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Factors Influencing Asiatic Oak Weevil Interactions with Native Ecosystem Engineers Over Time

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B.S., Biology, Albion College, 2006

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

in partial Fulfillment of the Requirements for the degree of

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THESIS ABSTRACT

I sought to build a model to predict current and future abundance of Asiatic oak weevil (Coleoptera: Curculionidae: Cyrtepistomus castaneus) by using the relative abundance of leaf tying and leaf rolling caterpillars. The Asiatic oak weevil is an exotic species that has been observed inside leaf ties and leaf rolls made by native Lepidoptera caterpillars. Chapter one is a review of the known relationships between animal constructs and exotic species. Within this review I transition from natural structures, to animal architects, and to ecosystem engineers and how they have a population dynamic impact on the invasive species. I also discuss the mechanisms behind why the exotic species is using the construct, and the ecological implications for the engineer and the natural community. In chapter two I present the meta-data analysis I performed on the Missouri Ozark Forest Ecosystem Project data that were collected over a period of 11 years. The focus of this analysis was to evaluate which variables are important for understanding the relationship between Asiatic oak weevils and leaf tying caterpillars and the relationships between Asiatic oak weevils and leaf rolling caterpillars. I found four main relationships. First, canopy counts from both types of shelter builders can be used to accurately predict Asiatic oak weevil abundance. The second finding was that if we are evaluating a region where the trees are mostly the same age then having understory and canopy counts from either group of shelter builders will increase the accuracy of predicting Asiatic oak weevils in that region. Third, clear cutting has a dramatic impact on the abundance of many species of insects including shelter building species and the Asiatic oak weevil. Finally, one can predict Asiatic oak weevil abundance two and three years into the future, based on the abundance of leaf rolling caterpillar.

KEYWORDS: construct, ecosystem engineer, animal architect, construct, exotic species, invasive species, shelter builder, leaf tiers, leaf rollers, Asiatic oak weevil

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Chapter 1

Use of Native Animal Constructs by Exotic Species

Abstract

This chapter reviews how animal constructs have a population dynamic impact on exotic species and how exotic species can significantly affect ecological communities through the use of native animal constructs. Natural and anthropocentric examples are examined identifying the possible mechanisms and ecological implications behind these relationships. The studies reviewed indicate exotic species use animal constructs to capture prey, avoid predation, obtain specific nutrients, find a mate, protect their young, and attract a host. Many of the studies examined are relatively limited in their depth and timespan, some of which with no experimentation. Although this lack of depth can be a significant limitation, indications are that success of exotics may in part be determined by the availability of constructs built by native engineers. More studies are needed to investigate the population dynamic impact of these relationships in the field, the larger community level implications of these relationships, and spatial associations between exotic species and native constructs.

Introduction

This chapter is a review of the current literature of how and why exotic species utilize structures within their colonized habitat. I distinguish between natural structures, like a tree hollow, from animal constructs, like a bird's nest. The sources of the structures are also discussed distinguishing abiotic forces, such as a storm, from an animal architect, such as a bee or a beaver. How these relationships might affect local communities and the native architect are also discussed. Significant impacts are measured in terms of changes in fitness. These measurements are changes in reproductive and death rates, and changes to their inhabited geographical range. This chapter gives examples of exotic species and native construct relationships and describes the ecological significance behind each. After the natural examples, this chapter discusses briefly how human structures are utilized by exotic species. This is important because by understanding how and why exotics use human structures might help clarify unexplained or misunderstood relationships found in nature. At the end of this chapter the commonalities of these different types of relationships are discussed highlighting what areas of this topic have been well studied and what areas of this topic need further research.

I. Background

Ia. Tests for Factors Influencing Population Dynamics

Decades of ecological research have focused on identifying the biotic and abiotic factors that impact populations of biological species. The variables commonly analyzed to determine if an impact is significant are changes to a population's reproductive rate, death rate, or geographic range, also known as species range limits (Benton and Grant 1999, Sexton et al. 2009). This chapter supplements research conducted within the Missouri Ozarks, a region that is mostly deciduous forest, on a variety of insect species using or building constructs. Numerous abiotic and biotic factors have already been shown to impact populations of forest dwelling insects. Such abiotic factors include; temperature (Karuppaiah and Sujayanad 2012), humidity (Antvogel and Bonn 2001), soil pH (Antvogel and Bonn 2001), and light levels (Antvogel and Bonn 2001). The known biotic factors include; leaf litter cover (Antvogel and Bonn 2001), availability of particular compounds (Pare and Tulinson 1999), inter- and intraspecific competition (Harvey et al. 2013), host plant richness (Knops et al. 1999), predators (Rosenheim 1998), parasites (Rosenheim 1998), pathogens (Rosenheim 1998), and the community’s biodiversity (Knops et al. 1999). Each species is affected by the listed variables differently. If light levels, for example, become too extreme, the reproductive rate or death rate will change, potentially influencing the geographic range of the evaluated species.

How might one determine the impact of changing temperature, for example? A researcher will begin by making observations about temperature in the field. He or she will then test the effects of different temperatures in a lab, and finally will experiment with temperature effects in the field. The researcher would measure the temperature at specific relevant sites and count individuals from the evaluated species. After the data has been collected, he or she would analyze it to see if there is a correlation between changes in temperature and changes in the abundance of the evaluated species at those specific locations. That analysis should reflect if there is an unbalanced change in the evaluated specie’s birth rates, death rates, or geographic range. This analysis would then provide support for whether temperature has a population dynamic impact on the evaluated species.

Much current research focuses on how global climate change will influence the biosphere because so many species are dependent upon a narrow temperature range. For example, Asian lady beetle (*Harmonia axyridis*) eggs were tested in a lab against a variety of monitored temperatures, ranging from 25-41°C. Naturally these eggs would be resting around 25°C. Each egg was exposed to higher temperatures for an hour at their designated temperature and then an hour at the natural temperature. The results showed an impact of heat exposure on successful egg hatching. Specifically, as the eggs were exposed to more heat, the likelihood of those eggs hatching decreased. The larvae from the eggs that were exposed to the highest temperature

(41°C) did not emerge, suggesting that this temperature extreme is intolerable for Asian lady beetles. The significance of this paper and many others is to highlight that global climate change may impact the reproductive rates of many species and the severity of that impact will depend on how much the temperature changes (Khaliq et al. 2014). However, maybe in normal conditions parasites, predation, or pathogens naturally prevent the same temperature intolerant eggs of the Asian lady beetle from hatching. If that is the case, then the temperature rising 5 to 10 degrees will likely not have a population dynamic impact on the Asian lady beetle.

This study highlights the importance of field tests and understanding the fundamental ecology of the population being studied. Field experiments are more desirable because their results are thought to more accurately represent what may occur naturally than the results from laboratory experiments. However, field experiments can be difficult because a researcher cannot control for all the variables that might influence their study like they can in a laboratory, not to mention maybe the variables being evaluated do not naturally occur today at the extremes being tested, such as in the Asian lady beetle study, so must be studied in a lab. Here is a different example of a study on the topic of population dynamics, but in this example the experiments were done in the field. The study aimed at gaining a better understanding of what contributes to the southern pine beetle's (*Dendroctonus frontalis*) oscillating populations, specifically evaluating predation. Within the field researchers sectioned off areas with cages to control for predators and recorded how the beetle population densities changed over time within and outside those protected cages across an entire five year increase-peak-decrease oscillation cycle. The results from this study strongly suggested that predation plays a significant role in the southern pine beetle population cycle (Turchin et al.1999). When the southern pine cycle was increasing the population measurements within and outside the protected cages were relatively the same, suggesting during this phase predation does not play a significant role. However, at the peak and decrease phases the southern pine beetle abundance dropped significantly outside compared to inside the protected cages, suggesting during these phases predation plays a significant role. The authors recognize that there are limitations to their study design, such as pathogens impacting the population densities, which they did not evaluate, but overall field studies like this one add tremendous value in understanding the ecological mechanisms behind natural interactions.

As mentioned earlier, controlling for all the natural variables acting upon the subjects of a study in the field is likely not possible, and is a common issue for field experiments. The methodologies described from the Asian lady beetle example and this southern pine beetle example show how scientific tests on the topic of population dynamics are performed within the lab and the field and the pros and cons of each. The results from a study suggesting a population dynamic impact should show how a population's abundance is changing at specific sites, like in the southern pine beetle example. Changes in abundance at specific sites likely reflect changes in the population's death rate, reproductive rate, or geographical range, which are our changes in fitness for evaluating population dynamic impacts. The evaluated variable and other influencing factors should be controlled for, experimentally or mathematically, to show as clear as possible the association being purposed. This typically consists of a treatment group and a natural group being studied, like how cages were used to control for predation within the southern pine beetle example and how those researchers assessed the beetles in both groups. For meta-analyses having a consistent experimental control is likely not possible. For these studies the variables being evaluated can be controlled for mathematically. An ANOVA is often used when testing variables across multiple groups and correlations or partial correlations are often used when testing variables within the same group. Incorporating the natural history and the known ecological relationships of the population being studied is also critical to showing how any one variable has a population dynamic impact.

Ib. Invasive vs Exotic Species

Invasive species are one of the biggest environmental problems today (Allendorf 2003). Invasive species can disrupt existing niches and outcompete natives. A common result is that invasive species increase interspecific competition (Sanders et al. 2002), prey upon native flora and fauna (Roemer et al. 2001), and bring new parasites to a region (Torchin et al. 2002). These factors are all known variables listed previously for influencing population dynamics.

Invasive species are often introduced into new areas by humans. Species that have their geographical range changed, for example when they are brought from one region to another, are called exotics. Exotic species can be outcompeted by the local flora and fauna (An et al. 2007). However, occasionally, and there are numerous cases of this, the exotic species starts spreading rapidly across the new area. This is an invasion. These successful invasions are typically the result of no to little local predation on the invasive species and the species' high reproductive capacity (Perkins et al. 2011).

Ic. Ecosystem Engineers and Animal Constructs

Living things use structures to avoid predation, capture prey, and to modulate abiotic factors such as temperature and humidity (Laland et al. 1999). When structures are nowhere to be found or already under intense competition, like in the open ocean, little fish, like the remora (family Echeneidae), often use bigger animals, like the manta ray (genus *Manta*), as structures to avoid getting eaten and help capture food. Other animals, such as termites, make huge mounds in a specific orientation to help regulate temperature (Korb 2003). Such mounds also are utilized by the local flora and fauna for example, the spotted gecko (*Gehyra pilbara),* to avoid predation and capture prey (Pringle et al. 2010). Additional animals that make structures are the prairie dog (*Cynomys)* which makes underground dens, the beaver (*Castor canadensis)* which make dams in bodies of water, and honey bees (*Apis*) which make hives above and below ground. The act of making, modifying, and reusing structures in the animal kingdom is common and the builder is referred to as an animal architect (Allred 1986). The structures built by animal architects are known as constructs. These constructs are critical for the survival of the architect but they often impact other species by influencing the availability of biotic and abiotic factors. Under these circumstances the animal architect is additionally known as an ecosystem engineer (Jones et al. 1996). Ecosystem engineers can be critically important to the functional health of many ecosystems and are often thought of as keystone species (Wright and Jones 2006).

Id. Exotic Species and Native Constructs

There has been little research on how invasive species interact with native constructs. The publications that exist on this topic suggest that the native constructs are used by the invasive species to help them survive in the new regions, for example, to help the invasive species capture prey, avoid predation, or raise their young. A recent study from the Missouri Ozarks showed that the exotic species, Asiatic oak weevil (*Cyrtepistomus castaneus*) selected host plants based on the abundance of leaf ties (Baer and Marquis 2014). Leaf ties are an animal construct made by many various species of caterpillars. These leaf ties have been shown to increase arthropod species density on trees (Wang et al. 2012). This is important because now there is clear evidence for ecosystem engineers' constructs influencing host plant choice by exotic species.

This then leads to additional questions such as what factors besides the presence of certain constructs influence the choices exotic species make in these new regions, and can we utilize the relationships between exotic species and native constructs to better predict and manage an invasion?

II. Exotic Species Utilizing Native Constructs

IIa. Exotic Species Utilizing Natural Structures to Avoid Predation

Exotic species have been shown to compete with native species over common habitat, causing the populations of those natives to crash, driving ecological shifts throughout natural communities (McNatty 2009). Tree cavities are an example of a natural structure, derived typically from abiotic forces such as a storm, which many animals use as a home. These structures are often under intense pressure from inter- and intraspecific competition because they provide a protective shelter against predation (Robertson and Rendell 1990). In the forests of Europe and northern Asia the Ural Owl (*Strix uralensis*) is facing a new threat from the invasive feral raccoon (*Procyon lotor*). The raccoon and the owl are both nocturnal and use tree cavities as shelters during the day. The raccoon population is on the rise and with that the availability of tree cavities for owls is declining. It is hypothesized that this competition for tree cavities will negatively impact the native owl because their suitable habitat to survive during the day will greatly diminish (Kobayashi et al. 2014). This is a smaller study but the relationship it highlights shows how an invasive species can reduce the availability of natural structures believed to be critical to the survival of native species.

IIb. Invasive Species Utilizing Native Constructs to Protect their Young

Within North America the European Starling (*Sturnus vulgaris*) is a common invasive exotic species that often steals other birds' nest material (Veiga et al. 2013). There are many bird species that share this behavior but it can be particularly problematic when an exotic species has this behavior because they directly displace native birds. Bird nests shelter assist in attracting mates and protecting eggs and chicks. Roughly 200 years ago both the European Starling was introduced to North America (Chapman 1906). Since then they have spread across the United States and Canada taking material from native bird nests to use in their nests for attracting a mate and protecting their eggs and chicks. This has negatively impacted many native bird species and even displaced several from specific regions for years, such as Olive-sided fly catcher (*Contopus borealis*) in parts of northwestern Nevada (Weitzel 1988). These birds are also very territorial increasing interspecific competition within many sought after nesting locations (Weitzel 1988). The European Starling is a clear example of how invasive exotic species can utilize native constructs to help attract a mate and protect their young.

Another less well known example is the Buffalo Bird (*Molothrus*). These birds used to live across the northern plains with the native Buffalo (*Bison bison*) but after humans plowed the plains into farmland the range of the Buffalo Bird changed (Friedmann 1929). The Buffalo Bird has a unique behavior, and that is it lays its eggs in other birds' nests (Friedmann 1929). This behavior relieves the parenting duties of the mother Buffalo Bird by entrusting the well-being of their offspring to another bird that is unaware of the situation. When the Buffalo Bird's starting invading the rest of the Midwest it soon started laying its eggs in new species of bird nests. Like the sparrow and starling example, this too has had negative impacts on many species of native birds evolutionarily not adapted to living with Buffalo Birds (Hill 1976). Over the past few hundred years this relationship has reshaped many populations of North American bird species across the plains, such as horned larks (*Eremophila alpestris*) which have adapted to have an earlier breeding season likely due to the Buffalo Bird (Hill 1976). With the extermination of the American Buffalo, the Buffalo Bird became known as the Cowbird. This Cowbird example is another way invasive species utilize native constructs to benefit their offspring.

IIc. Exotic Species Utilizing Native Constructs to Capture Prey

In southern Florida is a region that is one of the most diverse places in the United States, the Everglades. Exotic species are a big problem in the Everglades, in fact at least 37 non-native reptile and amphibian species live in southern Florida and they all have established themselves within the last 25 years (Meshaka 2000). One of those invasive problems is the Burmese Python (*Python bivittatus*). The Burmese Python is one of the largest snakes in the world and is from southern Asia. Within the Everglades the number of these pythons is exponentially growing because they have established a healthy breeding population causing native populations of small mammals to crash, such as the marsh rabbit. It has been hypothesized that by driving these small mammals to possible extinction, community level changes across the ecosystem will occur (Holbrook and Chesnes 2011). A common hunting strategy for these pythons is to find holes, typically near river banks, and slither their way in looking to catch unsuspecting prey. Holes, burrows, and dens are common constructs. Many animals use these tunnels besides the animal architect, but for the small mammals of the Everglades, they are not evolutionarily adapted to share these constructs with exotic pythons. This example shows how an exotic species can use native constructs to prey upon the natives that naturally use constructs. The natives in this scenario are suggested to be negatively impacted by this relationship because they are being eaten, specifically their death rates are increasing (Dorcas et al. 2011), and the exotic is benefiting from this relationship because they are being well fed, possibly playing a significant role into why their reproductive rate is exponentially growing (Dorcas et al. 2011).

IId. Exotic Species Utilizing Native Constructs to Obtain Nutrients

Ant mounds are constructs built to benefit ant colonies that consequently change the nutrient makeup of the surrounding soil. Similar to termite mounds, ant mounds are thought to help regulate the temperature of the eggs and the young inside the mounds. The impact from the nutrient changes in the soil near ant mounds has been shown to positively influence exotic plant species invasions (Berg-Binder et al. 2012; Farji-Brener 2010). Specifically the mounds from the ant species, *Acromyrmex lobicornis*, can increase the abundance of exotic plant species, *Carduus nutans* and *Onopordum acanthium*, 600% compared to areas away from ant mounds (Farji-Brener and Ghermandi 2008). These exotic plants can flourish in new areas because of the impact of native ants' constructs. This example illustrates how the relationship between an exotic species and native's constructs can help the exotic obtain needed nutrients.

III. Exotic Species Modifying Native Constructs

IIIa. Exotic Species Adding to Native Constructs

The nutria (*Myocastor coypus*) is a large South American rodent that spends most of its life in or around freshwater. The nutria has been introduced to various other parts of the world by people wanting to sell their fur (Jojola et al 2005). The nutria has established in several regions of the US, including the East Coast and the South. Native North American animals with overlapping niches include groundhogs (*Marmota monax*), muskrats (*Ondatra zibethicus*), beavers (*Castor* *canadensis)*, and river otters (*Lontra canadensis*). The Nutria often uses abandoned burrows and lodges from these North American mammals and make them their own for protection against predators. The Nutria will customize their new home to fit their needs. This typically means making the tunnels and underground dens bigger. The act of expanding these existing holes creates instability in the ground above (Jojola et al 2005), often causing the lake or river banks to crumble. This is particularly a problem for the native vegetation and the humans that have houses built on these sensitive spots. The nutria is an example of how exotic species can add to natives’ constructs and the possible negative implications of making such additions.

IIIb. Exotic Species Destroying Native Constructs

One of Earth’s most critical yet often overlooked ecosystem engineers is the coral reef. The largest coral reef system is the Great Barrier Reef (GBR) off the coast of Australia. Thousands of species relay on the coral of the GBR for shelter and food. In 1975 management of GBR began by the Great Barrier Reef Marine Park Authority. Between 1985 and 2012, the GBR saw nearly a 50% drop in coral cover (De’atha et al 2012). Roughly 47% of the coral decline during these years was attributed to the crown of thorns starfish (COTs, *Acanthaster planci*) (Lucas 2013). The COTS is an invasive species that feeds directly on the tissue of many hard corals. The COTS can reproduce extremely fast, resulting in regional outbreaks. Throughout the years of these COTS outbreaks, the unmanaged reefs had up to a 60% decline in biomass in their reef fish compared to their adjacent ecologically managed reefs (Bellwood et al. 2004). This suggests that the impact from the COTS on the GBR transcended the physical damage of the corals to the greater community of organisms living on and depending on coral reefs. This is a well-studied example of how the destruction of an ecosystem engineer's constructs can alter the composition of an entire ecological community.

IV. Exotic Species Directly Altering Ecosystem Engineers

IVa. Exotic Species Acting as Parasites to Ecosystem Engineers

A new addition to the research being done on ecosystem engineers is behavior changing parasites. There are many examples of parasites altering the behavior of their host but until recently no one has investigated this relationship for ecosystem engineers. Parasites are often found within the stool of animals. This begs the question, what about ecosystem engineers that interact a lot with fecal material, are their constructs impacted by parasites? The dung beetle (order *Coleoptera*, subfamily *Scarabaeoidea*) was studied just for this purpose. Dung beetles are ecosystem engineers that build structures out of fecal material on the forest floor. Many plant species, such as *Micropholis* guyanensis, get their seeds dispersed through the structures and activity of dung beetles (Andresen 2001). The parasites that live within some dung beetles were shown to impact their behavior specifically influencing their abilities to build constructs (Boze et al. 2012). This research team compared infected to uninfected dung beetles and measured how much fecal material they consumed. Their results show infected dung beetles remove less overall stool from the forest floor and at a slower rate than uninfected dung beetles. The parasites in this relationship are nematodes (*Streptopharagus pigmentatuss* and *Physocephalus sexalatuss*) and they are hypothesized to change the behavior of the dung beetle to make them more susceptible to predation so these parasites can enter their final host, various birds and mammals. When changing dung beetle behavior they impact their ability to dig and move dung. By changing the amount of available fecal material in the forest, which is used by many different species of plants, animals, and fungi for nutrients, these parasites become a proxy ecosystem engineer. We know exotic parasitic nematodes can become an invasive species, such as the *Anguillicola crassus* on the American Eel (*Anguilla rostrata*) (Barse and Secor 2011) but too little is known about *Streptopharagus pigmentatuss* and *Physocephalus sexalatuss* to suggest that they are invasive species. This example is from a small study, but it illustrates a very possible relationship that might or one day may exist that currently is not being evaluated in population dynamics research, and that is invasive behavior chaing parasites the influence the constructs built by ecosystem engineers.

IVb. Exotic Ecosystem Engineer Mutually Benefiting Other Exotic Species

Many ant species help disperse the seeds of a variety of plant species. This example is unique in that an exotic ant species is promoting the recruitment of an exotic plant species over native plant species. The exotic ant species is the European fire ant (*Myrmica rubra*) and the exotic plant species is the tetterwort (*Chelidonium majus*). This system was studied in southern Ontario where native ant species and this exotic ant species were evaluated in the lab and in the field to understand their choices on selecting seeds. Ants often collect plant seeds to take them back to their colonies to eat. Their colonies live within constructs above and below the ground. These fire ants live within nests. These nests change the availability of surrounding resources impacting the regional soil quality (Lafleur et al. 2005) making them an ecosystem engineer. The native ants did not gather and hence did not disperse the invasive plant’s seeds whereas the invasive ant did gather and disperse the invasive plant’s seeds (Prior et al. 2015). In this example, both exotic species are benefiting from each other’s presence. The ants are getting the seeds they need for their colony and along their journey some of the seeds fall onto the ground helping disperse the tetterwort's seeds. The behavior and relationship of multiple exotic species acting upon each other is rarely studied but in this example we see how an exotic ecosystem engineer can help other exotic species establish themselves within a new area. This is important because these exotic synergistic relationships can significantly drive ecological change (Prior et al. 2015).

IVc. *Exotic Species Benefiting Native Ecosystem Engineer*

An exotic microbe from the Indian and Pacific Oceans, *Symbiodinium trenchii,* is helping to momentarily reduce coral bleaching in the Caribbean Sea from rising water temperatures and other coral stresses (LaJeunesse et al. 2009). Dinoflagellates live inside most corals. They obtain their energy from the sun and the corals can use energy but in return their coral provide a suitable and stable home for these algal-like organisms. Unfortunately for Caribbean corals the native dinoflagellate, *Symbiodinium zooxanthellae,* is very sensitive to changes in temperature. When these dinoflagellates die the color of the coral changes to white, and the reef slowly starves to death, which is referred to as coral bleaching. Recently this exotic dinoflagellate, *S. trenchii*, has been introduced to the Caribbean and because they are more temperature tolerant than the native dinoflagellates they are reviving many regions by occupying the stranded but still alive corals. In this relationship the native corals and the invasive dinoflagellate benefit each other. For the time being the only obvious negative impacts are on the Caribbean's native dinoflagellates. The future of the Caribbean's coral reefs are undoubtedly in jeopardy, but this is one very rare case where an exotic species may be beneficial to a critically important native ecosystem engineer.

IVd. Exotic Species Preying upon Animal Architects

Australia has a number of exotic invasive pests, one of which is the house gecko (*Hemidactylus frenatus*). As this may be obvious, this species of gecko has become an urban wildlife issue for many home owners because it lives on and inside houses. A group of animal architects and critical pollinators for most of the country are bees and wasps specifically the paper wasp (*Polistes*) and the stingless bee (*Trigona*). Both the paper wasp and the stingless bee build nests for the protection of their young and the queen. These nests are an easy visual target for house geckos. House geckos are insectivores and feed upon bees and wasps at a rate of eight individuals per hour (Vyas 2012). Some have questioned what the larger impact of this predation will have on many regions of the country. In this relationship the exotic house gecko is benefiting from being able to easily identify and obtain a food source because they can see the nest constructs. The bees and wasps are likely being impacted negatively because the death rates for the worker bees are increasing. It has also been shown that the plants these wasps and bees pollinate are declining in number in and around urban areas (Cisterne et al. 2014). There are many factors influencing the population decline of these plant species but these house geckos targeting and consuming large numbers of their pollinators is thought to play a significant role. This example is from a small study but it illustrates how animal constructs can be used by exotic species to target and prey upon the architect.

V. Exotic Species Benefiting from Human Made Structures

Va. *Exotics Taking a Ride on the Vessels of Human Transportation*

The human (*Homo sapiens*) species has attracted many hitchhikers over the millennia. Exotic species have established populations in many new areas because of human travel. Humans travel across the globe by many different types of vessels. In Hawaii airplanes brought the brown tree snake (*Boiga irregularis*). This invasive species has caused ecological and anthropocentric problems (Fritts 2002). Their path of destruction spans from eating native bird eggs to electrocuting themselves in transformers and electrical boxes bringing hundreds of power outages every year.

Across most of North America many lakes and streams have had to deal with the impacts of the zebra mussel (*Dreissena polymorpha*). These tiny mussels are very efficient at filtering water. Most bodies of water where zebra mussels have invaded eventually see increases in underwater visibility because of how more effective they are at filtering water compared to the native mussels. However, they also communally grow in tight places, like the exhaust systems of boats. Zebra mussels have been shown to drive the extinction of native mussels because of competition (Baker and Levinton 2003) and have caused countless boat owners havoc (Ricciardi et al 1998). Zebra mussels are notorious for traveling via boats to new bodies of water, setting the stage for a new invasion.

However, the most common type of vessel exploited is the automobile. Our cars transport moths, pets, seeds, and more all across the land. An example in southern California is the Asian mustard (*Brassica tournefortii*) (Trader et al. 2006). This plant is not native to North America but has established itself in many regions of the southwest. A common method for how this plant is dispersing is through its seeds attaching themselves to cars and those cars then drive many miles to places such as California. The seeds eventually detach from the automobiles and get picked up by the wind landing in a new home. For California and regions of the Southwest these Asian mustard plants are outcompeting native species, significantly changing those natural communities. How humans travel directly influences how the spectrum of life moves across our planet. Without a conscience effort on our part exotic species will continue to hitch a ride with us where ever we go, even outer space (Kim et al. 2013).

VI. Conclusion

VIa. The future of Exotic Species and Animal Construct Research

There is still a lot to be studied for us to gain a better understanding of exotic species and how they interact with native constructs and animal architects. Just within the examples from this chapter I have identified the following mechanisms for which exotic species can and do benefit from animal architects: avoiding predation, enabling predation, raising their young, obtaining nutrients, finding a host, and expanding their range. Examples of exotics using constructs to capture prey or avoid predation are well established. However, more studies are needed investigating when, why, and how exotics alter an animal architect to affect its constructs. An additional mechanism we discussed from how exotics use human structures but not ecologically discussed is exotic species utilizing a construct to assist in finding a suitable mate. All of these mechanisms directly influence the fitness of the individuals within the populations being evaluated. Additional studies should investigate what factors and combination of factors impact exotic species with how and when they utilize native constructs. Having a better understanding of these relationships will enable scientists to better predict invasions and possibly be able to help manage their ecological and anthropocentric impacts. On this same topic, another question that should get researched further is the spatial relationships between native constructs and exotic species. Specifically, do we see native constructs influencing what regions exotic species invade successfully? This is has yet to be fully investigated. Hopefully by obtaining some of these results common lessons and patterns can be defined so that they can be utilized by conservation departments across the globe.

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Chapter 2

Title Factors Influencing Asiatic Oak Weevil Interactions with Native Ecosystem Engineers Over Time

Abstract

The Asiatic Oak Weevil (*Cyrtepistomus castaneus*) is an exotic species found in deciduous forests throughout the eastern and midwestern regions of the United States. The Asiatic oak weevil has been shown to preferentially choose host plants based upon native ecosystem engineers' constructs (Baer and Marquis 2014). This study's focus was on investigating what factors influence Asiatic oak weevil's relationships with native ecosystem engineers. Specifically leaf tiers and leaf rollers from the Missouri Ozarks were the ecosystem engineers studied, and the ecological and anthropocentric factors analyzed were host plant species, slope face of host plant, stratum, diameter of host plant, site age, and land management history of region. The data contributing to this study was from an eleven year meta-analysis derived from the Missouri Ozark Ecosystem Project. There are four main results from this study. First, counts of leaf tying caterpillars (r=0.604) and leaf rolling caterpillars (r=0.645) from the canopy are the single best variable for estimating current year Asiatic oak weevil abundance. Second, knowing the age of the forest being evaluated and having leaf tying caterpillar (r=0.976) and leaf rolling caterpillar (r=0.987) counts from both the canopy and the understory is the best combination of variables for estimating a region's Asiatic oak weevil population. Third, whether or not a region has experienced clear cutting impacts overall insect abundance (p=0.0263). Fourth, to accurately predict future Asiatic oak weevil abundance in a region, only leaf rolling caterpillar counts are needed (r=0.81 for two years into the future and r=0.92 for three years into the future). These findings would not be possible without the support of years of data collection from funded basic

ecological research. The implications of these findings could help conservation departments prevent, monitor, and control exotic species outbreaks.

Introduction

Many factors have been hypothesized, evaluated, and shown to help establish populations of exotic species into new areas, such as the number of invasion events, the number of exotics at each invasion event, the native species diversity of the invaded site, and the rate of reproduction of the exotics (Kolar & Lodge 2001). Exotic species are the source of some of the most significant environmental problems today, as approximately 42% of the species on the US threatened or endangered list are there because of alien-invasive species (Pimentel et al. 2005). Non-native forest insects cost the U.S. roughly 2.5 billion dollars annually (Aukema et al. 2011), and exotics across all avenues of life cost the U.S. roughly 120 billion dollars annually (Pimentel et al. 2005).

There are many examples in which exotic species directly impact native constructs. Engineered constructs alter the micro environment, mitigate predation, and often provide access to food benefiting the animals utilizing those structures (Crain & Bertness 2006, Jones et al. 1994). The success of these exotic species might be tied to how they use or inhibit others from using these native constructs. A few examples include the crown of thorns starfish invading the Great Barrier Reef eating away at the coral tissue for sustenance, consuming the reef structure, resulting in many native fish populations crashing (Bellwood et al. 2004), European Starlings invading North America forcefully taking over native bird nesting sites (Linz et al. 2007), and the Asiatic oak weevil (*Cyrtepistomus castaneus*) utilizing leaf tying caterpillar leaf shelters to possibly avoid predation (Baer and Marquis 2014).

The focus of this study was to investigate the possible relationships between the Asiatic oak weevil and native ecosystem engineers. Relationships between exotic species and native animal constructs are understudied but recently the Asiatic oak weevil was shown to preferentially select host plants where leaf-ties, a type of ecosystem engineered construct, were present (Baer and Marquis 2014). The implications from such research could impact our fundamental understandings of evolutionary ecology and practically impact our methods of conservation management.

The Asiatic oak weevil is an exotic species in North America that has invaded many forested regions spanning from the east coast of the United States to the Midwest (Frederick and Gering 2005). The Asiatic oak weevil was first detected in 1933 in New Jersey and has been observed feeding on a wide variety of deciduous tree species (Frederick and Gering 2005). Asiatic oak weevil larvae feed on the roots of their host plant while their adults feed on leaves (Baer and Marquis 2014). Orkin classifies the Asiatic oak weevil as a pest because they are attracted to houses when in search for a place to hibernate but they are believe to not cause any damages (Sanders 1997). However, certain weevils can and do kill trees across large geographic regions (Nordlandera et al. 2011).

Forest insect ecosystem engineers acting on the leaves of trees are categorized by the shape of the leaf structure they create, such as leaf-ties, leaf-rolls, leaf-tents, and leaf-curls. These structures around the Missouri Ozarks are produced by many different species of leaf chewing arthropods. Approximately 25% of herbivores found on Missouri Ozark oaks (*Quercus* sp.) build leaf shelters (Marquis unpublished data). The derived leaf structures might act as micro roads, highways, and rest stops for insects, spiders, and other arthropods to utilize for accessing the various regions of a tree safely. These structures get used as shelters for laying eggs, places to feed, and locations for pupation (Aiello and Solis 2003). All shelter builders identified for this study were lepidopteran larvae. Previous studies have shown a positive relationship between Asiatic oak weevil adult abundance and leaf tying caterpillar leaf tie abundance across trees of white oak in the same year, signifying that the effects of an ecosystem engineer can impact local distribution of an invasive species (Baer and Marquis 2014). The goal of this particular study was to identify the ecological and anthropocentric variables that impact the relationships between Asiatic oak weevils and leaf tying caterpillars' leaf ties and identify any new relationships between Asiatic oak weevils and leaf rolling caterpillars' rolled leaves. The driving hypothesis was Asiatic oak weevil abundance is dependent upon the abundance of leaf ties and leaf rolls, which are dependent upon the host oak species, slope face from the sampled tree, stratum, tree diameter, how long the surrounding forest has been managed (site age), and the regional land management practices. Spillover impacts, which are the byproducts of a relationship, and delayed impacts of leaf tying caterpillar and leaf rolling caterpillar abundance may also be important to Asiatic oak weevil success.

Methods

The data sets used in this study were derived from the Missouri Ozark Forest Ecosystem Project (MOFEP). At least a dozen research studies contribute to MOFEP, with an overarching goal to conduct the scientific research needed to understand how to keep the forests of the Missouri Ozarks safe while enabling the economic development of the timber industry.

The experimental design and collection procedures consisted of gathering data from trees within defined stands. The stands were often defined by a shared ecological factor such as slope aspect. Stands exist within plots, which are semi equally spaced out across each site. Sites were defined by their local management treatment history and range in age from 63 to 90 years old for how long they have been under the management of the Missouri Department of Conservation. Before being acquired by the state, these sites were mostly farmed. Further details can be found in Forkner et al. (2006). Figure 1 shows the geographic regions survived. This region consists of nine sites and 78 plots. From all the plots surveyed 1,438 trees were found to have Asiatic oak weevils, leaf rolling caterpillars, or leaf tying caterpillars. These collections happened from the years 1993 through 2004, with the exception of 1996. In the year 1996 no trees were surveyed because tree harvest took place. Many people throughout the study participated in the collection process. The collection process consisted of traveling to our defined sites and meticulously searching through the leaves of the oak trees within each site for hours at a time. Traveling to these sites typically happened weekly, often multiple times a week, between Spring and Autumn. When specimen were found, the participant then identified them, counted them, and recorded how many leaves at that tree they investigated. When possible, the participants would also record; the slope aspect of the tree, GPS coordinates, and the host plant species. Bucket trucks were used to collected canopy data from trees that could be sampled safely. Across the 10 years sampled, Asiatic oak weevils, leaf rolling caterpillars, or leaf tying caterpillars were counted from 101 trees every year sampled. These 101 trees add extra value because they show how Asiatic oak weevil, leaf rolling caterpillar, and leaf tying caterpillar abundance fluctuates year to year on any one specific tree. This set of 101 trees is referred to as the subset group throughout the analysis.

Statistical Analysis

The host plant species, tree diameter, local forest management history, stratum, slope, and site age, were the variables analyzed to model what factors significantly play a role in Asiatic oak weevil, leaf rollers and leaf tiers abundance. Many of the variables could not be gathered from every tree. For instance, canopy collection only happened from trees on ridge tops. Trees on ridge tops are not on a slope. Also, there were no canopy collections from the paired analysis when clear cut plots were compared to adjacent untouched plots. All relationships found to be significant across the study were then evaluated across the subset group and across the entire study again but with staggered years (1,2,3, & 4). For example, an analysis of one staggered year would compare a current year's leaf tying caterpillar and leaf rolling caterpillar normalized counts to the following year's Asiatic oak weevil normalized counts (Fig.2). These added evaluations help clarify tree specific biases and help identify spillover or delayed impacts.

Raw Asiatic oak weevil, leaf tying caterpillar, and leaf rolling caterpillar roller counts were normalized based by leaf area censused per tree. To do this the number of insects encountered was divided by the average leaf size for the tree species (*Quercus alba*: 0.00587 m^2 and *Q. velutina*: 0.00967 m^2 respectively (Forkner et al. 2006)) multiplied by the number of leaves sampled from that tree that year. Pearson product-moment correlation coefficients and Ps were calculated with R version 2.15 using the cor and cor.test functions for each variable. Groups of variables were also tested to check for possible synergistic significance. For example, maybe the tree species and the slope aspect are independently not explaining any Asiatic oak weevil relationship, but together can expose a significant finding. Tables and figures were produced with Excel v2010 and the data manipulation for extracting and organizing each piece for analysis was performed with perl and bash scripting.

The following variables were tested for effects on Asiatic oak weevil abundance: tree species (black versus white), stratum (canopy versus understory), land management history type (clear cut vs paired non clear cut plots), and north east vs south west slope facing trees, bins of tree trunk diameters (broken up into five ranges) and bins of site ages (broken up into five age groups ranging from 1925 – 1952). I did not define an arbitrary correlation coefficient cutoff value to define significance. Instead I compared correlation coefficients to identify what factors were most significant for predicting current year Asiatic oak weevil abundance and future Asiatic oak weevil abundance. To evaluate combinations of multiple factors I calculated the correlation coefficients from a model utilizing all possible variables and then removing variables one by one in order of their least importance from the single variable correlation values. This was accomplished by taking the sum of each year's leaf tying caterpillar, leaf rolling caterpillar, and Asiatic oak weevil normalized counts from the trees sharing the combination of variables being evaluated and calculating the correlation coefficients and p-values. When removing a single variable from the combination of variables being evaluated if the correlation coefficient increased or stayed the same then I deemed that single variable as insignificant. Also any single variable or combination of multiple factors deemed significant had to have support from both the study's entire 1,438 trees sampled and the subset group analysis (if applicable). If any findings from the entire analysis were not supported from the subset group analysis they were deemed insignificant and vice versa. After this multifactor analysis was complete I then determined which combination of variables was most influential for predicting Asiatic oak weevil abundance from leaf tying caterpillar and leaf rolling caterpillar abundance. To test if the model derived from the best combination of variables was biased by a handful of trees, I randomly down-sampled our data many times and reran those same analyses. Down-sampling is when you take a portion of your data from your larger dataset and run analyses on it for a variety of purposes, such as in our case, to test if our results change. If the results do not change then that supports the claim that the identified relationships from our study are not being biased by a handful of trees. For example, if one tree gave us 5 years of Asiatic oak weevil, leaf tying caterpillar, and leaf rolling caterpillar data, we randomly took only one of those five years of data and only one of the Asiatic oak weevil, leaf tying caterpillar, or leaf rolling caterpillar counts for this down-sample analysis.

Results

Ecological and Anthropocentric Factors

The evaluated variables that had the most significant correlations on same year leaf tying caterpillar abundance to Asiatic oak weevil (r=0.976 & P=0.000017) and leaf rolling caterpillar abundance to Asiatic oak weevil (r=0.987 & P=0.000002) were stratum (canopy vs understory) and site age. Though, figure 2 shows that site age alone does not significantly influence any leaf tying caterpillar or leaf rolling caterpillar relationship with the Asiatic oak weevils. However, the land management history of the trees sampled had a universal impact on Asiatic oak weevil (P=0.032) and leaf rolling caterpillar (P=0.024) abundance. It was also found that the factors most relevant for the same year analyses were not significant variables for predicting future Asiatic oak weevil counts. For predicting future Asiatic oak weevil counts the best indicator is years of normalized leaf tying caterpillar counts. The rest of the variables evaluated did not add significance for modeling leaf tying caterpillar or leaf rolling caterpillar relationship with Asiatic oak weevils (same year or future years). Table 1 shows the statistical results across the entire study for each individual variable; white oaks vs black oaks, canopy vs understory, northeast vs southwest facing slope, site age, plot land management history, and tree trunk diameter.

Same Year Significant Relationships

Canopy counts are the leaf tying caterpillar and leaf rolling caterpillar normalized counts from the canopy of trees. This variable was the single best factor for predicting current year Asiatic oak weevil abundance. The correlation coefficient from leaf tying caterpillar canopy counts was 0.627 and for leaf rolling caterpillars was 0.492. The combined r-value for leaf tying caterpillar and leaf rolling caterpillar canopy counts correlating with Asiatic oak weevil abundance 1, 2, and 3 years into the future were -0.06, 0.28, and -0.07 respectively, strongly suggesting that using canopy counts alone for predicating future Asiatic oak weevil abundance will not produce accurate results.

By grouping the normalized counts I hoped to find an even better set of variables to build a model from to predict current year and future year Asiatic oak weevil abundance. A snapshot of some of those combinations of variables evaluated for the same year analysis is found in Table 2. As shown in Table 2 by combining stratum (canopy and understory) and site age we found an even stronger correlation to Asiatic oak weevil abundance than by just having the canopy counts, keep in mind this is agnostic to the year of collection, meaning we are treating counts from 1994 the same as counts from 2004. The correlation coefficient between leaf tying caterpillars and Asiatic oak weevils with this combination of variables was 0.976 with a P of 0.00001687 and for leaf rolling caterpillars the r-value was 0.987 with a P of 0.00000241. To clarify, this is comparing leaf tying caterpillar and leaf rolling caterpillar normalized counts to Asiatic oak weevil normalized counts from sites with the same age with samples taken any year from both the canopy and understory of trees. To eliminate the possible bias from samplings taken from the same tree, I down-sampled the data and ran a test only accepting collection counts once (at random) from any tree and recalculated the r-values and Ps. The results from this test were; 0.981 and 0.009 for the correlation coefficient and P for leaf rolling caterpillars and 0.996 and 0.002 for the correlation coefficient and P for leaf tying caterpillars. I reran this test several times to check for consistency and every time the results were similarly significant. These results are meaningful because they weigh all trees equally, meaning a tree that was sampled 10 times vs a tree that was sampled once both only contributed once to this test. In addition to controlling for the number of times a tree was sampled, trees where leaf tying caterpillars, leaf rolling caterpillars, and Asiatic oak weevils were all identified only contributed one of those count values, making it equal to a tree where only leaf rolling caterpillars were found. This highlights a larger community level significance between Asiatic oak weevils and leaf tying caterpillars and Asiatic oak weevils and leaf rolling caterpillars by not getting skewed results from a handful of specific trees. To test if Asiatic oak weevil abundance was correlated solely with stratum and site age independent of leaf tying caterpillar and leaf rolling caterpillar abundance we ran a linear regression analysis without leaf tying caterpillar and leaf rolling caterpillar counts. This test compared the Asiatic oak weevil abundance across each site age in both strata. The r^2 value from this Asiatic oak weevil test was 0.0005, suggesting that this relationship is legitimately dependent upon the abundance of our evaluated ecosystem engineers.

Another same year finding from this study was that the land management history of a site was shown to play a significant role in insect abundance. Six plots were clear cut in the 1996. Those plots had fewer Asiatic oak weevil (one-tail $P = 0.032$) and leaf rolling caterpillar (one-tail $P = 0.024$) abundance than their paired plots that were not clearcut. Leaf tying caterpillar abundance was not statistically impacted (two-tail P = 0.64) (Table 4). These data were gathered between the years 2002-2004.

Accurately Predicting Future Asiatic oak weevil Abundance

It has been shown that Asiatic oak weevil abundance is correlated with leaf tying caterpillar abundance (Baer and Marquis 2014) from counts gathered that same year. Our data supports that finding (r = 0.55, P = 0.04). However, an even stronger relationship was identified when comparing leaf tying caterpillars to Asiatic oak weevils and leaf rolling caterpillars to Asiatic oak weevils across time. The persistent pattern was that leaf rolling caterpillar abundance has a very strong positive impact on Asiatic oak weevil abundance two and three years into the future. These findings are significant when analyzing across all 1,438 trees (PP = 0.001 and P = 0.013 respectively) and when analyzing the subset group (P = 0.007 and P = 0.002 respectively). Figure 3 shows the offset years evaluated and how the leaf tying caterpillar to Asiatic oak weevil and leaf rolling caterpillar to Asiatic oak weevil relationships change across the subset group of trees. Table 3 shows those same relationships but across all 1,438 from the entire study. Notice leaf rolling caterpillar abundance was not shown to significantly impact Asiatic oak weevil abundance 4 years into the future. This however might be largely due to a lack of sample size. Correlation coefficients for all of the ecological and anthropocentric factors were evaluated in these offset year analyses, but the addition of these factors did not add significance to any future predicting leaf tying caterpillar to Asiatic oak weevil or leaf rolling caterpillar to Asiatic oak weevil model.

Discussion

For predicting the current year's Asiatic oak weevil abundance within an area, all that is needed is an accurate estimate of the leaf tying caterpillars or leaf rolling caterpillars in that area. That estimate needs to come from sampling the canopy of black or white oaks. For predicting future Asiatic oak weevil abundance, specifically two and three years into the future, having the leaf rolling caterpillar counts is all that is needed. However, we do see that knowing a region's recent land management history is important because it influences many different types of insects. The other factors evaluated, host plant species, slope face of the tree, and diameter of the tree, were not helpful for predicting future or current year Asiatic oak weevil abundance. Based on these results a few new questions should now be further assessed, such as why are leaf rolling caterpillars driving future Asiatic oak weevil abundance and not leaf tying caterpillars? I believe the likely mechanism behind what is driving leaf rolling caterpillar abundance to be a better indicator for future Asiatic oak weevil abundance is predation. It that is true, I would expect that rolled leaves do a better job of protecting Asiatic oak weevils from predators than leaf ties. The surviving Asiatic oak weevils then reproduce and their offspring persist in the same area. Specifically, what I believe is happening is that leaf ties fall apart on Asiatic oak weevils more often than rolled leaves leaving them exposed or falling to the ground, which increases their chances of being preyed upon. I also believe it is possible that there might be more inter-species competition for the leaf ties. If so, then other arthropods might be forcing the Asiatic oak weevil to leave the leaf tie and while it is searching for a new shelter it is exposed and its chances of being preyed upon increase. One could test how leaf ties and rolled leaves stand up to Asiatic oak weevils by observing these conditions within a greenhouse over an entire season. In the field this can be evaluated by getting the relative number of leaf ties and rolled leaves on a particular tree, then get a relative number of Asiatic oak weevils on that tree, and finally count how often birds are observed finding prey on that tree. The counts would have to be recalculated several times across a season for each tree being studied. Having more insight on how effective leaf ties and rolled leaves are at protecting Asiatic oak weevils from predators I believe would complement the findings from this study.

An interesting spatial observation was made from this study. Specifically, that longitude appears to be influential when predicting future Asiatic oak weevil abundance two and three years into the future, however no spatial analysis was performed. The trees from plots of a similar longitude appear to have more comparable abundance of Asiatic oak weevils than the trees from plots of differing longitudes. A more in-depth spatial analysis on all the plots surveyed throughout the study to investigate possible spillover impacts by pockets where leaf rolling caterpillars strongly drive Asiatic oak weevils to succeed and invade new areas should be performed.

Missouri's timber industry annually accounts for $5.7 billion dollars (Timber Industry and Harvest) towards the state's economy and in the year 2013 Missouri's gross domestic product (GDP) was $228 billion dollars (JP Morgan Missouri Economic Outlook 2014) making it one of the largest single revenue sources for the state. Missouri's timber industry also employees over 32,000 people making it one of the largest sources of jobs for the state. Back in 2002 the emerald ash borer (EAB), an exotic Asiatic beetle, was detected in North America (Emerald Ash Borer Management). In 2008 this beetle was only present in one of Missouri's counties, Wayne County. At that time they estimated the loss to Missouri's GDP if the EAB could not be contained and spreads across the state to be $180 million dollars annually (Missouri Timber Price Trends July – Sept 2008). To put that figure in context, in 2011 Missouri was hit with widespread flooding and one of the state's worst tornado catastrophes ever in Joplin. When all was said and done the state contributed $36 million dollars in response to those natural disasters (usatoday). In order to better inform our institutions and land owners of the state, we need to have a better understanding of what ecologically makes a region vulnerable to an exotic species invasion. Monitoring native leaf rolling caterpillar species abundance within the Missouri Ozarks will enhance our abilities to predict and hopefully one day control the Asiatic oak weevil impact on local forests and Missouri's economy.

Ecologically this study reflects a growing trend in our understanding of invasive and exotic species. Having a greater understanding of the fundamental ecology of an area drastically improves conservation departments' abilities to react successfully to local problems. This study has shown in order to understand inter-species relationships many years of data collection and research is required in order to identify key relationships. Without long term support for basic science, local communities suffer the economic consequences. The Asiatic oak weevil is just one of over 50,000 exotic species invading the United States (Pimentel et al. 2005). Understanding the fundamental principles behind its ecological relationships may lead to incalculable improvements for conservation departments across the planet to deal with their own local ecological crises.

Tables and Figures

Tables:

1. The single variable correlation coefficients explaining same year Asiatic oak weevil cumulative normalized counts

Variable	**leaf tying caterpillars**	**leaf rolling caterpillars**	**leaf tying caterpillars**	**leaf rolling caterpillars**
Black Oaks	0.607	0.303	0.024	0.182
White Oaks	0.234	0.085	0.244	0.402

Canopy	0.627	0.492	0.020	0.062
Under Story	0.696	-0.085	0.009	0.402
Slope-17	0.572	-0.079	0.033	0.409
Slope-18	0.323	-0.024	0.166	0.472
Clearcutting	0.043	0.408	0.467	0.211
Site Age	0.564	0.619	0.218	0.190
Tree Diameter	0.463	0.190	0.004	0.149
	r-value	**r-value**	**P**	**P**

These values show the associations between leaf tying caterpillars to Asiatic oak weevils and leaf rolling caterpillars to Asiatic oak weevils for the variables evaluated across the study. Several factors have Ps less than 0.05, such as black oaks, slope-18, clearcutting, and tree diameter for leaf tying caterpillars, but only the "Canopy" variable alone was significant across the entire study and the subset group. The terms 17and 18 refer to the slope face of the tree sampled; 17 = southwest and 18 = northeast.

2. The multi variable correlation coefficients explaining same year Asiatic oak weevil normalized counts

Variables	**CC**	**P-Value**	**Species**
Year, Oak Sp, Paired Clearcut, Site Age, Slope	0.273258361	0.00420137	leaf rolling caterpillar
Year, Oak Sp, Paired Clearcut, Site Age, Slope	0.239629732	0.01070842	leaf tying caterpillar
Year, Oak Sp, Site Age, Tree Diameter, Slope	0.264277591	0.00007221	leaf rolling caterpillar
Year, Oak Sp, Site Age, Tree Diameter, Slope	0.28178558	0.00002426	leaf tying caterpillar
Year, Oak Sp, Stratum, Site Age, Slope	0.448721177	0.00007879	leaf rolling caterpillar
Year, Oak Sp, Stratum, Site Age, Slope	0.609796119	0.00000003	leaf tying caterpillar
Year, Oak Sp, Stratum, Site Age	0.801509484	0	leaf rolling caterpillar
Year, Oak Sp, Stratum, Site Age	0.784357192	0	leaf tying caterpillar
Year, Stratum, Site Age	0.831132127	0	leaf rolling caterpillar
Year, Stratum, Site Age	0.824934315	0	leaf tying caterpillar
Stratum, Site Age	0.987513933	0.00000241	leaf rolling caterpillar
Stratum, Site Age	0.976051156	0.00001687	leaf tying caterpillar

This table illustrates how our multi variable combinations were filtered to find our most significant factors. Single variables were removed by the order of their r-value (from table 1), with the least significant variables first. To accurately predict Asiatic oak weevil abundance in an area, one should group years of leaf tying caterpillar and leaf rolling caterpillar counts by the age of the sites and by where in the stratum the specimens were found.

3. Leaf tying caterpillar to Asiatic oak weevil and leaf rolling caterpillar to Asiatic oak weevil abundance sampled from across the study over different offset years

	leaf rollers	leaf tiers	leaf rollers	leaf tiers
-4	-0.51981	**-0.7108**	0.115882	**0.036695**
-3	-0.26103	-0.44172	0.285899	0.160538
-2	**-0.72377**	0.321206	**0.021191**	0.218941
last year (-1)	-0.39452	**0.624507**	0.146687	**0.036097**
current year	-0.19917	**0.546404**	0.278562	**0.041005**
next year (+1)	**0.613043**	0.195751	**0.03959**	0.306868
2+	**0.813684**	0.159665	**0.006997**	0.352839
3+	**0.922138**	-0.4496	**0.001557**	0.15574
4+	0.33946	-0.34229	0.228168	0.226174
	r-value	r-value	P	P

These values show the association patterns of leaf tying caterpillars to Asiatic oak weevils and leaf rolling caterpillars to Asiatic oak weevils over different offset years. The values bolded have a P less than 0.05. The patterns highlighted suggest that Asiatic oak weevil abundance positively influences leaf rolling caterpillar abundance 1, 2 and 3 years into the future. The negative offset years would mean Asiatic oak weevil abundance was impacting future leaf tying caterpillar or leaf rolling caterpillar abundance which was not supported when we calculated these values from the subset group.

4. The effect of forest management (clear-cutting versus intact forest) on insect abundance

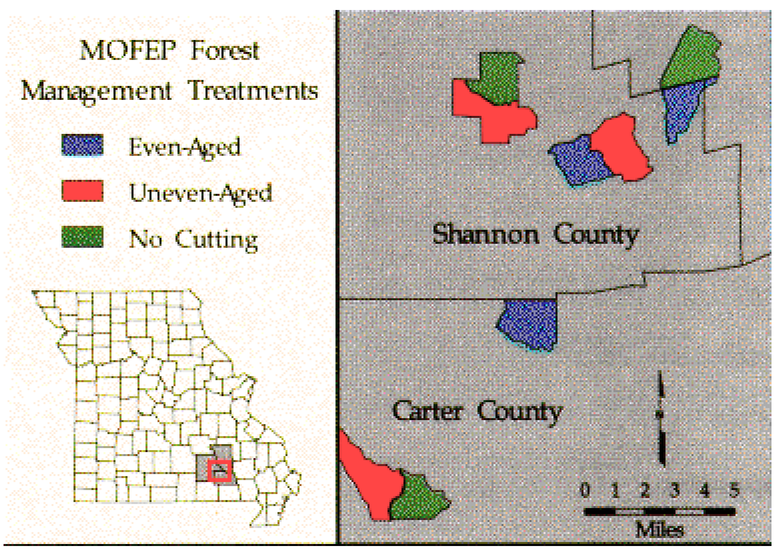
Year	Oak	Species	P-Value
2002-04	Black	Asiatic oak weevil	0.219858649
2002-04	Black	leaf rolling caterpillar	0.153132896
2002-04	Black	leaf tying caterpillar	0.230760381
2002-04	White	Asiatic oak weevil	0.107105397
2002-04	White	leaf rolling caterpillar	0.263126387
2002-04	White	leaf tying caterpillar	0.015273276

2002-04	- (ignoring oak type)	Asiatic oak weevil	0.064773583
2002-04	- (ignoring oak type)	leaf rolling caterpillar	0.048096497
2002-04	- (ignoring oak type)	leaf tying caterpillar	0.639068997
2002-04	- (ignoring oak type)	- (ignoring species)	0.026364816

Cutting occurred in 1996, and sampling took place during the years 2002-04. These values show how the paired-site analysis is impacted by the type of oak and by the type of leaf structure. From these data incorporating the oak species hindered our ability to see the Asiatic oak weevil and leaf rolling caterpillar relationship, as shown in the Asiatic oak weevil and leaf rolling caterpillar rows ignoring oak type. It is also worth mentioning that when ignoring oak type and species group of insect, the P keeps dropping. This suggests that clear cutting universally impacts insect abundance on nearby trees within that region. The anomaly in this table is the "White leaf tying caterpillar 0.015 P". These Ps are 2 tailed and that specific case is suggesting that the sites enduring more cutting result in higher abundance of leaf tying caterpillars on their white oak trees. This anomaly was not further investigated.

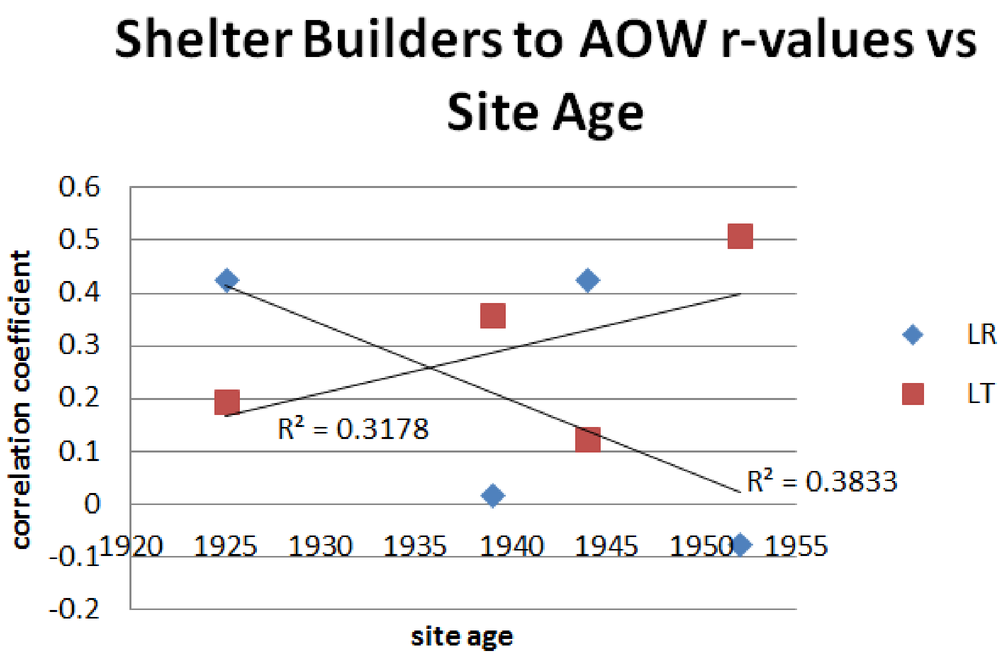
Figures:

1. The MOFEP geographical area



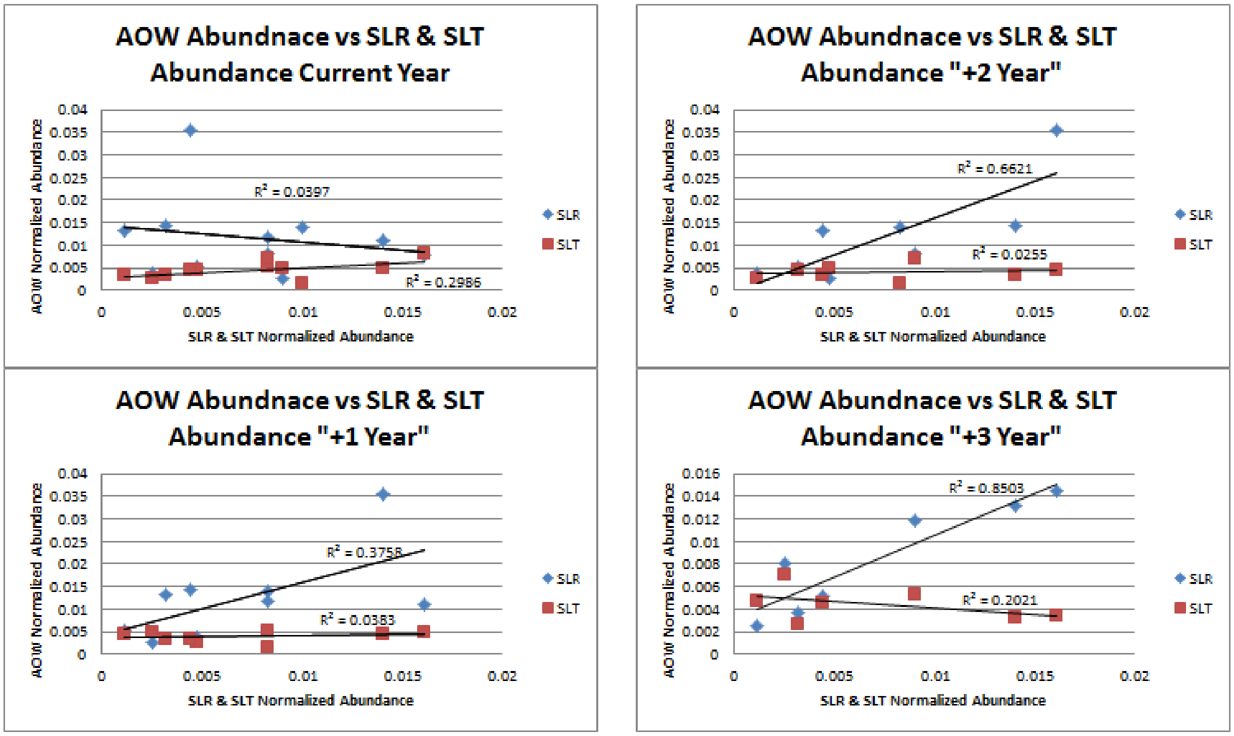
This map is displaying where in the state of Missouri the MOFEP sites are located. Every plot exists within one of the specified sites. Notice there are 3 even-aged, uneven-aged, and no cutting sites.

2. Linear regression plot of leaf tying caterpillar to Asiatic oak weevil and leaf rolling caterpillar to Asiatic oak weevil correlation coefficients from same aged sites



This figure shows how a site's age impacts our shelter builders' relationship with the Asiatic oak weevil. These are not statistically significant (see table 1) but the trend suggests leaf tying caterpillars have a stronger correlation to Asiatic oak weevils from younger sites and leaf rolling caterpillars have a stronger correlation to Asiatic oak weevils from older sites. From the 9 sites there are only 4 unique site ages (1925, 1939, 1944, & 1952), having a n of 4 is a major hindering factor to determine if the described trend is significant.

2. Linear regression plots of Asiatic oak weevil vs leaf tying caterpillars & leaf rolling caterpillars from the subset group over different offset years



As these plots compare normalized counts further into the future, the leaf rolling caterpillar correlation becomes stronger, suggesting that leaf rolling caterpillar abundance positively impacts future Asiatic oak weevil abundance. The offset years displayed go from "+1" to "+3". This means for the example of "+1", that the leaf rolling caterpillar and leaf tying caterpillar normalized counts were plotted against the following year's Asiatic oak weevil normalized counts.

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