60.0% of cases were correctly classified (Table 5, Fig. 5).

Leafties and arthropod densities

Repeated measures ANOVA showed significant seasonal variation in the percentage of leaves tied on control trees ($F_{2,68} = 17.206$, $P < 0.0001$). Percentage of tied leaves was lowest in August, while it was equally high in July and September (Fig. 6). Linear regression found a positive relationship between percent tied leaves and non-leaftying arthropod species richness on control trees in July, and a marginally significant positive relationship in September (Fig. 7; July: $r^2 = 0.175$, $F_{1,33} = 7.012$, $P = 0.0123$, September: $r^2 = 0.081$, $F_{1,33} = 2.911$, $P = 0.0973$). There was no significant relationship between percent tied leaves and arthropod species richness in August. Positive relationships were found between percent leaves tied and non-leaftying arthropod abundance in July and September (Fig. 8; July: $r^2 = 0.388$, $F_{1,33} = 20.909$, $P < 0.0001$, September: $r^2 = 0.174$, $F_{1,33} = 6.931$, $P = 0.0128$), but not in August.

Leaf quality

Repeated measures ANOVA indicated that hydrolysable tannins and total phenolics declined over the course of the season, while condensed tannins accumulated (Fig. 9; condensed tannins: $F_{1,69} = 96.253$, $P < 0.0001$, hydrolysable tannins: $F_{1,69} = 238.955$, $P < 0.0001$, total phenolics: $F_{1,69} = 56.855$, $P < 0.0001$). Percentage dry weight nitrogen and carbon also declined over the season (Fig. 10; %N: $F_{1,69} = 250.761$, $P < 0.0001$, %C: $F_{1,69} = 116.155$, $P < 0.0001$). Leaf water content slightly increased over the course of the season, from a mean of 58.1% in June to 61.6% in September ($F_{1,69} = 43.287$, $P < 0.0001$). Leaf toughness did not significantly change during the season, remaining relatively consistent with a mean value of 188 g/mm^2. There were no significant differences in any of the measured leaf quality variables between treatments.

Parametric correlations suggested that individual trees had consistent within-season hydrolysable tannin and total phenolic concentrations (hydrolysable tannins: $\rho = 0.360$, $P = 0.002$, total phenolics: $\rho = 0.264$, $P = 0.0279$). June and September condensed tannin concentrations were not correlated, suggesting significant within-season variation on individual trees. Concentrations of condensed tannins were positively correlated with the percentage of dry weight carbon, but only in June ($\rho = 0.469$, $P < 0.0001$).

Leaf quality, leaftiers, and the arthropod community

In both July and September, PCAs of leaf quality variables explained over 50% of the variance using the first two principle components (Table 6); these components explained 54% of the variation in July, and 52% in September. High levels of condensed

tannins and hydrolysable tannins were correlated with low nitrogen levels; these variables were strongly associated with PC1 in July and PC2 in September. High nitrogen content was correlated with low condensed tannins and hydrolysable tannins in PC1 in September, and PC2 in July. In September, trees with high nitrogen content tended to have higher carbon content and tougher leaves.

Leaf quality PCs were not significantly correlated with the percentage of tied leaves or leaftying caterpillar richness in July. In September, percent tied leaves and leaftying caterpillar richness were both negatively correlated with PC2, which was associated with high tannin concentrations and low nitrogen content (Fig. 11; % tied leaves: $\rho = -0.345$, $P = 0.043$, richness: $\rho = -0.431$, $P = 0.01$).

Analysis of total non-leaftying arthropod richness and abundance MANCOVAs showed that the effects of PC1 were marginally significant, but that the model had no significant overall effects in July (Table 7). ANCOVAs revealed that PC1, associated with high tannin concentrations and low nitrogen content, had significant negative effects on arthropod abundance in July ($F_{1,64} = 5.370$, $P = 0.024$). The September MANCOVA revealed significant overall model effects on arthropod species richness ($F_{5,64} = 2.453$, $P = 0.043$), but no significant effects on abundance. ANCOVAs showed that PC1, which was associated with high nitrogen content and low tannin concentrations, had a marginally significant positive effect on species richness ($F_{1,64} = 3.873$, $P = 0.053$). There was a significant negative effect of PC2 on species richness ($F_{1,64} = 6.392$, $P = 0.014$). Considering the variable loading of these PCs, the pattern is consistent with the conclusion that trees with lower tannin levels and higher levels of nitrogen and water had

more arthropod species. Treatment × PC interaction effects were not significant in July or September.

Leaf quality groups created based on PC variable loadings were able to accurately describe low and high quality trees. Leaf toughness, and both condensed and hydrolysable tannin concentrations were higher in the low quality group than in the high quality group, in both the early and late season. Nitrogen content was significantly higher in the high quality group across the season (Table 8). Two-way repeated measures ANOVAs of leaf quality groups showed significant positive effects of leaf quality on species richness, but neither treatment nor treatment × quality interactions were significant (Table 9). Treatment and treatment × quality had significant and marginally significant positive impacts, respectively, on species diversity across the season, but quality alone had no effects (Table 10). Arthropod abundance was not affected by leaf quality or treatment alone, but there was a significant treatment × quality interaction effect (Table 11). When leaf quality was low, control trees had higher abundances of arthropods (0.16 individuals/leaf), but when leaf quality was high, removal trees had higher abundances (0.18 individuals/leaf).

DISCUSSION

Removal of leaftying caterpillars had significant impacts on the diversity and structure of arthropod communities. In addition, the proportion of leaves tied by caterpillars on control plants was positively related to arthropod species richness and abundance. These ecosystem engineering effects were influenced by the quality of foliage on plants; higher foliage quality magnified the ecosystem engineering effect on

arthropod diversity, suggesting that leaf quality can influence how ecosystem engineering affects arthropod communities.

Arthropod communities

Estimation of species richness using rarefaction showed that control trees had consistently higher richness, but the difference between treatments was not statistically significant (Figs. 1a-c). This is in contrast to a previous study, which found that removal of leaftying caterpillars for a three-week period early in the season resulted in reduced species richness for the duration of the season (Lill and Marquis 2003). The abundance of arthropods varied during the season, but was not significantly different between treatments (Fig. 4). Arthropod community metrics, including abundance, were expected to be low in August on both removal and control trees, because this is typically before the second leaftier generation appears, and the proportion of leaves tied are lowest (Fig. 6). August abundances were higher than either July or September, however, due to high abundance of plant lice (Psocoptera).

Comparison of species diversity, a metric that takes into account species richness as well as the relative abundance (evenness) of species, showed significant differences between treatments and across censuses (Fig. 3). In addition to having different levels of species diversity, community similarity between treatments was significantly lower than similarity within treatments in September, as measured by the Morisita-Horn index (Fig. 4). The pattern of differences in species diversity and low between-treatment similarity suggests that by the end of the season, the communities on control and removal trees consisted of different species.

Community structure between treatments was significantly different. Discriminant analysis suggested that two arthropod guilds, non-lepidopteran chewing herbivores and free-feeding caterpillars, were much less abundant on removal trees. These two guilds have been shown to be associated with the shelters constructed by leaftying caterpillars (e.g., Lill and Marquis 2003, 2004), suggesting that the differences in species diversity and species assemblages between treatments is a result of the ecosystem engineering effect. Previous studies suggest that these effects may be occurring due to preferential colonization by certain guilds of arthropods (e.g., chewing herbivores) of trees that have leafties over those that do not, or that have fewer such ties (Lill and Marquis 2004).

Leafties

The proportion of leaves tied on control trees was consistent with a previous study in July and September, but slightly lower in August (Lill and Marquis 2003). This inconsistency is likely due to the fact that in this study, the August census occurred before the emergence of the second generation of leaftying caterpillars. As a result, proportion of tied leaves was lowest in August, but equally high in July and September (Fig. 6).

During July and September, when leaftying caterpillars were active, species richness and arthropod abundance shared a positive relationship with the percentage of leaves tied (Figs. 7 and 8). These relationships were not found in August, probably due to the fact that leaftying caterpillars are between generations, making the number of tied leaves much lower as a result. Ecological theory suggests that landscapes will have

higher species richness at an intermediate point between completely unmodified habitat (e.g., no leafties) and entirely modified habitat (e.g., every leaf tied) (Connell 1978; Marquis and Lill 2006). Because the natural amount of leaves tied on a tree rarely exceeds 5-10%, I predicted that no intermediate point would be reached. The fact that both species richness and abundance generally increased along with the proportion of tied leaves supported my prediction.

Leaf quality, leafties, and arthropod communities

There was significant seasonal variation in all measured leaf quality traits, with the exception of leaf toughness (Figs. 9 and 10). Seasonal variation of condensed tannins, hydrolysable tannins, total phenolics, and percent dry weight nitrogen is consistent with previous studies of *Q. alba* leaf chemistry (Forkner *et al.* 2004; Marquis and Lill 2010). Water content and leaf toughness were relatively similar to, but did not share the same seasonal patterns as previous studies (Marquis and Lill 2010). Principal components constructed from leaf quality variables were associated with either high tannin concentrations and low nitrogen content or low tannin concentrations and high nitrogen content (Table 6).

Leaf quality had several impacts on ecosystem engineering and the arthropod community. In September, the proportion of leaves tied on control trees and the species richness of leaftying caterpillars had a negative association with a PC associated with low quality foliage (e.g., high tannin concentrations and low nitrogen content), suggesting that adult moths of the leaftying caterpillars prefer to oviposit on trees whose leaves are traditionally thought as being high quality (Fig. 11). Additionally, PCs associated with

low quality foliage had a negative impact on the overall non-leaftying arthropod community in both July and September (Table 7).

When the arthropod community was compared between low and high quality plants in addition to treatment, a difference in the ecosystem engineering effect was found. There were no significant treatment effects on arthropod species richness, even when foliage quality was taken into account. There was, however, a significant difference in the effect of ecosystem engineering on species diversity at low and high qualities; on plants with higher quality foliage, the presence of leaftying caterpillars increased arthropod species diversity much more than on plants with low quality foliage (Figs. 12a-b). Additionally, arthropod abundance was higher on control trees when leaf quality was low, but higher on removal trees when quality was high. These differences in mean arthropod abundance between quality levels were due to high abundances of Psocoptera during the study (Figs. 13a-b). The data suggest that Psocoptera prefer high quality trees but avoid leafties. Overall, the differences in arthropod species diversity and abundance between treatment and quality levels (as illustrated by Figs. 12 and 13) suggest that environmental context (i.e., foliage quality) can change the dynamics of how ecosystem engineering can affect ecological communities.

In summary, this study showed that ecosystem engineering can increase the diversity of *Q. alba* arthropod communities at the whole-plant level, and that these effects were influenced by the quality of foliage on study trees. While previous work in this system has shown that removal of leaftying caterpillars for three weeks early in the season can have significant impacts on arthropod communities (Lill and Marquis 2003), this study has shown how plants with and without leaftiers differ throughout the entire

season; by September, trees with leaftiers had arthropod communities that were

significantly more diverse, and the species assemblages between treatments shared

relatively little similarity. Furthermore, this is the first study to show that the quality of

plant foliage can impact the way that ecosystem engineering affects arthropod

communities, in addition to the direct influence of leaf quality on arthropods documented

in previous studies (Forkner *et al.* 2004). These results emphasize the importance of both

ecosystem engineering and leaf quality in determining the spatial distribution and

population dynamics of arthropods among trees.

Considering the results of this study, it seems likely that other environmental

factors could also have an impact on ecosystem engineering and arthropod community

dynamics. Plant architecture is one such factor; it has been shown to affect colonization

by leaftiers (Marquis and Lill 2010), and may have an indirect impact on arthropod

community diversity. Future studies in this system should include leaf architecture in

conjunction with leaf quality, and attempt to identify other factors that may influence

ecosystem engineering effects.

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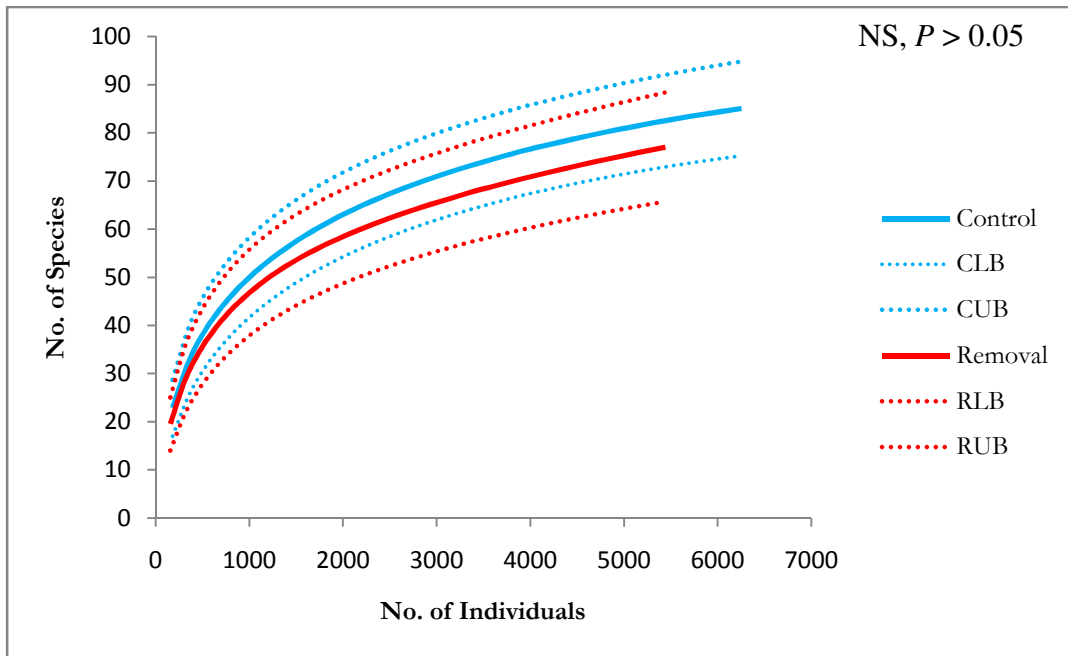
FIGURES AND TABLES

Figure 1a. Incidence-based accumulation curves for all non-leaftying arthropods for both treatments. Dashed lines indicate the upper (CUB, RUB) and lower (CLB, RLB) bounds of the 95% confidence intervals.
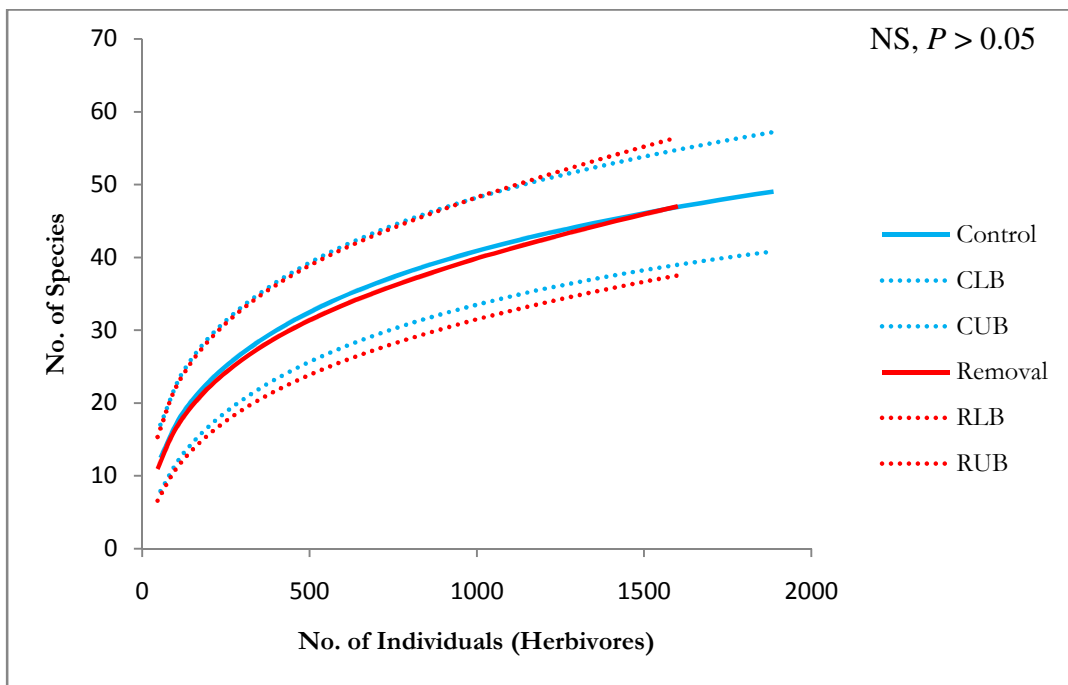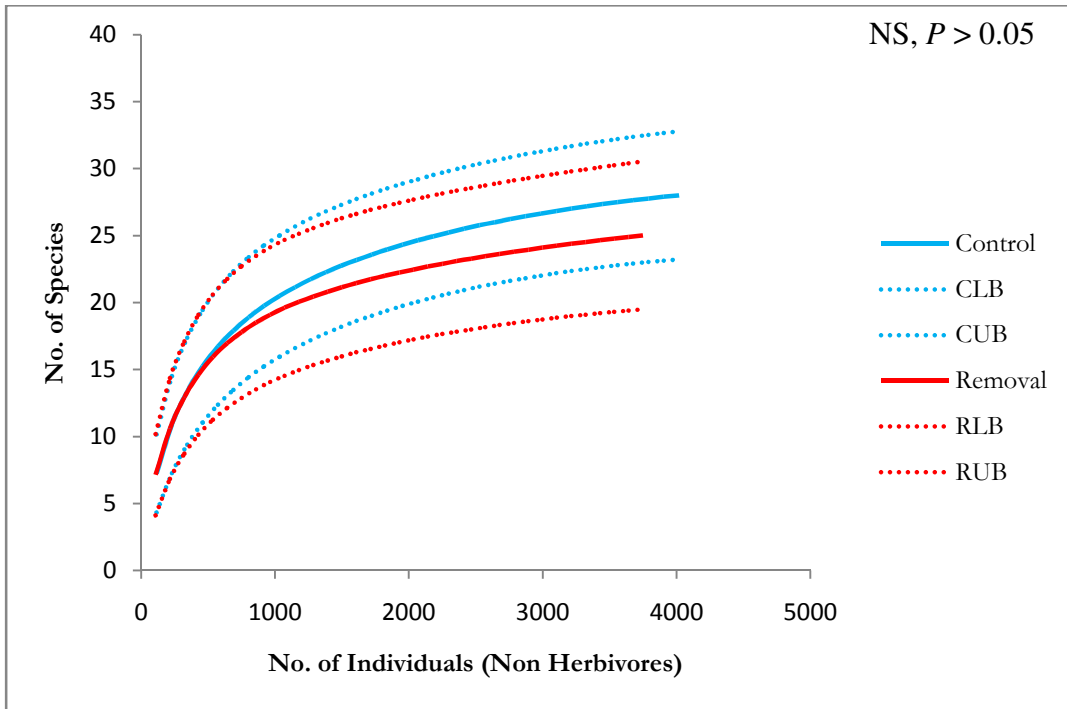

Figure 1b. Incidence-based accumulation curves for all non-leaftying herbivores for both treatments. Dashed lines indicate the upper (CUB, RUB) and lower (CLB, RLB) bounds of the 95% confidence intervals.
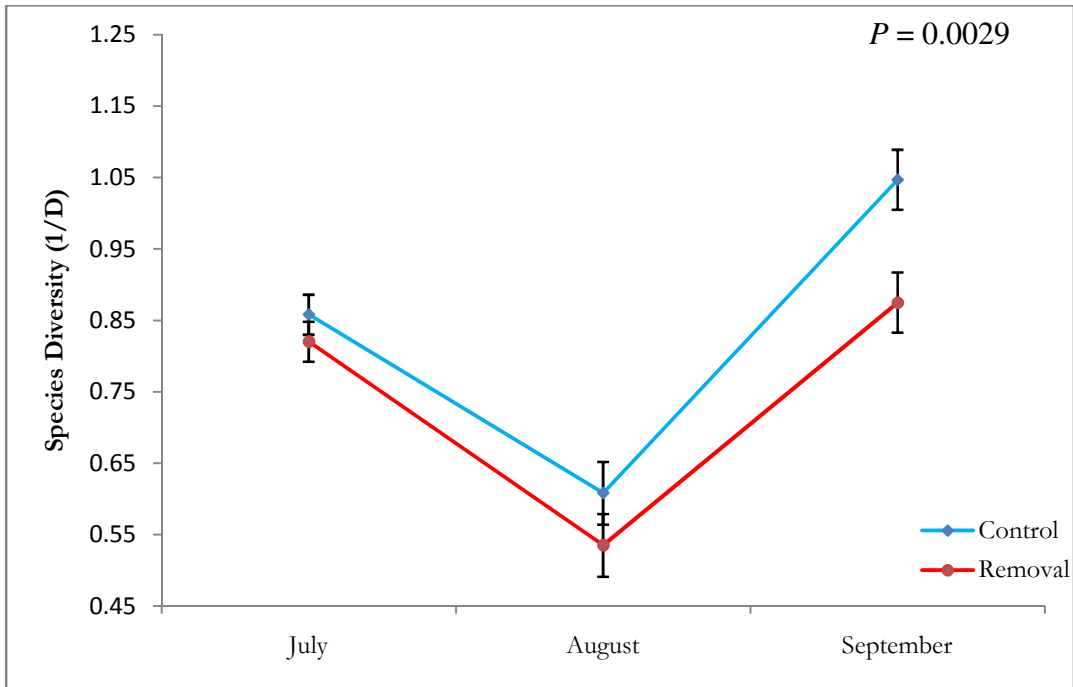
Figure 1c. Incidence-based accumulation curves for all non herbivores for both treatments. Dashed lines indicate the upper (CUB, RUB) and lower (CLB, RLB) bounds of the 95% confidence intervals.

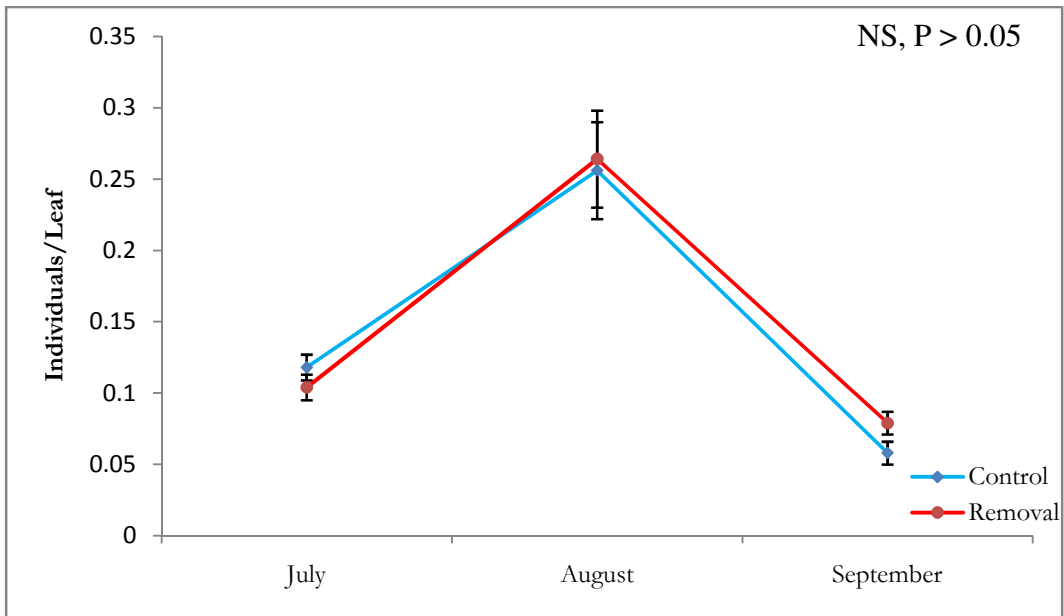Figure 2. Seasonal patterns of species diversity (1/D, mean ±1 SE), for control and leaftier removal treatments.

Figure 3. Seasonal patterns of non-leafying arthropod abundance (individuals/leaf, mean ±1 SE), for control and leaftier removal treatments.
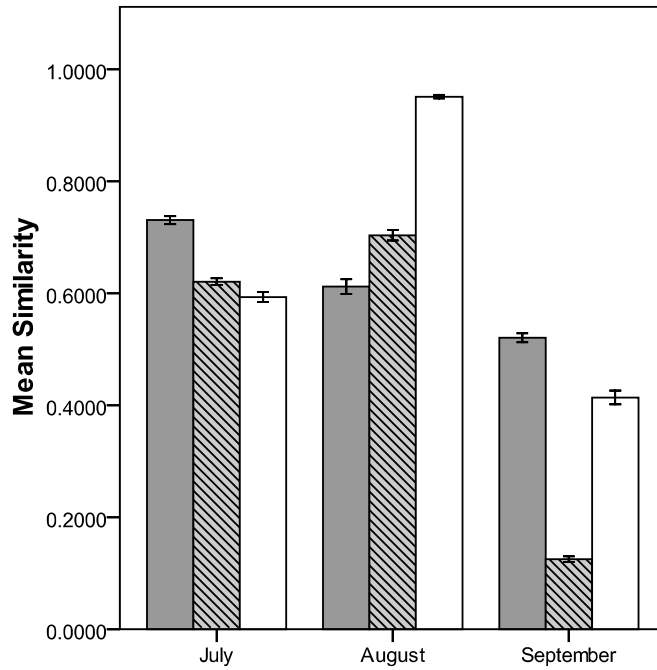
Figure 4. Seasonal patterns of arthropod community similarity (as measured by the Morisita-Horn index, mean ±1 SE), within and between treatments. Solid gray and white bars indicate similarity within control and removal trees, respectively. Striped bars indicate similarity between treatments.
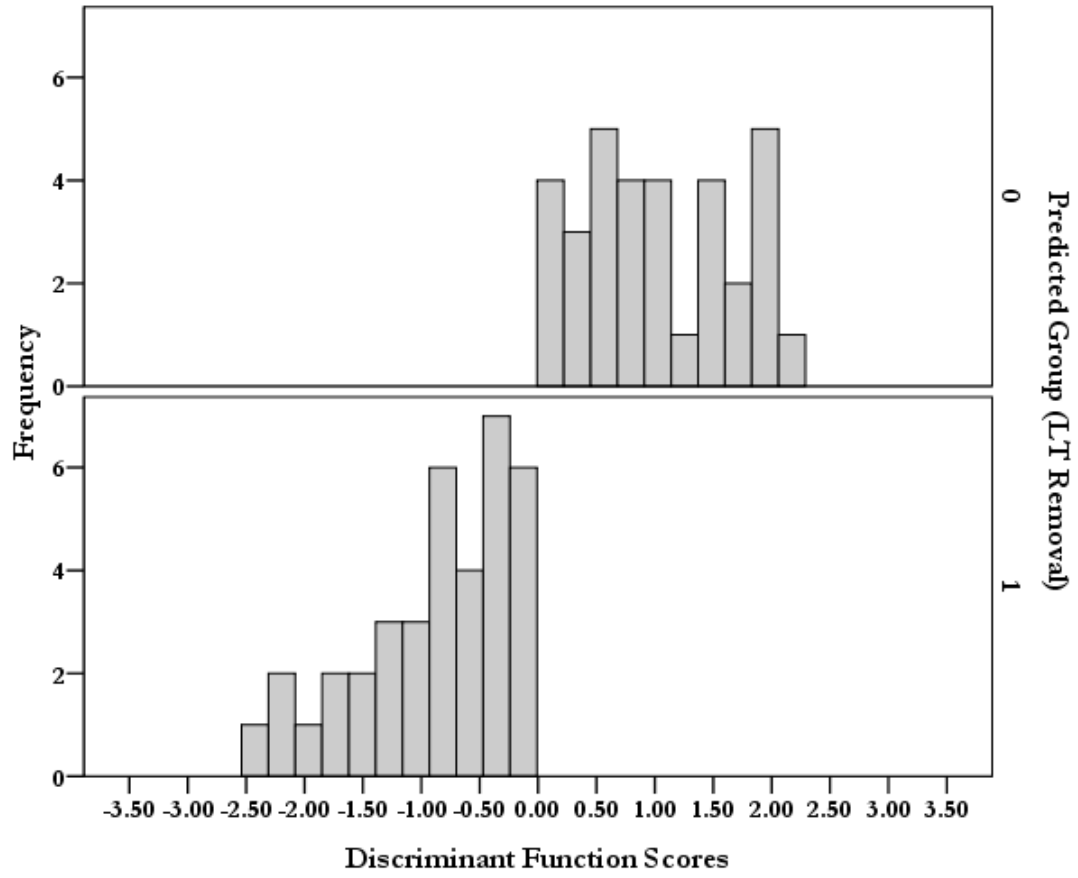
Figure 5. Histogram of the distribution of discriminant function scores for the two treatments.
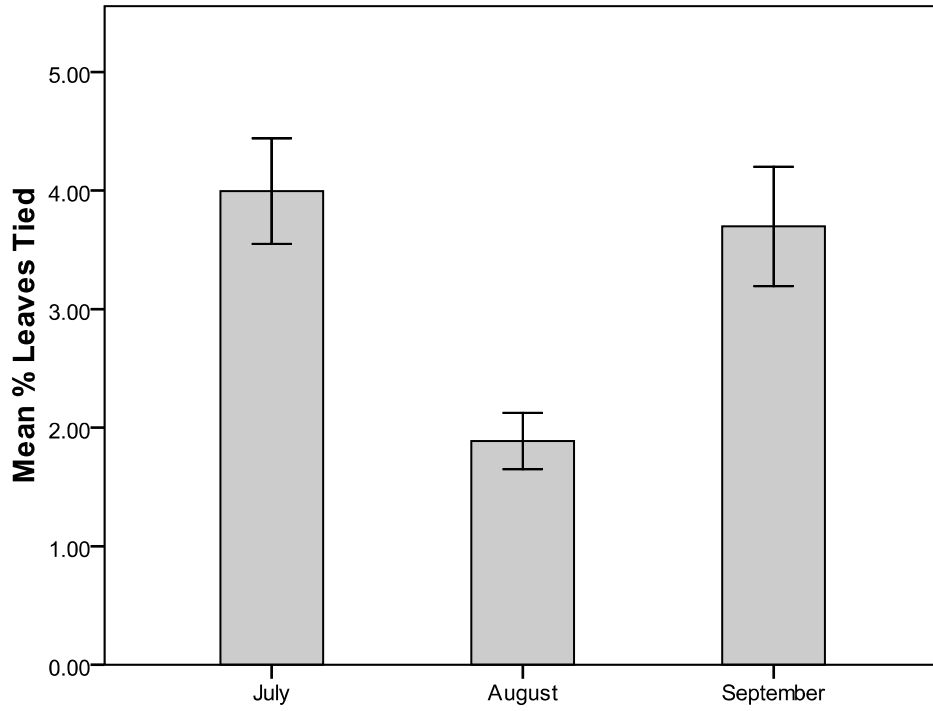
Figure 6. Seasonal variation in the percentage of leaves tied on control trees. Means ±1 SE.
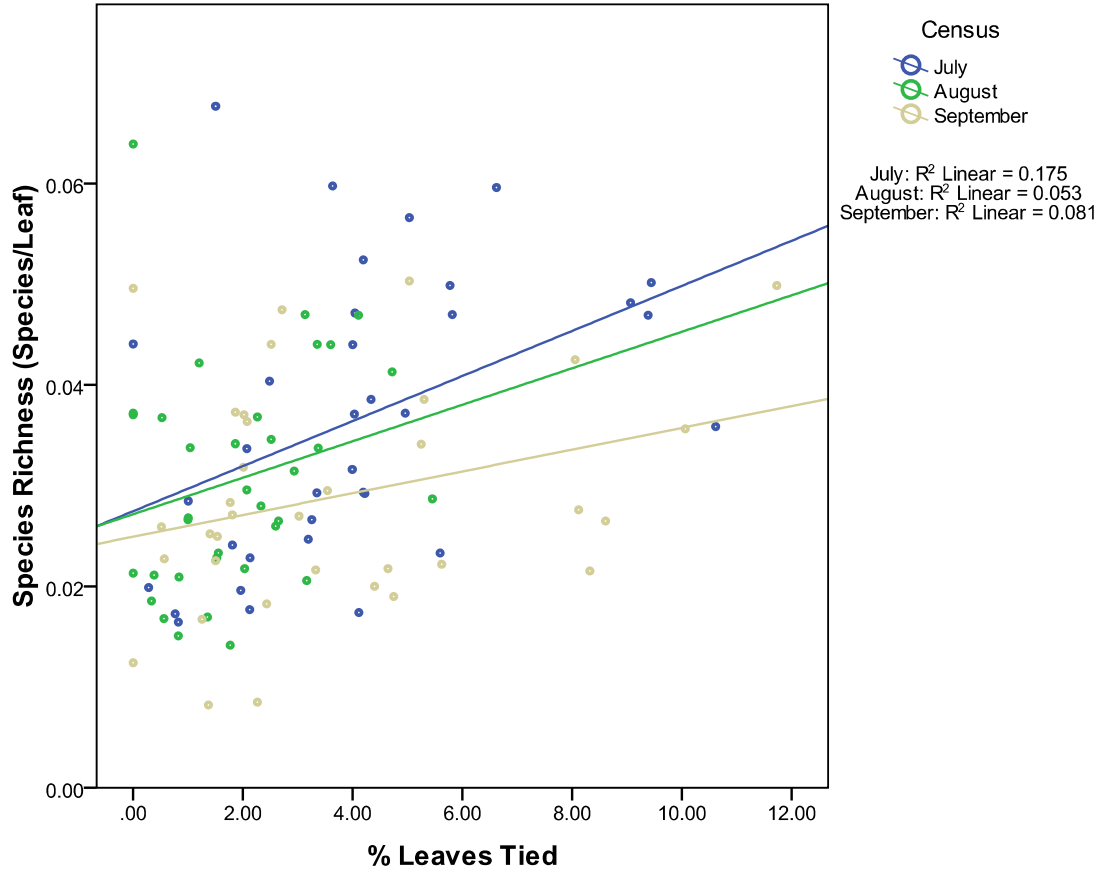
Figure 7. Scatterplot illustrating the within-census correlations between non-leaftying arthropod species richness and the percentage of leaves tied on each tree. July: *P* = **0.0123**, August: *P* > 0.10, September: *P = 0.0973*.
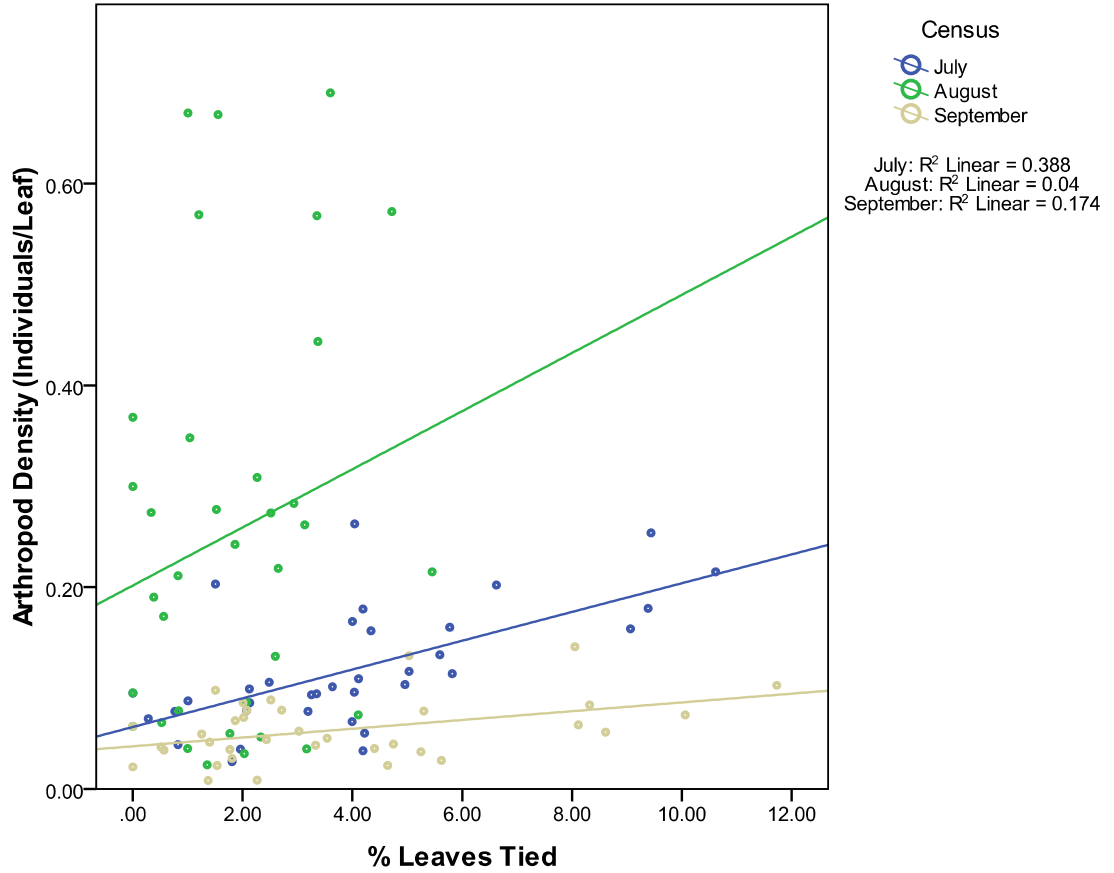
Figure 8. Scatterplot illustrating the within-census correlations between non-leaftying arthropod abundance and the percentage of leaves tied on each tree. July: *P* < **0.0001**, August: *P* > 0.10, September: *P* = **0.0128**.
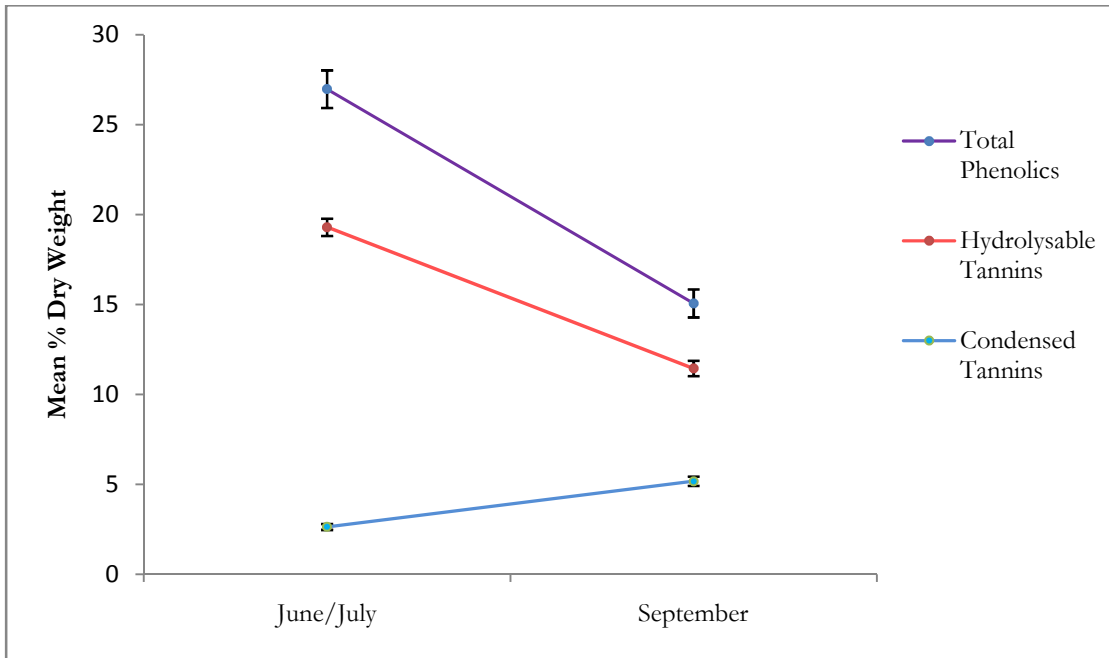
Figure 9. Seasonal variation in phenolic concentrations (% dry weight, ±1 SE) on all sample trees.

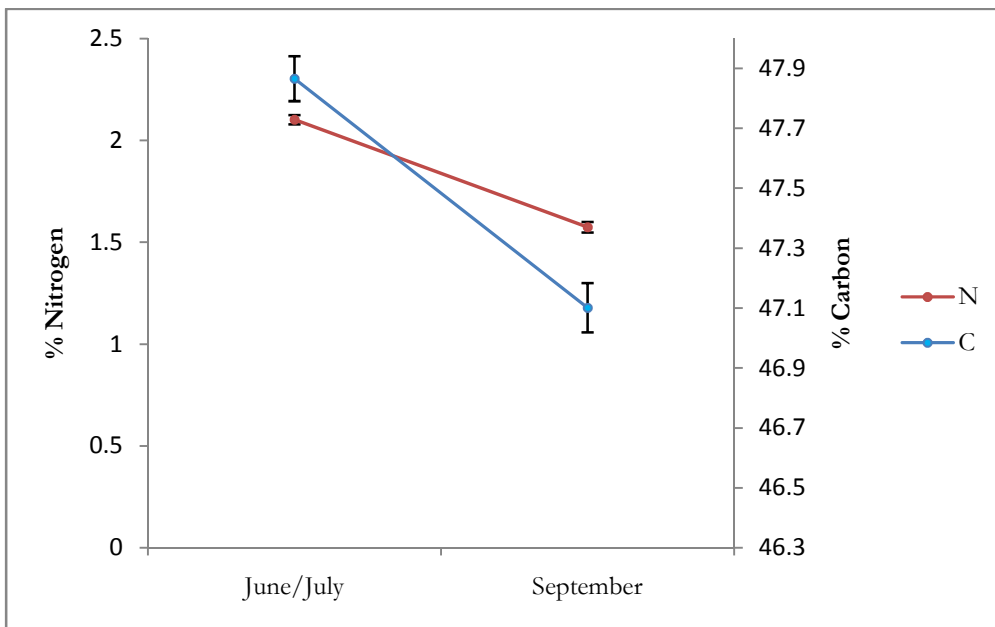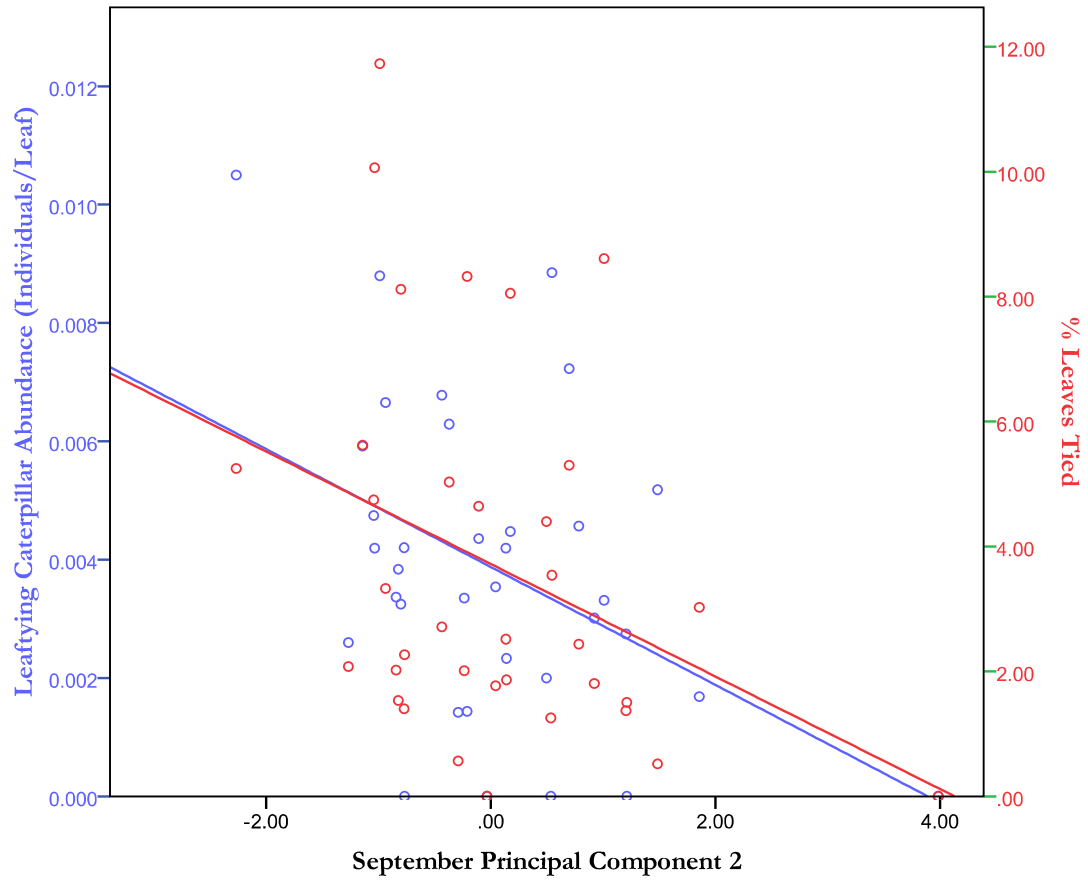Figure 10. Seasonal variation in elemental composition (±1 SE) on all sample trees.

Figure 11. Scatterplot illustrating the relationship between leaftying caterpillar abundance and percent tied leaves with September PC2, which was associated with high tannin concentrations and low nitrogen content. % Leaves tied: $r^2 = 0.120$, $P = \textbf{0.0430}$; Leaftying Caterpillar Abundance: $r^2 = 0.186$, $P = \textbf{0.0101}$.
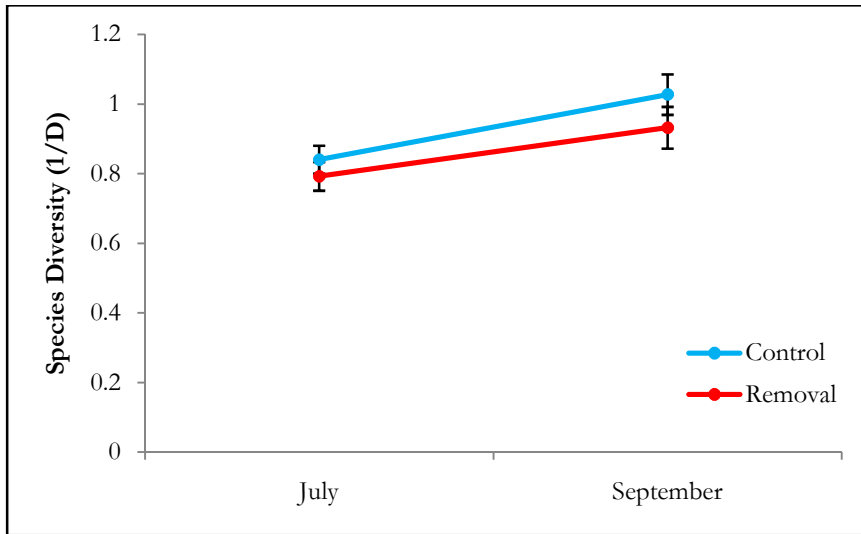
Figure 12a. **Low** quality plants, as determined by percent dry weight nitrogen and tannin concentrations. Seasonal variation in non-leaftying species diversity (1/D, mean ± 1 SE) between treatments.
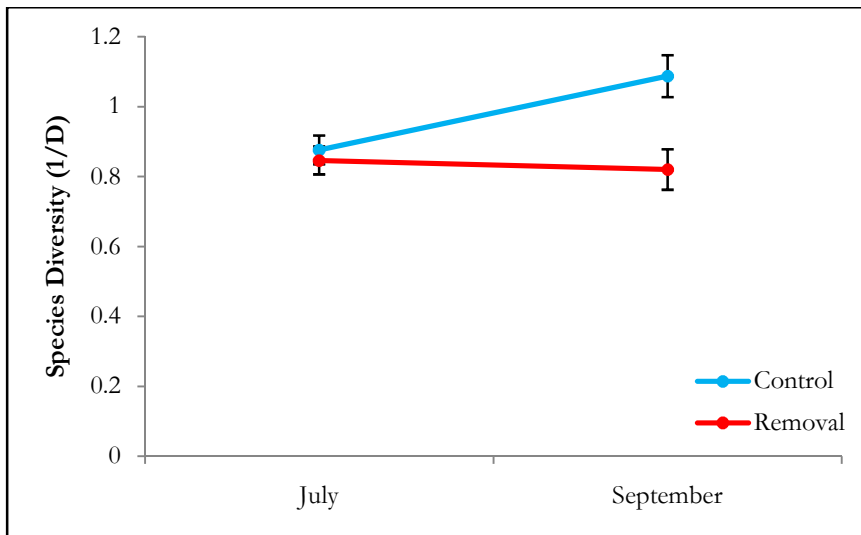
Figure 12b. **High** quality plants, as determined by percent dry weight nitrogen and tannin concentrations. Seasonal variation in non-leaftying species diversity (1/D, mean ± 1 SE) between treatments. Treatment x Quality effect was marginally significant; *P = 0.0740*.

Figure 13a. Mean arthropod abundance (**all** non-leaftying arthropods) between control and treatment trees of different quality levels. Treatment x Quality effect was significant at $P =$ **0.0110**.
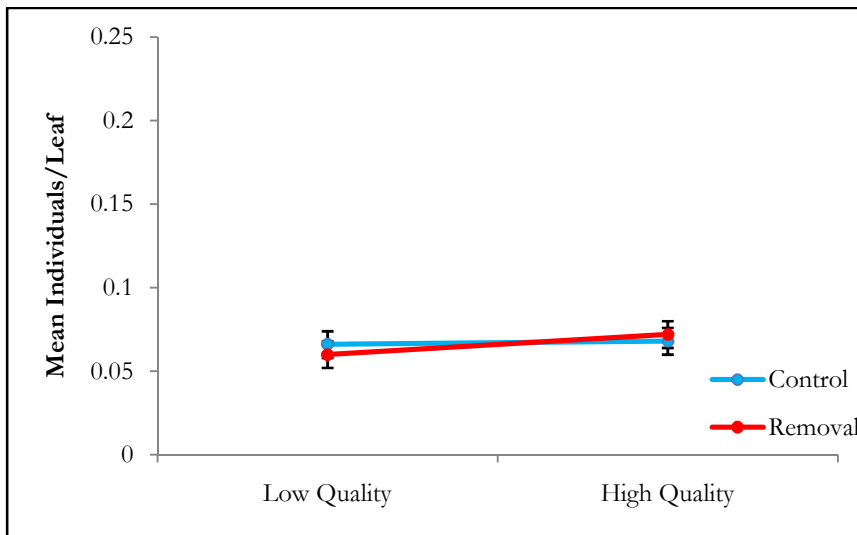
Figure 13b. Mean arthropod abundance (**excluding Psocoptera**; non-leaftying arthropods) between control and treatment trees of different quality levels. Treatment x Quality effect was not significant; $P = 0.4445$.

Table 1. Repeated-measures ANOVA for non-leaftier species diversity between two leaftier treatments across three censuses.

Source	df	F	P
Between subjects			
Treatment	1, 68	9.523	**0.0029**
Within subjects			
Census	2, 136	51.453	**< 0.0001**
Census x Treatment	2, 136	1.573	0.2110

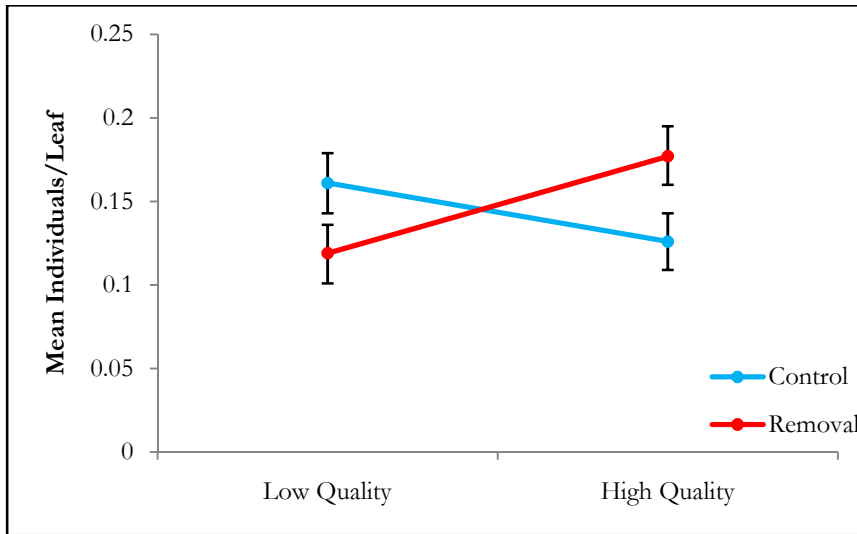Table 2. Repeated-measures ANOVA for non-leaftying arthropod abundance between two leaftier treatments across three censuses.

Source	df	F	P
Between subjects			
Treatment	1, 68	0.067	0.7970
Within subjects			
Census	2, 136	51.643	**< 0.0001**
Census x Treatment	2, 136	1.573	0.6733

Table 3. Repeated-measures ANOVA for non-leaftying arthropod community similarity within and between treatments across three censuses.

Source	df	F	P
Between subjects			
Treatment	2, 2374	37734.728	**< 0.0001**
Within subjects			
Census	2, 4748	1671.067	**< 0.0001**
Census x Treatment	4, 4748	332.924	**< 0.0001**

Table 4. Correlations between guilds and the standardized discriminant function. Guilds are ordered by size of structure matrix correlation within the function.

Predictor	Structure matrix correlations[a]	Standardized discriminant function coefficients[b]
Chewing herbivores	0.736	0.554
Free-feeding caterpillars	0.336	-0.394
Leaf miners	-0.175	0.802
Insect predators	-0.17	-0.338
Sucking herbivores	-0.094	-0.582
Arachnids	0.094	0.169
Detritivores	0.085	0.208
Non-leaftying shelter builders	0.037	0.001

[a]Pooled within-groups correlations between guilds and the standardized discriminant function.
[b]Discriminant coefficients (weights) of each guild in the discriminant function.

Table 5. Classification table for the discriminant function. Rows indicate observed categories, while columns indicate predicted categories. Cross-validation is performed by classifying each sample by the function derived from all other samples.

			Predicted Group Membership		
		Treatment	Control	Removal	Total
Original[a]	Count	Control	25	10	35
		Removal	8	27	35
	%	Control	71.4%	28.6%	100.0%
		Removal	22.9%	77.1%	100.0%
Cross-validated[b]	Count	Control	19	16	35
		Removal	12	23	35
	%	Control	54.3%	45.7%	100.0%
		Removal	34.3%	65.7%	100.0%

[a]74.3% of original grouped cases correctly classified.
[b]60.0% of cross-validated grouped cases correctly classified.

Table 6. Leaf quality variable loadings in July and September for the first and second principal components (PCs). Total variance explained is the percent of total variation in leaf quality explained by each PC for that month.

Variable	July		September	
	PC1	PC2	PC1	PC2
Condensed tannins	.756	-.131	-.113	.884
Hydrolysable tannins	.531	-.316	-.395	.405
Nitrogen	.159	.632	.587	-.255
Carbon	.812	-.146	.587	.088
Water	-.033	.727	-.595	-.525
Toughness	.544	.568	.774	.059
Total variance explained	30.6	23.2	30.2	21.6

Table 7. MANCOVA tables illustrating the effects of treatment, leaf quality, and treatment x leaf quality interactions on arthropod species richness and abundance.

	July			September		
	Wilks λ	F	P	Wilks λ	F	P
Treatment	0.961	1.282	0.285	0.999	0.039	0.962
PC1	0.914	2.963	*0.059*	0.934	2.225	0.116
PC2	0.971	0.936	0.398	0.893	3.766	**0.029**
Treatment x PC1	0.976	0.787	0.460	0.983	0.546	0.582
Treatment x PC2	0.984	0.497	0.611	0.991	0.274	0.761

Table 8. Leaf quality trait means (± 1 SE) for each of the designated quality groups for each census. Condensed tannins, hydrolysable tannins, total phenolics, nitrogen content, and carbon content are measured in percent dry weight. *F* and *P* values for differences between quality groups were determined using univariate ANOVAs.

	July				$F_{1,68}$	*P*
Variable	Low Quality		High Quality			
Condensed tannins	0.0298	(0.0027)	0.0208	(0.0013)	10.0450	**0.0022**
Hydrolysable tannins	0.2127	(0.0061)	0.1948	(0.0073)	2.9160	*0.0920*
Total phenolics	0.2985	(0.0160)	0.2719	(0.0133)	0.8681	0.3553
Nitrogen content	0.0206	(0.0033)	0.0216	(0.0032)	4.9702	**0.0291**
Carbon content	0.5529	(0.1014)	0.5492	(0.1071)	3.9333	*0.0510*
Water content	0.5694	(0.0194)	0.5985	(0.0205)	21.1920	**< 0.0001**
Toughness (g/mm²)	188.8860	(0.7905)	187.8075	(0.7911)	6.3573	**0.0141**

	September				$F_{1,68}$	*P*
Variable	Low Quality		High Quality			
Condensed tannins	0.0614	(0.0038)	0.0412	(0.0026)	22.1651	**< 0.0001**
Hydrolysable tannins	0.1315	(0.0060)	0.1019	(0.0051)	12.2266	**0.0011**
Total phenolics	0.1624	(0.0131)	0.1431	(0.0083)	1.4300	0.2361
Nitrogen content	0.0150	(0.0037)	0.0165	(0.0033)	7.9124	**0.0062**
Carbon content	0.5492	(0.1028)	0.5413	(0.1299)	0.0080	0.9310
Water content	0.5992	(0.0424)	0.6110	(0.0430)	0.3884	0.5351
Toughness (g/mm²)	189.0079	(0.8280)	187.5917	(0.8280)	6.0152	**0.0175**

Table 9. Repeated-measures ANOVA for non-leaftying arthropod species richness between two quality levels and two leaftier treatments across three censuses.

Source	df	*F*	*P*
Between subjects			
Treatment	1, 66	0.287	0.5941
Quality	1, 66	4.235	**0.0440**
Treatment x Quality	1, 66	0.887	0.3503
Within subjects			
Census	2, 132	9.108	**< 0.0001**
Census x Treatment	2, 132	0.148	0.8622
Census x Quality	2, 132	3.043	*0.0514*
Census x Treatment x Quality	2, 132	2.066	0.1310

Table 10. Repeated-measures ANOVA for non-leaftying arthropod species diversity (1/D) between two quality levels and two leaftier treatments across three censuses.

Source	df	*F*	*P*
Between subjects			
Treatment	1, 66	9.751	**0.0031**
Quality	1, 66	0.072	0.7890
Treatment x Quality	1, 66	3.273	*0.0740*
Within subjects			
Census	2, 132	50.932	**< 0.0001**
Census x Treatment	2, 132	1.510	0.2255
Census x Quality	2, 132	0.548	0.5801
Census x Treatment x Quality	2, 132	1.035	0.3579

Table 11. Repeated-measures ANOVA for non-leaftying arthropod abundance between two quality levels and two leaftier treatments across three censuses.

Source	df	*F*	*P*
Between subjects			
Treatment	1, 66	0.062	0.8041
Quality	1, 66	0.400	0.5289
Treatment x Quality	1, 66	6.789	**0.0110**
Within subjects			
Census	2, 132	54.951	**< 0.0001**
Census x Treatment	2, 132	0.405	0.6679
Census x Quality	2, 132	0.572	0.5657
Census x Treatment x Quality	2, 132	7.244	**0.0008**