

FUNCTIONAL DIVERSITY THRESHOLDS IN COLEOPTERAN COMMUNITIES IN HARDWOOD FOREST LANDSCAPES

Introduction

Human endeavors are the leading cause of current changes to biodiversity (Sala et al. 2000). Among anthropogenic activities, increasing habitat fragmentation and loss are primary contributing factors to this decline (Brook et al. 2003, Pereira et al. 2010, Rands et al. 2010). The spatial extent of this disturbance combined with increased susceptibility to exotic species invasion can disrupt normal cycles of succession (Seastedt et al. 2008). Such disturbances generally have deleterious effects on diversity and community phylogenetic structure by eliciting changes in species assemblages (Winter et al. 2009, Turvey & Fritz 2011). For example, the intensive management of agricultural lands affects communities through the modification of their composition (Kremen et al. 2002, Stefanowicz et al. 2008) and trophic interactions (Benton 2002, Tylianakis et al. 2007). Humans have broken the geographic barriers that once separated species, and the introduction of exotic species by anthropogenic activity further disrupts the current system causing biotic homogenization of contemporary ecosystems (Clavero & García Berthou 2005, Olden et al. 2004). In addition, climate change is exacerbating pressures on biodiversity by altering global temperature and precipitation patterns (Thuiller 2007) as well as community interactions (Harley 2011) and disease dynamics (Pounds et al. 2006). Thus, interactions between disturbance events such as harvesting (Holland et al. 2012) or severe storms (Darwin et al. 2004) and changing conditions caused by chemical inputs, invasive species, and climate change may result in the creation of “no-analog conditions” which challenge traditional strategies for ecosystem management (Seastedt et al. 2008) and make defining the biodiversity of these altered systems difficult.

Functional Diversity

There is empirical evidence that species loss affects ecosystem function (Naeem et al. 1994), but in many cases it is the identity of the lost species that ultimately determines the extent of change that may occur after a disturbance event (Cardinale et al. 2006). Specifically, functional diversity, the number of functionally distinct roles that a community of species has in an ecosystem, is a more exact measure of change after disturbance (Díaz & Cabido 2001, Ernst et al. 2006). Functional diversity has a greater impact on ecosystem services than species richness alone (Dang et al. 2005, Díaz & Cabido 2001, Heemsbergen et al. 2004, Scherer-Lorenzen 2008, Tilman et al. 1997) and has two facets, functional redundancy and functional insurance (Díaz & Cabido 2001). The Functional Redundancy Hypothesis states that after an extirpation event in a community, species with similar roles as the lost species are able to compensate for the loss (Walker 1992). In addition, the Functional Insurance Hypothesis states that stability in ecosystems is maintained by species performing similar functions but have different responses to disturbance (Johnson et al. 1996; Yachi and Loreau 1999). Any extinction event that takes place in a community increases the probability of losing functionally-unique species (O’Gorman et al. 2011). But, by providing numerous species that are functionally similar, functional redundancy assuages the consequences of losing some species from a community because other species can insure against this loss (Loreau et al. 2001, Walker 1995, Walker et al. 1999).

Thresholds for Predators and Their Prey

In addition to understanding how disturbance impacts community composition, knowledge on how it influences the interactions among species is important for maintaining processes crucial for ecosystem services. Because of the economic importance that pest species have in human-modified landscapes, there is the need for a pragmatic strategy that controls them. A functional diversity approach may provide insight to predator-prey dynamics, the potential for biocontrol in a system, and further the understanding about ecosystem thresholds to disturbance. It is also important to consider that disturbed landscapes may have a more negative impact on certain predator communities and their ability to suppress pests (Thies and Tschardt 1999) than on pests. For instance, the parasitism of caterpillars has been found to decrease with climatic variability, and this may cause larger lag times and disconnections between predators and their prey (Stireman et al. 2005). Under these conditions, specialist predators may be more vulnerable to disturbance than generalist predators due to being more susceptible to population lags of prey (Stireman et al. 2005). More specifically, predator and wood boring beetles vary in their response to habitat disturbance due to differences in their dispersal patterns and edge behavior (Costa et al. 2013), the availability of native vegetation (Bianchi et al. 2013), and plant diversity (Albrecht et al. 2007). Even though certain beetle predators demonstrate superior dispersal ability than their prey, it has been shown that some are more sensitive to forest edges than prey species (Costa et al. 2013). The mechanism behind this observation was not determined by the authors. Specific to cerambycid beetles, herbaceous fringes adjacent to forest habitat harbors greater diversity than agricultural, forest, and forest mantel habitat (Wermelinger et al. 2007). In other communities, predators may prefer areas of disturbance where woodborers are abundant. For example, Ulyshen et al. (2004) found that new gaps created by uneven timber harvests, which contained a greater amount of wood debris, harbored a greater abundance of cerambycid and clerid species than surrounding edge and forest habitats. In the gaps, resource availability and quality was increased for the cerambycids which attracted a greater number of them. This promoted a trophic cascade to clerid predators.

Response to disturbance may be due to inherent sensitivities of functional groups, but functional groups may also vary in their response to disturbance due to differences in functional redundancy, or the number of species each contain. Functional groups with more members may be more resilient to change than those with fewer member analogues (Redundancy Hypothesis, Walker 1992). Findings by Bellwood et al. (2003) are in support of this hypothesis. In Indo-West Pacific coral reefs, parrotfish are responsible for bioerosion through their feeding on coral (Bellwood et al. 2003). Bioerosion is a critical process that forms the physical structure of the coral community structure by reducing the calcium accumulation rates of the reef (Bellwood et al. 2003). In their study, Bellwood et al. (2003) found that out of the 35 species of parrotfish observed, one was principally responsible for performing the important function of bioerosion of coral. This species is likely a keystone species, being a principal driver of a coral community's physical structure (Bellwood et al. 2003). Population densities of this parrotfish were very low, and without it, bioerosion would only be a periodic occurrence (Bellwood et al. 2003). This would impair normal ecosystem function, resulting in a loss of resilience in that system (Bellwood et al. 2003). Therefore, in addition to various responses among trophic levels, functional redundancy may cause groups to respond differently to disturbance events.

Stabilizing Mechanisms

Three mechanisms have been proposed through which biodiversity may stabilize ecosystem services: density compensation (Naeem & Li 1997), response diversity (Chapin III et al. 1997, Chillo et al. 2011, Elmqvist et al. 2003, Nyström 2006, Walker et al. 1999), and cross-scale resilience (Peterson et al. 1998, Steffan-Dewenter et al. 2002). Density compensation occurs when the decrease in abundance of one species is followed by an increase in the abundance of another species (Naeem & Li 1997). For instance, in an experiment using microbial food webs in aquatic microcosms, approximately half of the species had a negative correlation with species richness, three had a positive correlation with species richness, and five had a non-linear correlation with species richness (McGrady-Steed and Morin 2000). The authors concluded that density compensation was occurring in these systems (McGrady-Steed and Morin 2000). In a second study that investigated ant species assemblages along an elevation gradient, it was found that, with increasing elevation, species density and richness increased more rapidly than species occupancy and density, which provided evidence for density compensation in these systems as well (Longino and Colwell 2011).

Unlike density compensation, response diversity is said to occur when an environmental change causes populations of some species to increase while causing other populations to decrease (Chapin III et al. 1997, Walker et al. 1999). A study by Li et al. (2006) used ecotypes of *Arabidopsis thaliana* to examine differences in gene expression and metabolite profiles under elevated CO₂ conditions. Plant ecotype metabolite responses differed under ambient and elevated CO₂ conditions (Li et al. 2006). Furthermore, the ecotypes' biosynthetic pathways and processes were influenced differently by the elevated CO₂ conditions (Li et al. 2006). This was thought to influence the plants' phenotypic expression of growth and development (Li et al. 2006). Other differences in response to environmental change by the plant ecotypes include the transcription for the allocation and transport of carbon (including sucrose phosphate synthase and ADP-glucose pyrophosphorylase), nitrogen metabolism, and changes among hormonal response circuits (Li et al. 2006). Considering that response changes were noted among these pathways, the authors concluded that response diversity occurs between these ecotypes (Li et al. 2006).

Cross-scale resilience is a third possible stabilizing mechanism, and it occurs when an environmental change influences species' abundances at various spatial scales (Peterson et al. 1998, Steffan-Dewenter et al. 2002). Winfree and Kremen (2009) found evidence for cross-scale resilience in their study examining bee pollinator response to a gradient of natural vegetation around watermelon farms. To identify which spatial scale each pollinator species had the strongest response, seven spatial scales were chosen (Winfree and Kremen 2009). At these spatial scales, the relationship between natural vegetation and abundance was explored (Winfree and Kremen 2009). It was found that pollinator species respond differently to disturbance level at different scales, so cross-scale resilience was supported by these systems (Winfree and Kremen (2009).

Out of these three proposed stabilizing mechanisms, response diversity and cross-scale resilience may be the key factors contributing to ecosystem resilience in landscapes where resource availability varies (Winfree and Kremen 2009). Winfree and Kremen (2009) tested for the presence and significance of density compensation, response diversity, and cross-scale resilience in wild bee communities present in watermelon farms. In their study, there was no support for density compensation, which they attributed to there being a heterogeneous distribution of resources across landscapes where sampling efforts took place (Winfree and Kremen 2009). In studies that have shown support for density compensation, the distribution of

resources was homogeneous across space and time. However, Winfree and Kremen (2009) found evidence for response diversity and cross-scale resilience since species demonstrated a different response to natural vegetation loss and also responded to that loss at different spatial scales, respectively.

Research problem, objectives, and importance

As ecosystems continue to be altered by an increasing, global human footprint, a greater understanding of system thresholds is paramount for maintaining the provision of ecosystem services for a growing human population (Butler & Oluoch-Kosura 2006, MEA 2003). This proposed study aims to adopt the perspective of system thresholds by using functional diversity as an indicator of ecosystem response and resilience to change from disturbance. Specifically, this study will be focused on a beetle community composed of cerambycid wood borers (consisting of both species that cause economic damage to timber and those species that provide ecosystem services) and generalist predators of wood borers. The aim of this study is to gain important ecological insights that can augment current and future projects that aim to tailor management decisions of timber harvests in temperate forests. This study will investigate how habitat disturbance impacts species' functional groups among beetle communities on a landscape scale and will then identify the ecological mechanisms that stabilize processes important for the provision of ecosystem services by these groups.

Research question and objectives

Stability maintenance in ecosystems is aided by a multitude of species performing similar functions but responding differently to environmental change (Insurance Hypothesis, Johnson et al. 1996; Yachi and Loreau 1999). Furthermore, with regards to maintaining ecosystem function, members within larger functional groups are more expendable than those species without functional analogues [Redundancy Hypothesis (Walker 1992)].

Objective 1:

Determine how functional redundancy and response diversity, including that of predator and prey groups, are influenced by a gradient of human disturbance.

Research Hypothesis 1: Functional groups respond according to the surrounding landscape.

Prediction 1: Anthropogenic land use intensification will cause a decrease in functional diversity, response diversity, and functional redundancy within beetle communities.

Prediction 2: More species-rich functional groups will be more resilient (undergo less change) to ecosystem disturbance than functional groups containing fewer species.

Prediction 3: Among functional groups, more intense habitat disturbance will have a greater, negative impact overall on predator beetle and beneficial cerambycid functional diversity than on pest cerambycid functional diversity.

Objective 2:

Examine how land use affects the linkages between predator and prey trophic levels.

Research Hypothesis 2: Resource availability influenced by habitat disturbance impacts linkages between predator and prey functional groups.

Prediction 1: An inverse relationship exists between predator and prey functional diversity.

Prediction 2: A direct relationship exists between functional redundancy among groups at lower trophic levels and at higher trophic levels.

Objective 3:

Identify the stabilizing mechanisms (density compensation, response diversity, and/or cross-scale resilience) that are best supported by cerambycid and predator beetle groups.

Research Hypothesis 3: Biodiversity stabilizes ecosystem services through several proposed mechanisms: density compensation, response diversity, and cross-scale resilience.

Prediction 1: Density compensation is indicated by a decrease in one species causes an increase in another.

Prediction 2: Response diversity is the result of an environmental change causing a simultaneous decrease in the abundance of one species and increase in another.

Prediction 3: Cross-scale resilience occurs if species respond to environmental change at different spatial scales.

Methods

Identifying Functional Groups

There are several methods for quantifying functional diversity, but all methods are based on functional trait data (Pla et al. 2011). Methodology preference depends on the type of available data and research purpose (Pla et al. 2011). The approach used for quantifying functional diversity in the proposed study will be to estimate the number of functional groups in the community. A functional group can be defined as a subset of species present within an assemblage that shares similar trait profiles, and it is identified by a combination of ordination methods and a cluster analysis of the trait profiles (Pla et al. 2011). To identify functional groups in the current study, methods established by Laliberté et al. (2010) and Pla (2011) will be followed.

Species traits can be classified into two types: response traits and effect traits (Lavorel and Garnier 2002, Walker et al. 1999). Response traits are those that indicate which species will respond successfully to a disturbance event (Lavorel and Garnier 2002, Walker et al. 1999) and include traits such as dispersal potential, root length, leaf area, beak size. Effect traits, however, are those that directly influence ecosystem functions (Lavorel and Garnier 2002, Walker et al. 1999). Examples of effect traits include traits related to biochemical cycling, pollination, and predation. In the current study, a mixture of response and effect traits of taxa will be selected *a priori* based on how well they collectively capture variation in response to environmental change and with respect to contribution to ecosystem processes. Values for functional traits will be collected from specimens and literature sources. Traits will first be standardized to avoid having variables with larger scales affecting the statistical analyses such as the cluster analysis and so that all traits will have the same mean and variance. Since it is likely that traits will be composed of quantitative and qualitative variables such as size and body form, respectively, a Gower dissimilarity matrix will be computed. This distance matrix is appropriate for mixed (continuous, categorical, and ordinal) variable types (Gower 1971, Laliberté et al. 2010, Pla 2012). Ward's minimum variance clustering will then be used to classify species into functional groups because it tends to form more-defined clusters that are more evenly distributed in trait

space, thus it will facilitate functional group identification (Laliberté et al. 2010, Pla 2011). The clusters will be visually-inspected with screen plots, and functional group membership will be assigned to all species (Laliberté et al. 2010).

Disturbance effects on response diversity and functional redundancy

Once functional groups are established for cerambycid and predacious beetle species, I will determine how habitat modification is affecting their functional redundancy and response diversity. For this step, methods established by Laliberté et al. (2010) will be followed. Functional redundancy will be measured by the number of species in each functional group. Response diversity of each group will be measured by the multivariate functional dispersion (FDis) of the species within functional groups in response trait space based on the Gower dissimilarity matrix of species computed from response traits. Laliberté et al. (2010) recommends the use of FDis, the average distance of individual species to their group centroid in response trait space, because it is not strongly influenced by species number. Therefore, if FDis is used, the response diversity measure will not be related to functional redundancy. For any given functional group, a loss of response diversity is indicated by a decrease in multivariate dispersion in response trait space which implies that the community's composition has shifted toward species that are more similar to one another in how they respond to environmental change.

Analysis will be conducted to estimate how timber harvests affect response diversity and functional redundancy of cerambycid and predacious beetle groups and to test Prediction 1. Laliberté et al. (2010) considered the number of observations as the number of functional groups (their analysis only considered effect groups) multiplied by the number of plots where each plot was an independent measurement. To control for intergroup differences, response diversity and functional redundancy within each functional group will be ranked within each functional group. Then, the Pearson correlation coefficient will be calculated between land-use intensity and, within each group, response diversity and functional redundancy will be ranked. Correlation coefficients will be used as effect sizes in the analysis, which will use a random-effect model permitting more general inferences to be made about the population.

Null models will then be used to see whether the changes in functional redundancy and response diversity can be distinguished from one another. Species will be randomly selected within each functional group while holding functional redundancy (species number) constant, and a null distribution of response diversity values will be generated for each functional group. Then I will test whether the response diversity value for the functional group within each land use category is lower than the null distribution. If there are more cases where the response diversity is significantly lower than expected from the null distribution, then species' responses to disturbances are limited.

Stabilizing Biodiversity

To examine three possible mechanisms for biodiversity stabilizing ecosystem service provision, this study will follow the methods of Winfree & Kremen (2009) but will use data on cerambycid and predacious beetles, and analyses will be performed with both species and functional groups as the taxonomic unit. The degree to which density compensation occurs will be verified by determining if there are differences in overall abundance of beetle species across the range of forest harvest intensities. A frequency distribution of all pairwise correlation coefficients (Pearson's r) between species' abundances will be plotted. If density compensation

is occurring, distributions will be shifted to the left. Then, a variance ratio test (ratio <1 indicates density compensation) will be used to statistically test for density compensation, and significance will be assessed by a Monte Carlo simulation.

In the proposed study system, response diversity would be represented by different species or functional groups being more common in treatments where other species or functional groups are less common. This is quite similar to the expectation for density compensation, except now it is predicted that changes will be driven specifically by the different forestry treatments in the different landscapes. A two-way ANOVA will be used to examine this with factors of species and forestry treatment. A significant negative interaction term will indicate response diversity.

Cross-scale resilience may refer to the spatial scale at which species respond to some aspect of their environment (habitat loss in Winfree & Kremen 2009). In the proposed study, the intensive grid of overstory plant data from the HEE project (plots located on a 150 m x 75 m grid) will be used to determine the spatial scales at which the species respond to habitat type. UWEP sites will be used to examine scales of response to forest fragmentation. In addition to tree species, the insects may be responding to many local (e.g., moisture, vertebrate predators, dead-wood availability) and landscape factors [habitat fragmentation, density of habitat edges, variation in habitat quality (Abdel Moniem and Holland in press)]. Cluster analysis with the tree plot data will be used to delineate different conditions according to the tree communities. These conditions will be digitized onto the maps in GRASS GIS (GRASS Development Team 2012).

The proportion of different habitat conditions will then be correlated with each species or functional group to determine the scale at which they most strongly respond to these using the Focus program (Holland et al. 2004). Cross-scale resilience will be indicated by having different species respond to the same habitat condition at different spatial scales. Simply predicting different spatial scales to reject the null hypothesis of the same scale is not a conservative approach, as this is more likely simply by chance than the same spatial scale for different species. A Monte Carlo randomization method for testing cross-scale resilience will be developed. These analyses will be repeated for the cerambycid and predacious beetles, with measures of habitat amount at different spatial scales made using the National Land Cover Data (NLCD) as appropriate for each group.

Data for the Proposed Study

We will examine the changes in functional groups of cerambycid beetles and predacious beetles as well as identify ecosystem service stabilizing mechanisms along a landscape gradient using data from across the state of Indiana. Insect trapping followed the methods of Holland (2006). Sites of beetle collection include those within the Upper Wabash Ecosystem Project (UWEP), at Purdue University Agricultural Centers (PAC), within Purdue research forests (PRF), and within the Hardwood Ecosystem Experiment (HEE). For sites within UWEP, PAC, and PRF, beetles were surveyed in 2006 at 23 forested sites throughout Indiana that were chosen to both represent the majority of the state (Holland 2006). Furthermore, sites were selected to maximize where vegetation data were previously collected through the UWEP, at PAC's or at PRF's (Holland 2006). For each site included in these locations, a point was randomly-selected within 50 m from the nearest edge on digital air photographs in ArcGIS (Holland 2006). Furthermore, two arrays of four traps were set at each point: two Lindgren multiple funnel traps (12-funnel size; Phero Tech, Delta, Canada), one Intercept panel trap for bark beetles (Integrated Pest Management Tech, Portland, OR), and one multi-pane window trap (Holland 2006). Because species respond differently to different trap designs (Chénier and Philogéne 1989),

multiple trap types were used to maximize the probability that the community will be adequately sampled. Two most distant sites were selected at HEE (samples collected in 2007) where trapping consisted of two arrays of one Lindgren multiple funnel trap, one Intercept panel trap, one multi-plane window trap, and one purple sticky trap (specimens collected from the latter being excluded for this study). In all sites, from the central point, each trap was positioned approximately 10 m away and randomly placed in one of the four cardinal directions (Holland 2006). Traps were hung with their bottoms 1 – 2 m from the ground, and a 125 ml Nalgene bottle with 2 mm holes on the top containing 60 ml of 99% EtOH was hung on each trap (Holland 2006).

The trapping surface of the multi-pane window traps consisted of two sheets of perpendicular clear plastic (Hines and Heikkinen 1977). Each of the four vanes of the trap was 0.6 by 0.3 m. Plastic sheets were used to make a flat rain cover and a large funnel (0.3 m diameter, 0.3 m high) for these traps (Holland 2006). Collection jars were made from 2-liter plastic bottles with their tops removed (Holland 2006). Surface area varied between the different trap designs, but this was not considered since these traps are not passively sampling; it is assumed that the beetles are responding to the EtOH lure (Montgomery and Wargo 1983) or the dark vertical silhouette of the trap (Lindgren 1983) (Holland 2006).

All traps had several inches of ethylene glycol in the collection jar to kill and preserve the beetles (Holland 2006). In each trap, a few drops of liquid soap were added to the killing fluid to limit surface tension (Holland 2006). Sites were trapped for between 70 and 90 d over the summer and visited four to five times after the initial trap set up (Holland 2006). Approximately every 3.5 wks, all insects were removed from the traps by filtering the ethylene glycol through a strainer (Holland 2006). The remaining EtOH was measured to investigate the effect of EtOH evaporation rate on the diversity, richness, and abundance of beetles caught (Holland 2006). At each visit, after measuring the remaining EtOH, the Nalgene bottle was refilled to 60 ml (Holland 2006). All cerambycid beetles have been removed from the catch and pinned. Longhorned beetles were identified using Yanega (1996) and occasionally Linsley (1962a, b, 1963, 1964) and Linsley and Chemsak (1972, 1976). Currently, clerid, histerid beetles along with the two species, *Catogenus rufus* (Passandridae) and *Cucujus clavipes* (Cucujidae) are being removed from the catch in the laboratory and pinned. Clown beetles (Histeridae) are being identified using Arnett et al. (2002a) and Downie & Arnett (1996a). Checkered beetles (Cleridae) are being identified using Arnett et al. (2002b) and Downie & Arnett (1996b). All specimens currently reside in a reference collection in the laboratory.

Species identified to date so far include 120 species of longhorned beetles (Cerambycidae), 9 species of clerid beetles, 4 species of histerids, and two additional species, *Catogenus rufus* and *Cucujus clavipes* in the families Passandridae and Cucujidae, respectively. Most of the 120 long-horned beetle species surveyed in the HEE project are within the subfamilies Cerambycinae, Lamiinae, and Lepturinae which are economically-important members to hardwood ecosystems either because they are beneficial species that provide ecosystem services or due to damage that they cause as pest species to living trees and/or herbaceous plants. Approximately three-quarters of the 120 long-horned beetle species surveyed have larvae that feed during development by excavating galleries in decaying wood. These species, including almost all of the Lepturinae, play a large role in wood decomposition and nutrient flow (Gutowski 1987), and others are known to be pollinators of plants (Bond & Philips 1999). Furthermore, cerambycid larvae contribute significantly to food webs by being prey items for other animals such as woodpeckers (Beal 1911, Hanula & Franzreb 1995), and the galleries they create provide habitat for other

species as well (Holland 2009). However, the two families Cerambycinae and Lamiinae are important pests of living woody plants (Hanks 1999), can cause significant damage to stressed trees destined to be harvested for timber (Hanks et al. 1995), and others can vector pathogens to trees (Linit 1988). The Cerambycinae attack a myriad of hosts including living, dying, dead, and seasoned wood of woody plants (Hanks 1999). Many living woody angiosperms and a few herbaceous plants are hosts to species within the Lamiinae, and it is uncommon that members within this subfamily attack dead hosts (Hanks 1999). Considering the wide range of life histories between these groups, a hierarchical ranking of some general traits that can be used to separate them into functional groups is shown in Table 1.

Table 1: Cerambycid functional traits

Cerambycid Functional Traits
Size
Larval Host Condition
healthy tree, moribund tree, recently dead wood, decaying wood
Larval Wood Type
roots, stems, twigs
Adult Feeding Behavior
none, flowers, leaves, sap
Potential for Larvae Cannibalism
yes, no
Dispersal Potential
Landscape Scale Response
Color
Body Form
Taxonomy
Trophic Level
Time in Each Life Stage
egg, larvae, pupae, adult
Activity

Unlike the Cerambycidae, not much research has been conducted on the predacious beetle groups Cleridae, Histeridae, Cucujidae, and Passandridae. But it is known that they are generalist predators on wood-boring larvae (Arnett et al. 2002a,b), thus they have the potential of controlling cerambycid beetles. Most species within the family Cleridae are natural enemies of wood and bark boring insects, thus the group is economically important for the preservation of hardwood forests (Böving & Champlain 1920). Little is known about the biology feeding habits of *C. rufus* and *C. clavipes* (Arnett et al. 2002b). However, it is reported that larvae *C. rufus* is an ectoparasite of Cerambycid pupae (Arnett et al., 2002b; Knull 1930). Furthermore, the larvae of *Cucujus* are known to be predacious (Arnett et al. 2002). Many genera within the family Histeridae are considered economically-important because of them being generalist predators of soft-bodied eggs and larvae (Arnett et al., 2002a). Because these groups are known to inhabit areas where they may encounter wood boring beetles and are considered generalist predators, it can be assumed that they attack a wide variety of cerambycid beetles. Table 2 summarizes the

known prey groups of these predacious beetles, and Table 3 lists various important functional traits of these groups.

Table 2: Predator beetle species and known prey groups (Arnett et al. 2002a,b; Knull 1930; Leavengood 2008)

Predator	Predator Family	Known Orders, Superfamilies/Families Attacked	Known Cerambycid Species Attacked	Life Stage Attacked
<i>Catogenus rufus</i>	Passandridae	Cerambycidae		Pupa
<i>Enoclerus nigripes</i>	Cleridae	Scolytinae		Unknown
<i>Pyticeroidea laticornis</i>	Cleridae	Scolytinae		Unknown
<i>Madoniella dislocatus</i>	Cleridae	Cerambycidae, Colydiidae, Buprestidae, Scolytinae	<i>Elaphidion villosum</i>	Unknown
<i>Platysoma aurelianum</i>	Histeridae	Diptera and Coleoptera		Larvae
<i>Platysoma leonti</i>	Histeridae	Diptera and Coleoptera		Larvae
<i>Zenodosus sanguineus</i>	Cleridae	"lignicolous" boring insects		Unknown
<i>Platysoma gracile</i>	Histeridae	Diptera and Coleoptera		Larvae
<i>Hololepta aequalis</i>	Histeridae	Unknown		Unknown
<i>Hololepta lucida</i>	Histeridae	Unknown		Unknown
<i>Neorthopleura thoracica</i>	Cleridae	Cerambycidae, Curculionidae	<i>Obrium</i> sp., <i>Neoclytus confusus</i> , <i>Tilliclytus geminatus</i>	Unknown
<i>Platylomalus aequalis</i>	Histeridae	Subcortical larvae, Diptera		Larvae
<i>Paromalus bistratus</i>	Histeridae	Diptera		Eggs and Larvae
<i>Cucujus clavipes</i>	Cucujidae	Unknown		Unknown
<i>Cymatodera bicolor</i>	Cleridae	bark beetles, Cerambycidae, Buprestidae		Larvae
<i>Placopterus thoracicus</i>	Cleridae	Scolytinae, Buprestidae		Unknown
<i>Priocera castanea</i>	Cleridae	Lymexilidae, Curculionidae		Larvae
<i>Paromalus seminulum</i>	Histeridae	Diptera		Eggs and Larvae
<i>Cymatodera inornata</i>	Cleridae	bark beetles, Cerambycidae, Buprestidae		Larvae
<i>Paromalus seeversi</i>	Histeridae	Diptera		Eggs and Larvae
<i>Chariessa pilosa</i>	Cleridae	Curculionidae, Cerambycidae	<i>Xylotrechus</i>	Larvae
<i>Teretrius americanus</i>	Histeridae	wood-boring Coleoptera		Unknown

Table 3: Predator beetle functional traits

Functional Traits for Predator Species
Size
Larvae Free-living
yes, no
Larval Food Type
eggs, other larvae
Adult Food Type
eggs, larvae, adult insects
Potential for Larvae Cannibalism
yes, no
Dispersal Potential
Landscape Scale in which Beetles Respond
Color
Mimicry
yes, no
Taxonomy
Trophic Level
Time in Each Life Stage

Expected Outcomes

By adopting the perspective of system thresholds using functional diversity as an indicator of ecosystem response and resilience to change from disturbance, this proposed work will contribute valuable information on disturbance thresholds, an area of research that is rapidly growing. Furthermore, since little is known about these predators, acquiring more knowledge on these beetles will bolster the understanding of the interactions between them and their prey within these forest ecosystems. We hope to produce an estimation of how the provision of ecosystem services provided by these beetle groups is expected to change with habitat disturbance across Indiana hardwood forest landscapes. In addition, we plan to present the underlying ecological mechanisms behind the changes in the community composition and verify whether these changes conform to the Functional Insurance Hypothesis. The findings of this work will also have a broader impact by suggesting practices that promote the existence of beneficial species while suppressing wood-boring pests. Expanding the knowledge on how populations within this community shifts after an anthropogenic disturbance event will aid other work that will provide shareholders on a local scale by enhancing sustainable management decisions for forest systems destined for timber harvest. These strategies would be applicable to timber harvest management practices across many temperate hardwood forest systems. Furthermore, since little is known about these predators, acquiring more knowledge on these beetles will bolster the understanding of the interactions between them and their prey within these forest ecosystems.

Thesis Chapters/Papers

1. Influence of habitat modifications on the functional diversity, functional redundancy, and response diversity within cerambycid and predacious beetle communities
2. Using a functional diversity approach to examine changes in trophic interactions between woodborers (Cerambycidae) and their generalist predators
3. Ecological mechanisms stabilizing ecosystem processes within cerambycid and predacious beetle communities

Timeline

Since beginning my PhD program at Purdue University in August 2010, the fall and spring semesters have been focused on coursework. In January 2012, I joined Dr. Holland's research group, and by May 2012, I began to form my research topic. Now that I have completed my Plan of Study coursework and that document has been approved, I will be devoted to completing my research project. Table 4 outlines the expected completion times of my research projects and final degree.

Table 4: Timeline of completion for research and the PhD degree

Year	Beginning In	Ending In	Plan	Comments
2013	January	April	<ol style="list-style-type: none"> 1. Refining the proposal. 2. Sorting samples and beetle ID. 3. ID of important functional traits. 4. Begin Preliminary Exam review. 	
	May	August	<ol style="list-style-type: none"> 1. Completion of sample sorting. 2. Begin functional group identification 3. Finalize proposal. 4. Preliminary Exam review, help with field work 	
	September	December	<ol style="list-style-type: none"> 1. Begin writing Publication 1 2. Preliminary Exam? 	
2014	January	April	<ol style="list-style-type: none"> 1. Wrap up Publication 1 2. Trophic groups and functional diversity work 3. Start thesis writing 	
	May	August	<ol style="list-style-type: none"> 1. Publication 2 2. Help with field work 	
	September	December	<ol style="list-style-type: none"> 1. Complete Publication 2 2. Begin ID of stabilizing mechanisms 3. Continue thesis writing 	
2015	January	April	<ol style="list-style-type: none"> 1. Complete work on stabilizing mechanisms 2. Publication 3 3. Continue thesis writing 	
	May	August	<ol style="list-style-type: none"> 1. Finalize thesis 2. Defense...? 	
	September	December		

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