

PHYLOGENETIC COMMUNITY STRUCTURE OF AQUATIC BEETLE ASSEMBLAGES
IN A MULTI-WETLAND EXPERIMENT

by

SANDOR LAWRENCE KELLY
B.S. University of Central Florida, 2004

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ABSTRACT

Phylogenetic Community Structure (PCS) metrics are becoming more common in community ecology. PCS metrics estimate the phylogenetic relatedness among members of an ecological community or assemblage. If ecological traits are conserved, then phylogenetic clustering (i.e., taxa are more closely related than expected by chance) indicates habitat filtering as the key process in community assembly. On the other hand, a pattern of phylogenetic overdispersion (i.e., taxa are more distantly related than expected by chance) suggests competition is dominant. Most studies to date have used PCS of unmanipulated ecosystems, but the value of PCS metrics will be best revealed in experiments. This project used PCS for aquatic beetle (Coleoptera) assemblages in experimentally manipulated seasonal wetlands on a cattle ranch in south-central Florida, and compared PCS metrics to standard ecological metrics. Wetlands were experimentally treated with all combinations of pasture management, fencing to exclude cattle, and controlled burning during 2006-2009. Beetle assemblages in fenced wetlands were significantly more overdispersed compared to non-fenced wetlands, suggesting that this treatment decreases habitat filtering, causing competition to become the dominant process in community formation. There was also a significant pasture x fence x burn interaction effect, with assemblages in wetlands differing in PCS depending on what combination of the three treatments were applied. Phylogenetic Diversity (PD – a measure of branch length of a community or assemblage on a phylogenetic tree) was highly correlated with genera richness (number of genera), and these metrics along with the expected number of genera (D – an ecological diversity index) found significant differences among burn treatments and a pasture x

burn interaction. The results of this study indicate that PCS metrics complement classical ecological methods and should be widely applied.

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LIST OF ACRONYMS

BACI	Before-After Control-Impact design
D	Diversity index for calculating expected # of taxa
MAERC	MacArthur Agro-Ecology Research Center
MNTD	Mean Nearest Taxon Distance
MPD	Mean Phylogenetic Distance
NRI	Net Relatedness Index
NTI	Nearest Taxon Index
PCS	Phylogenetic Community Structure
PD	Phylogenetic Diversity

CHAPTER ONE: INTRODUCTION

Community Ecology

Community ecology studies groups of coexisting organisms (community or assemblage). The processes that form communities are both known and predictable (deterministic), and unknown. Deterministic processes, namely habitat filtering and competition, result from non-random (i.e. predictable) abiotic and biotic factors that contribute to the formation of communities. Abiotic factors are environmental phenomena such as landscape and weather patterns, hydrology, water chemistry, and geomorphology. Biotic factors include the regional species pool, presence of competitors, predators and disease, host availability, and behavioral habitat selection (Binckley and Resetarits 2005). *Habitat filtering* (also called environmental filtering) occurs when certain abiotic and biotic factors create environmental conditions in which only ecologically similar taxa can persist because of shared habitat requirements or adaptations to environmental disturbance (Keddy 1992, Webb et al 2002, Figure 1). *Competition* is considered to be an important process in community assembly when a limited resource causes ecologically similar organisms to exclude each other (Hutchinson 1959, Hardin 1960, MacArthur and Levins 1964, Figure 1). Unknown processes can be thought of as either stochastic (neutral theory – Hubbell 2001) or simply poorly-known deterministic phenomena, such as dispersal (Clark 2008). These processes are important at a broader scale because local conditions affect the metacommunity and regional species pool, which in turn affects the speciation rate and

historical biogeography of species and clades (Wiens and Donoghue 2004, McPeck and Brown 2000).

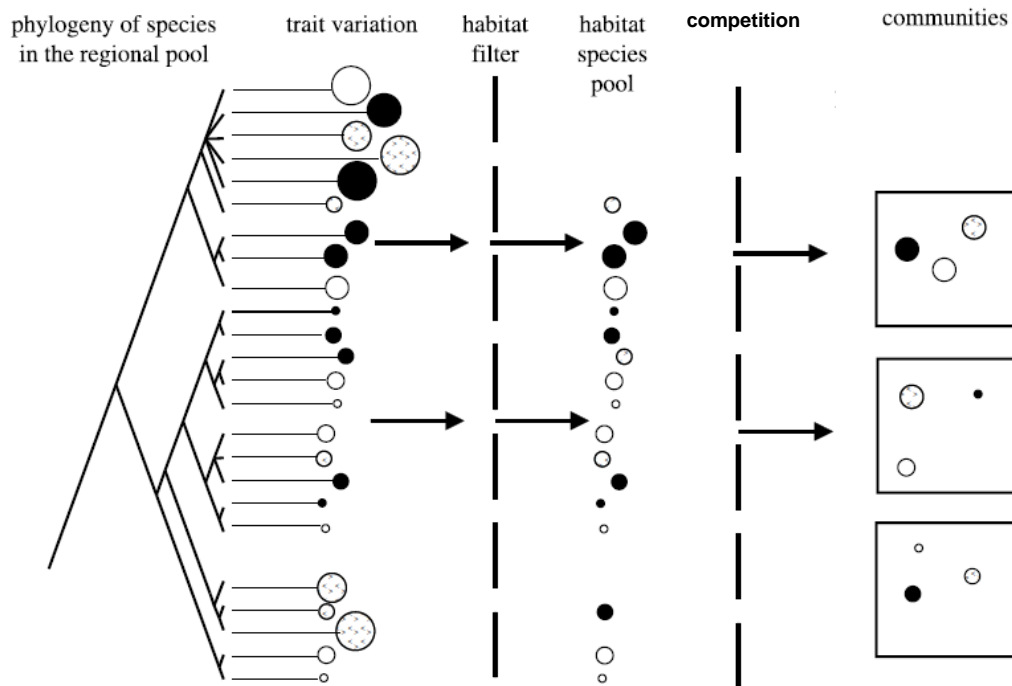


Figure 1: Local Communities Formed by the Processes of Habitat Filtering and Competition

The processes of habitat filtering and competition act upon the regional species pool to form local communities. Circle size and pattern represent traits of taxa in the regional pool; circle size is dependent on phylogeny (closer related species tend to be similar). Some species (largest circles) cannot tolerate habitat conditions and are “filtered” out. Competition may counter habitat filtering by excluding those species that are too similar (represented by pattern). Modified from Silvertown et al (2006).

The extent to which deterministic processes contribute to community formation varies (Gravel et al 2006, Ellis and Ellis 2009), but it can be generally stated that an organism’s ability to disperse to, and tolerate the abiotic conditions and biotic interactions within a community will

depend on its traits. Since an organism's traits are in large part determined by genotype, and genotype is inherited, then the phylogenetic relationships among taxa in a community will inform community ecology (Webb 2000, Figure 1).

Closely related taxa have long been expected to share similar traits because they share common ancestry (Darwin 1859, ch. 3); it is standard practice to account for phylogeny when comparing traits across species, as in studies of correlated trait evolution, adaptations, or allometry (Garland et al 1992, Arnqvist and Rowe 2002, Ackerly 2004, Whittall and Hodges 2007, Agrawal & Fishbein 2008). Under random, Brownian-motion evolution, species that share a recent common ancestor will have diverged less, and thus be more statistically interdependent than comparatively more distantly related species (Felsenstein 1985). Of course this will not be true for rapidly evolving traits in cases of strong character displacement or an adaptive radiation, or if selection is acting upon traits in a way that leads to convergent evolution (Cavender-Bares et al 2004, Losos 2008).

Community ecology has recently started to take phylogeny into account as an explanatory factor for community composition and assembly. Phylogenetic analysis for community ecology uses either trait similarity among closely related taxa (*trait conservatism*), or trait similarity among more distantly related taxa (*trait convergence*, whichever applies), and the overall relatedness of the taxa within the community (*phylogenetic community structure*) to infer the processes that shape the community (Webb 2000, Webb et al 2002, Figure 2, Table 1). Studies to date have found non-random patterns of phylogenetic community structure in natural communities, and have used these to explore the relative importance of competition, habitat filtering, and other deterministic factors in forming the community (Vamosi et al 2009,

Cavender-Bares et al 2009). However, few studies have applied phylogenetic community structure analysis in communities with experimentally modified habitats. Experimentation provides strong inference, and will be used in this study to test and build upon existing phylogenetic community structure research.

CHAPTER TWO: BACKGROUND INFORMATION

Phylogenetic Community Structure

Classical ecological methods for measuring communities or assemblages such as richness (number of taxa), diversity indices (number and abundance of taxa), and guild levels (number of different trophic levels) do not explicitly consider the identities of the taxa involved. However, since traits are generally correlated with phylogeny, metrics that take into account relatedness of community taxa can be more sensitive than classical ones (Crozier 1997, Cadotte et al 2008, Maherali and Klironomos 2007, Lessard et al 2009). Similarly, phylogenetic diversity (PD), a metric that measures the branch length of a sample community on a phylogenetic tree, is used to compare communities in conservation. Phylogenetic diversity inherently represents genetic diversity: greater genetic diversity represents greater niche diversity and presumed flexibility in response to future changes (Faith 1996). Phylogenetic community structure has also been used to help understand how local biotic interactions affect the regional species pool and feed back to evolutionary processes, and to predict resistance to invasive species and effects of climate change on communities (Cavender-Bares et al 2009).

There are many metrics for measuring phylogenetic community structure (Vamosi et al 2009), but most of these compare the relatedness of taxa in an observed community or assemblage to a distribution of communities or assemblages generated by a null model of random samples drawn from a regional taxa pool. The result of such a comparison is a test for non-random relatedness of the taxa in the observed sample, and one of three patterns can occur

(Table 1): (1) *clustering*, in which the observed community or assemblage is more closely phylogenetically related than expected by chance (2) *overdispersion* (also called evenness), in which the observed community or assemblage is significantly less related than expected by chance, and (3) no significant difference from random. Therefore, when comparing phylogenetic structure among communities or assemblages, one is not only measuring if they are different, but how they are different, by considering the identities and relationships of the taxa.

Several phenomena can lead to a pattern of phylogenetic clustering (Figure 2, Table 1). Most commonly it is attributed to habitat filtering in community assembly, assuming ecological trait conservatism in the community taxa. In this case, ecologically similar, closely related taxa are able to withstand some environmental stress that keeps ecologically different (distantly related) taxa out of a community. This mechanism has been found in rainforest trees (Webb 2000), Mediterranean woody plants (Verdu and Pausas 2007), bacteria (Horner-Devine & Bohannan 2006), yeast in the nectar of flowering plants (Herrera et al 2010), predaceous diving beetles (Vamosi and Vamosi 2007), Wisconsin lake fish (Helmus et al 2007), and tropical hummingbirds (Graham et al 2009). Clustering can also happen if there is strong competition amongst ecologically similar but more distantly related taxa due to convergence, or if competitive ability itself is a conserved trait (Vamosi et al 2009).

Phylogenetic overdispersion can also be the outcome of different processes (Figure 2, Table 1). Competitive exclusion of ecologically similar, closely related taxa is often invoked as an explanation for phylogenetic overdispersion and examples include sphenoid sedges (Slingsby and Verboom 2006), mycorrhizal fungi (Maherali and Kilronomos 2007), ants (Machac et al 2011), and Carnivora (Davies et al 2007). Overdispersion will also occur if there

is habitat filtering of less-related taxa that are ecologically similar due to convergence, as seen in Floridian oaks (Cavender-Bares et al 2004). Finally, a random pattern in phylogenetic community structure could be the result of deterministic processes canceling each other out, or of neutral processes dominating community formation (Kembel and Hubbell 2006).

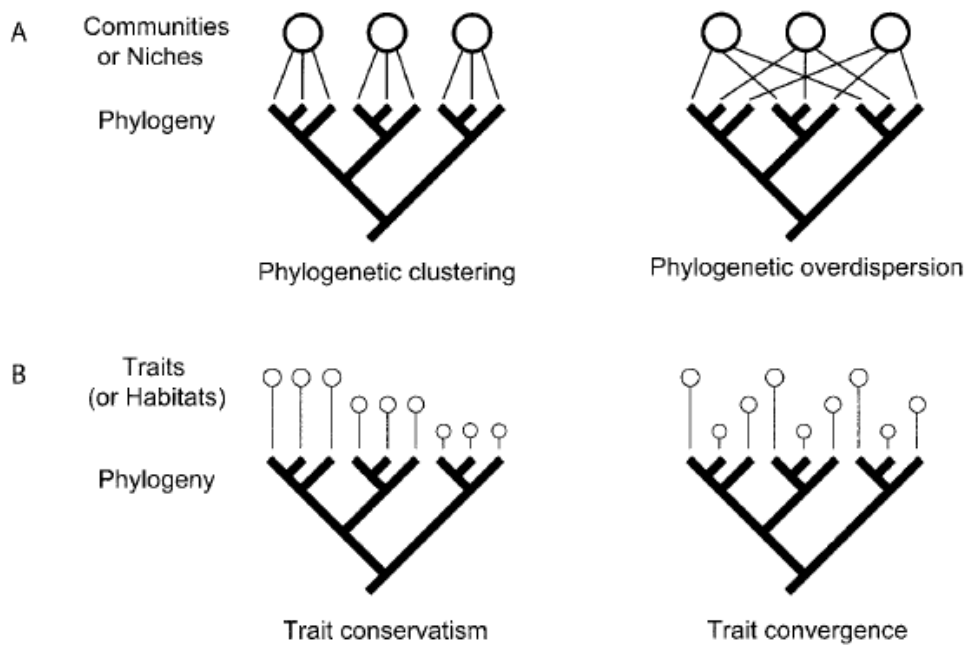


Figure 2: Different Possibilities of Phylogenetic Community and Trait Structure

(A) Communities, represented by circles, are phylogenetically clustered when the taxa are more closely related than expected by chance (all taxa from one clade). They are overdispersed when the observed taxa are more distantly related than expected by chance (taxa only from different clades). (B) Traits, represented by line length, are either conserved (taxa in same clade have similar traits) or convergent (taxa from different clades have similar traits) depending on whether closely or distantly related taxa are more similar. Modified from Cavender-Bares et al (2004)

Table 1
 Traits and Processes Drive Patterns of Phylogenetic Community Structure

	Habitat Filtering	Competition
Trait Conservatism	Phylogenetic Clustering	Phylogenetic Overdispersion
Trait Convergence	Phylogenetic Overdispersion	Phylogenetic Clustering or random

Patterns of phylogenetic community structure can be interpreted to have resulted from either filtering or competition being a dominant process, depending on whether relevant ecological traits are conserved or convergent (Cavender-Bares et al 2004).

Patterns of phylogenetic community structure depend on the spatial and taxonomic/phylogenetic scale observed, with generally more clustering with increasing scale (Silvertown et al 2006, Swenson et al 2006). At a species level, ecological traits may be more labile (i.e. less conserved) due to character displacement and/or adaptive radiations, or even divergent selection (Cavender-Bares et al 2009, Losos et al 2003). However, non-adaptive speciation events can also create species rich clades while maintaining ecological trait conservatism of close relatives (Kozak et al 2006, McPeck and Brown 2000). At relatively higher phylogenetic levels (i.e. genus), trait similarity within clades will generally be greater than among clades (Cavender-Bares et al 2006). Some studies have implied community processes from phylogenetic structure and the observation of ecological trait convergence (Cavender-Bares et al 2004), while most other studies have found evidence for or assumed ecological trait conservatism (Lovette and Hochachka 2006, Verdu and Pausas 2007, Lessard et al 2009). Indeed, the extent to which ecological traits are universally conserved remains unresolved (Wiens and Graham 2005, Losos 2008, Wiens et al 2010). Consequently, it is necessary to thoroughly understand the organisms and the deterministic factors affecting the communities being studied.

Most studies of phylogenetic community structure have inferred ecological processes from observed patterns of natural communities. The value of phylogenetic community structure metrics will be best revealed in experiments. To date, phylogenetic community structure has been evaluated after experimental manipulation of the phylogenetic structure of communities (Maherali and Kilronomos 2007) or abiotic factors (Dinnage 2009), but more experimental studies are needed to understand how different factors affect phylogenetic community structure and hence the processes that shape communities (Vamosi et al 2009).

Aquatic Coleoptera and Seasonal Wetlands

This was a study of aquatic beetle (Coleoptera) assemblages in experimentally manipulated seasonal wetlands on a cattle ranch in south-central Florida. The experimental units in this study were entire wetland ecosystems that dry out then refill annually, and so aquatic beetles also re-assemble annually (see below). The experimental factors were pasture intensification, fencing to exclude cattle, and controlled burning. The purpose of this study was to see how these factors influence community assembly by measuring the phylogenetic community structure of aquatic beetle assemblages, with the assumption of ecological trait conservatism.

Water beetles and other aquatic invertebrates are commonly used to study aquatic ecosystems because they are important in the food chain (Mitsch and Gosselink 2000), regulate decomposition and nutrient cycling (Batzer and Wissinger 1996), and influence species composition (Pearman 1995). Aquatic Coleoptera are used for assessing habitat quality and

biodiversity (Eyre et al 2003, Sanchez-Fernandez et al 2006), and for conservation (Fairchild et al. 2000, Eyre 2006) because they are collectively sensitive to environmental conditions due to their wide range in trophic levels and body size – consistent with a diversity of niche traits, and their high species richness (New 2010). This rich background of aquatic Coleoptera provides a strong foundation for life histories and phylogenetic analyses of community assembly.

Factors that influence aquatic Coleoptera assemblages include: hydrology, water chemistry, vegetation, geomorphology, and biotic forces such as the presence of other macroinvertebrates, amphibians, and especially predatory fish (Larsen 1985, de Szalay and Resh 2000, Fairchild et al 2003). Water beetles that inhabit temporary water bodies exhibit high dispersal ability (Ribera and Vogler 2000) and habitat selection (Binckley and Resetarits 2005, Yee et al 2009), which should weaken the influences of the unknown processes such as metacommunity demography on community structure. These facts lead to the expectation that aquatic beetle assemblages should be sensitive to the environmental treatments applied in this experiment (see Methods).

Although an aquatic lifestyle is itself a convergence among several lineages of Coleoptera (Hunt et al 2007), morphological and ecological traits are generally conserved within clades of aquatic beetles (Table 2). Moreover, this study focused on taxa within a suborder (Adephaga, Table 2). The Haliplidae, or ‘Crawling Water Beetles’ are tiny; the taxa in this study range in body size from 2-3 mm, and are often associated with each other (Epler 1996). The taxa of Noteridae, or ‘Burrowing Water Beetles’, found in this study range in body size from 2-5 mm. The Dytiscidae, or Predacious Diving Beetles vary greatly in body size (1.5-33 mm), but show phylogenetic signal for this trait, and were assumed to have ecological trait conservatism in a

previous study (Vamosi and Vamosi 2007). Furthermore, aquatic beetle larvae are so similar among congeners that morphological identification of most species has not been resolved (for the purposes of this study, genus-level identifications only were considered). The aforementioned details provide evidence that adepagan aquatic beetles display ecological trait conservatism.

Table 2
Adepagan Aquatic Beetle Habits

Taxa	Habit	Trophic Relationships
Haliplidae		
larvae	Aquatic (climbers)	Algivores (piercers and shredders)
adults	Aquatic (swimmers, climbers)	Algivores (piercers and shredders); Predators of insect eggs and polyps of Hydrozoa
Dytiscidae		
larvae	Aquatic (climbers, swimmers)	Predators (piercers, some engulfers) of micro/macroinverts, fish, amphibians, and reptiles
adults	Aquatic (divers, swimmers)	Predators (engulfers) of insects, fish, and amphibians; some communal feeding; some scavenging
Noteridae		
larvae	Aquatic (burrowers)	Predators (engulfers) of micro/macroinverts; some scavenging
adults	Aquatic (swimmers, climbers, burrowers)	Same

Data from Merritt and Cummins (1996), Arnett and Thomas (2001), and Arnett et al (2002)

This project complements a larger experiment on the interactive effects of rangeland management practices (i.e. pasture intensification, cattle grazing, and controlled burns) on seasonal wetlands in pastures. Wetlands in Florida cattle ranches provide habitat for endemic

and specialized plants and animals, function in water buffering and the cycling and storage of nutrients, and provide water, food and refuge to cattle (Steinman et al. 2003). Conversely, management practices can have negative effects on wetland ecosystems. Fertilization is a direct source of nitrogen and phosphorus which can alter water chemistry and both floral and faunal assemblages (Mitsch and Gosselink 2000), resulting in eutrophication and a loss in plant diversity (Gathumbi et al 2005, Boughton et al 2010).

Cattle grazing and fire can have mixed effects on wetlands. Selective grazing and nutrient loading from cattle can lead to eutrophication and changes in macroinvertebrate assemblage, vegetation, algae, and detritus (Hornung and Rice 2003, Steinman et al. 2003). However, grazing has also been shown to control non-native grasses and increase inundation time of ephemeral wetlands (Marty 2005), as well as control the invasion of woody plants (see below). Fire is a natural occurrence in these seasonal wetlands, and is applied by ranchers across pastures to control woody vegetation. A regular fire regime over time will result in a higher diversity of herbaceous plants and the exclusion of invasive and woody ones (Myers and Ewell 1990, Clark and Wilson 2001), although vegetation assemblages are sensitive to the frequency and season of burning (Main and Barry 2002). Controlled burning in wetlands can also increase invertebrate and plant abundance (de Szalay and Resh 1997). To test the effects of pasture intensification, fencing to exclude cattle grazing, and fire on seasonal wetlands, all combinations of these factors were experimentally applied to wetlands at the study site. *These different combinations should result in different intensities of habitat filtering, and therefore different phylogenetic structuring of assemblages of aquatic beetles among treatments.*

Hypothesis

Experimental treatment of wetlands on a south-central Florida cattle ranch will cause phylogenetic community structure to differ among treatments for adephagan aquatic beetle assemblages.

Assumptions

- Adepagan aquatic beetles display ecological trait conservatism, i.e. phylogenetic relatedness is positively correlated with ecological similarity
- Adepagan aquatic beetles have been adequately sampled, and the sum of all species collected in all experimental wetlands represents the regional species pool
- Phylogenetic tree used represents accurate relationships between taxa
- Adepagan aquatic beetle assemblages in the ranch wetlands study system are not dispersal-limited (i.e., every species has access to every wetland)

Predictions

- Pasture intensification will strongly affect habitat quality, resulting in habitat filtering and thus less phylogenetic diversity and more clustering of assemblages in wetlands in intensively-managed pastures compared to those in semi-natural pastures.
- Fenced wetlands will have increased habitat filtering, less phylogenetic diversity, and

more clustering compared to grazed wetlands

- Wetlands in intensively-managed pastures with fencing will have the overall strongest habitat filter and thus the least phylogenetic diversity and greatest clustering.
- The single fire treatment in this short-term study will have a negligible effect on aquatic beetle assemblages.
- Compared to classical ecological measures of diversity alone, adding phylogenetic community structure metrics will increase the sensitivity to measure beetle assemblage responses to experimental treatments.

Explanation of Predictions

Ecological (richness, D) and phylogenetic (PD, NRI, NTI) measures of adephagan aquatic beetle community structure were used as response variables to test the treatment effects of pasture intensification, fencing to exclude cattle, and controlled burns on wetlands within a cattle ranch. These metrics indicate ecosystem integrity and conservation value (Faith 1996, Gotelli 2004, Jost 2006). Therefore, statistically significant differences among treatment regimes can be interpreted as differences in wetland habitat quality and biodiversity. Comparatively low genera richness and PD can be interpreted as indicating lower quality habitat. Phylogenetic conservatism of ecological traits of adephagan aquatic beetles is assumed, so phylogenetic clustering is inferred to have resulted from habitat filtering being a dominant process in community formation, whereas phylogenetic overdispersion is inferred to have resulted from competition being more important. Inferences cannot be made from random patterns of

phylogenetic community structure because these can result from either neutral processes or a canceling out of clustering and overdispersion (Cavender-Bares et al 2009).

The prediction that community structures in the wetlands in intensively-managed pastures would be more clustered and less diverse was made because of the physical differences between the pasture types (fertilizer and ditching), and from quantitative evidence. Data collected from the MAERC experimental wetlands in 2006 showed intensively-managed pastures had significantly less plant richness and diversity, and less heterogeneity in plants and invertebrates compared to semi-native pastures. Wetlands among the two pasture types were also shown to be significantly different in ordination plots of the total community (plants, invertebrates, and vertebrates) (Medley et al in prep).

The prediction that fencing wetlands would negatively affect beetle assemblages comes from perceived effects of the fenced wetlands before data were analyzed. A drought in 2007 (after cattle exclusion by fencing) produced favorable conditions for the uncharacteristic overgrowth of dog fennel (*Eupatorium* sp.) in many fenced wetlands. Dog fennel is a hardy, normally herbaceous plant that in some fenced wetlands grew into dense woody thickets up to ten feet high. This change in vegetation structure was expected to affect beetle assemblages. The short-term effects of one year's prescribed fire were expected to be less obvious, because fire effects in wetlands have been found for long-term fire regimes.

CHAPTER THREE: METHODS

Study Site and Experimental Design

This study was conducted at the MacArthur Agro-ecology Research Center (MAERC), a 4,170-ha working cattle ranch with several thousand cattle managed by Archbold Biological Station in south-central Florida and is located at Buck Island Ranch, approximately 30 miles northwest of Lake Okeechobee, within the Indian Prairie basin (Figure 3). Much of this area is pastureland converted from dry and wet prairies and cabbage palm flatwoods. Depressional temporary wetlands are abundant here: over 600 wetlands are on MAERC alone. These wetlands are characterized by seasonal drying and frequent fires, which results in communities of specialized flora and fauna (Myers and Ewell 1990). Seasonal drying also results in an annual re-assembly of aquatic beetles in the wetlands. Wetlands at MAERC are embedded in either “intensively-managed” or “semi-natural” pastures. Intensively-managed pastures have been fertilized (annually with N, historically with N,P, and K – 1960’s-1986), extensively ditched, replanted with non-native Bahia Grass, *Paspalum notatum*, and are grazed in the summer. Wetland vegetation in these pastures is dominated by soft rush (*Juncus effusus*). “Semi-natural” pastures have never been fertilized, have fewer ditches, are dominated by native grasses, and are grazed in the winter. The wetland vegetation in these pastures is dominated by an assortment of sedges, emergent macrophytes, and maidencane (*Panicum hemitomon*). Cattle grazing and fire were experimentally manipulated by fencing and burning the wetlands in both pasture types.

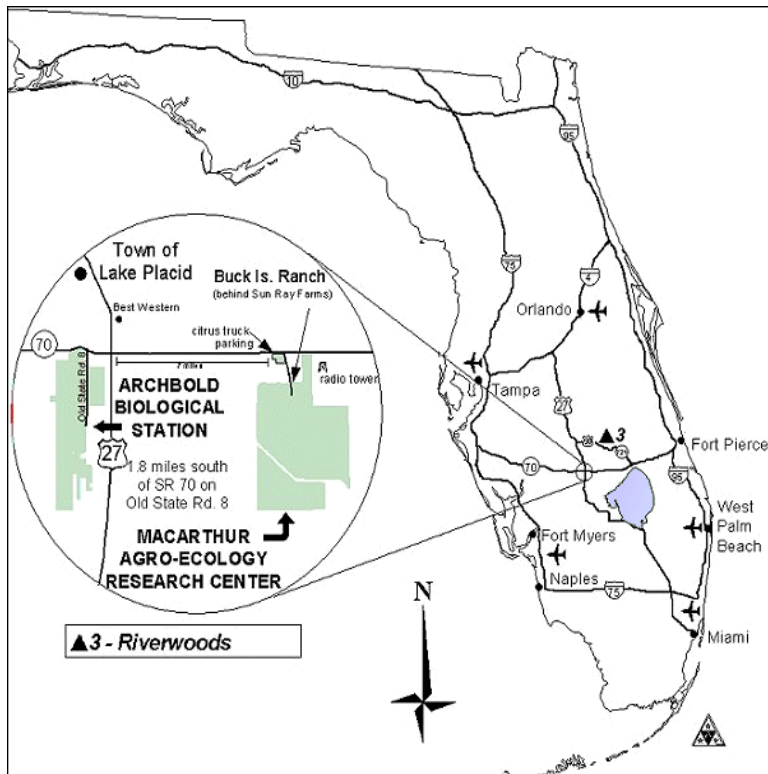


Figure 3: MAERC (maerc.org)

Samples were collected from 40 wetlands at MAERC in September 2006, September 2008, and July 2009. To control for confounding effects of variation in size and hydrology, wetlands of similar sizes (0.5 – 1.5 ha) were chosen from the two pasture types within 5 blocks across the ranch, and randomly assigned experimental treatment (Figure 4). The 2006 samples reflect only pasture intensification (semi-natural vs. intensively-managed). After 2006 samples were collected, 20 wetlands were fully fenced to exclude cattle. A drought in 2007 prevented complete wetland sampling for aquatic beetles. Prescribed fire was applied to 20 wetlands in winter 2007, and samples were collected in September 2008 and July 2009 to reflect the full combination of all three treatments (pasture intensification, fencing to exclude cattle, and fire).

Thus, two levels of pasture intensification treatment are crossed with two levels fencing treatment and two levels of fire treatment to yield 8 treatment combinations in a full factorial design. Five replicates of each treatment combination are arrayed in 5 blocks across the ranch, for a total of 40 wetlands in the experiment.

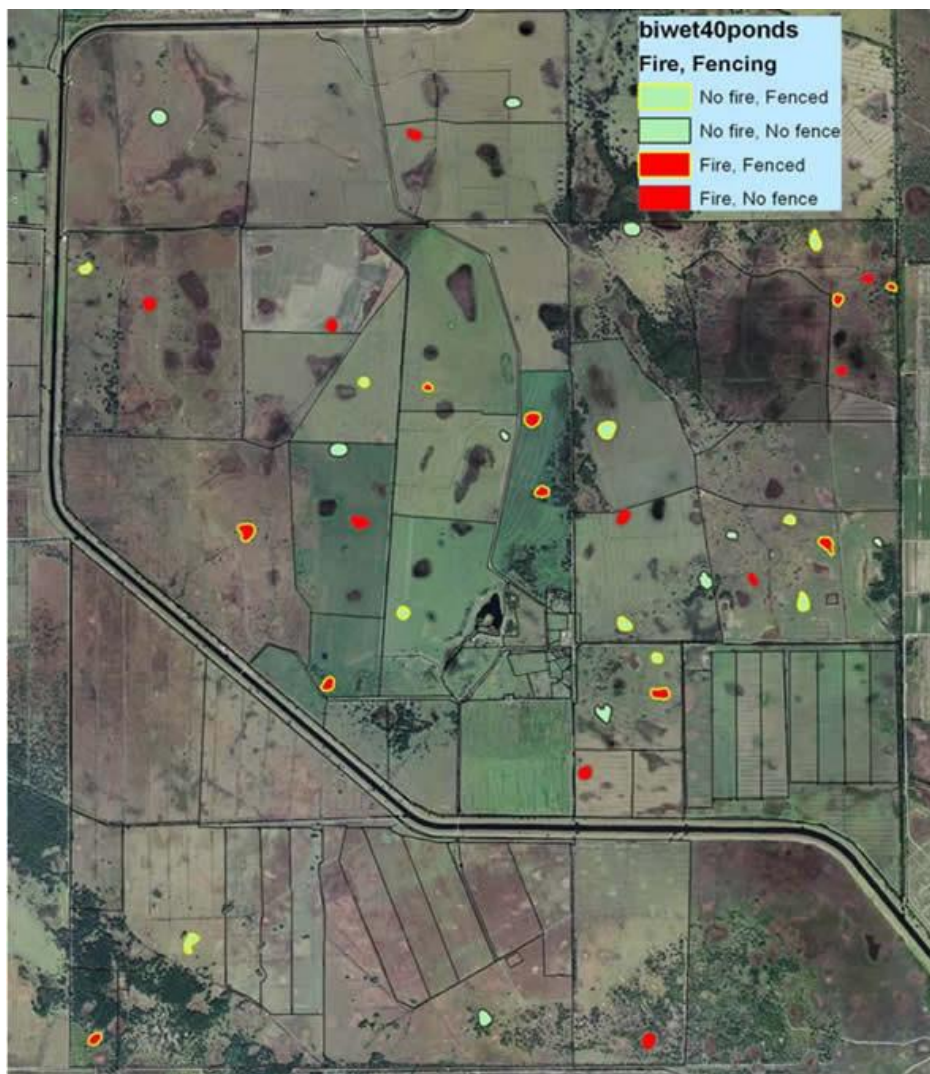


Figure 4: Aerial View of Experimental Wetlands Showing Fence and Fire Treatments

Sampling

Dip net sampling was conducted in September 2006, September 2008 and July 2009. Each wetland represents a single experimental unit, and was sampled with two standardized, 1-meter sweeps with a 500-micron dip net, within one meter of each steel pole that marked random sample locations. There were five randomly-selected locations, for a total of 10 sweeps per wetland. Organisms were preserved in 70% isopropanol.

Identifications were done in the lab at the University of Central Florida following Epler (1996) and Merritt and Cummins (1996). Voucher specimens will be deposited at the University of Central Florida Collection of Arthropods and Archbold Biological Station. Morphological identification of larvae of most species of aquatic beetles has not been resolved, so only genera were used in calculating metrics in this study.

Phylogenetic Analysis

Only genera in the three families of the suborder Adephaga were used in this study because sequences were not available for many of the genera in the families of the suborder Polyphaga. The aquatic adephagans are monophyletic (Hunt et al 2007, Ribera et al 2002). Therefore, some problems are avoided that arise from including distantly related taxa in calculating PCS metrics (Vamosi et al 2009); this would be the case if the aquatic polyphagans were incorporated, as an aquatic lifestyle is a convergence across distantly related lineages spanning the entire phylogeny of Coleoptera (Hunt et al 2007).

Three genes were used to estimate the phylogenetic tree to account for differing rates of genetic evolution: nuclear small subunit ribosomal RNA (18S rRNA), mitochondrial 16S rRNA, and mitochondrial protein-coding cytochrome oxidase subunit I (COI). Sequence data were acquired from GenBank (see Appendix for GenBank Accession Numbers) for each aquatic adephagan genus present in the study. Each gene partition was aligned with MUSCLE software (Edgar 2004) using default parameters and then concatenated into a single dataset using MaClade (Maddison and Maddison 2005). The best-fit model was determined using MrModelTest (Nylander 2008), which found GTR+I+G as the best model for each partition. The dataset was analyzed in a mixed-model partitioned Bayesian framework in MrBayes ver 3.1.1 (Huelsenbeck and Ronquist 2001). Bayesian analyses were conducted using four independent runs, each running 5 million generations, saving trees every 1,000 generations. Convergence of the runs was measured in Tracer (Rambaut and Drummond 2007), and 25% were discarded as burn-in. MrBayes was used to summarize the data and to generate posterior probability values. Graphical manipulation of the phylogenetic tree was done in Mesquite (Maddison and Maddison 2009).

Several genera in the dytiscid tribe Bidessini did not have available sequences from GenBank. This tribe consists of very closely related genera, and their monophyly is consistently recovered in other studies (Miller et al 2006, Ribera et al 2008), so in this study they were treated as a polytomy. This was done by assigning the six genera found in this study in Bidessini (*Liodessus*, *Andocheilus*, *Bidessonotus*, *Brachyvatus*, *Neobidessus*, and *Uvarus*) sequences of a single genus, *Liodessus* (Appendix: GenBank Accession Numbers).

Statistical Analysis

Adephagan aquatic beetle assemblages were evaluated using both phylogenetic and classical ecological metrics. The phylogenetic metrics used were phylogenetic diversity (PD), net relatedness index (NRI), and nearest taxon index (NTI). PD was originally created to compare habitat quality for use in conservation (Faith 1992), and is a measure of all the nodes or branch lengths of a sample of taxa on the larger phylogeny of the taxa pool (total taxa from all samples). The value of PD increases with both species richness and phylogenetic distance between species.

NRI and NTI are standardized indices for calculating phylogenetic relatedness, and so can be used to test for differences among treatments, and to directly measure the phylogenetic structure (clustering/overdispersion) of each sample or all samples within a treatment. NRI is calculated from the mean phylogenetic distance (MPD), which is a measure of the phylogenetic distance (nodal or branch length) between each taxon and every other terminal taxon in the sample (Figure 5). The mean MPD taken from a distribution of randomized null community samples is then subtracted from the observed sample MPD value, and standardized by the standard deviation of the null distribution to give the NRI value for the sample (Figure 6). Compared to NTI, NRI is more sensitive to clustering/overdispersion at higher taxonomic levels. The null distribution is produced by randomly generating a specified number (generally 1000) of sample iterations based on a null model. NTI is calculated similarly, except that it is a standardized measurement of mean nearest taxon distance (MNTD), which is the mean phylogenetic distance between each sample taxa and its closest related neighbor in the sample; it

is relatively more sensitive to lower level taxa relationships. Positive values of both NRI and NTI indicate phylogenetic clustering of a sample, negative values indicate overdispersion.

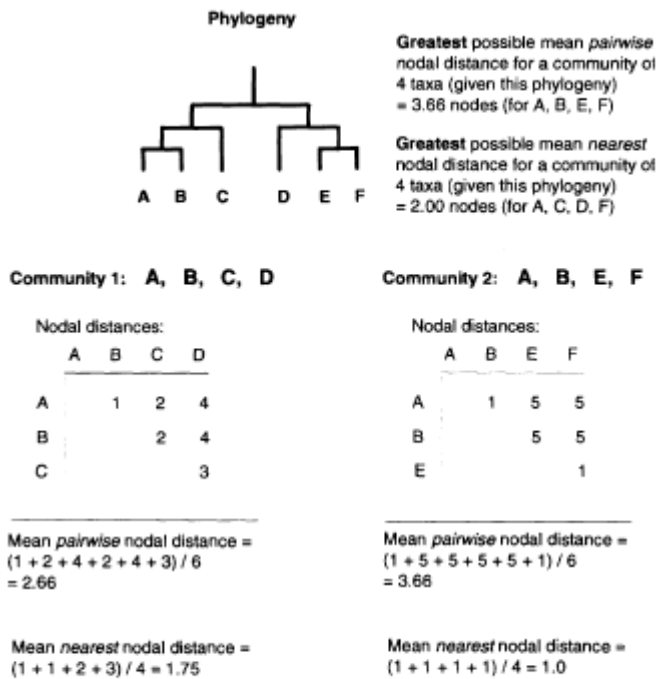


Figure 5: Calculation of MPD and MNTD

Example of how MPD (mean phylogenetic distance, here as mean pairwise distance) and MNTD (mean nearest taxon distance, here as Mean nearest nodal distance) are calculated (rearranged from Webb 2000)

$$\text{NRI}_{\text{sample}} = -1 \times \frac{\text{MPD}_{\text{sample}} - \text{MPD}_{\text{rndsample}}}{\text{sd}(\text{MPD}_{\text{rndsample}})}$$

$$\text{NTI}_{\text{sample}} = -1 \times \frac{\text{MNTD}_{\text{sample}} - \text{MNTD}_{\text{rndsample}}}{\text{sd}(\text{MNTD}_{\text{rndsample}})}$$

Figure 6: Calculation of NRI and NTI

NRI_{sample} = net relatedness index of observed community or assemblage, MPD_{sample} = mean phylogenetic distance of observed community, MPD_{rndsample} = mean phylogenetic distance from randomly generated null distribution, NTI_{sample} = nearest taxon index of observed community, MNTD_{sample} = mean nearest taxon distance of observed community, MNTD_{rndsample} = mean nearest taxon distance from randomly generated null distribution, sd = standard deviation.

A null model known as the independent swap algorithm was used to randomize genera co-occurrence while maintaining genera occurrence frequency across all samples and richness within samples (Gotelli & Entsminger 2003). This type of null model has been shown to have a low Type I error rate while remaining sensitive to patterns of non-random phylogenetic community structure when used in conjunction with NRI/NTI (Kembel 2009).

The classical ecological metrics used were richness (number of genera in an assemblage) and expected number of taxa (D). The expected number of taxa (D) is calculated as the antilog of H' (i.e. $D = e^{H'}$) (Krebs 1999). The D index was recently shown to be a robust measure of diversity (Jost 2006). The Shannon-Wiener index (H') is commonly applied in ecological studies, and is based on abundance data ($H' = -\sum (p_i)(\ln p_i)$, where p_i = the proportional abundance of species i).

NRI and NTI values within each treatment were tested for significant phylogenetic structure (i.e. different from 0, or random) using a one-sample t-test. To test for significant differences among treatment effects (and the differences in measurement sensitivity), all metrics (genera richness, D, PD, NRI, NTI) were analyzed with analysis of variance (ANOVA; Table 3),

after testing for homogeneity of variance with Levine's Test. Results are presented in summary form, but ANOVA tables are presented in the appendices.

Table 3
ANOVA Table for This Experiment (3-way factorial, randomized block)

Source	Degrees of Freedom (df)	Critical F-ratio
Blocks	4	4.2
Pasture	1	2.71
Fence	1	2.71
Burn	1	2.71
Pasture x Fence	1	2.71
Pasture x Burn	1	2.71
Fence x Burn	1	2.71
Pasture x Fence x Burn	1	2.71
Within groups (residual)	28	

The 2006, 2008, and 2009 results were analyzed separately, as aquatic beetles re-assemble annually in the seasonal wetlands. In addition, 2008 and 2009 results were analyzed as a Before-After Control-Impact (BACI) design by calculating the difference for each wetland beetle assemblage from the value obtained in 2006. This approach accounted for initial variation among wetlands recorded in 2006. Data were analyzed for treatment effects with R (R Development Core Team (2007) software. Metrics of phylogenetic community structure were calculated using the Phylocom (Webb et al 2008) software package based on the novel phylogenetic tree generated here.

CHAPTER FOUR: RESULTS

Sampling

A total of 23 genera in three families (Haliplidae, Noteridae, Dytiscidae) of aedepteran aquatic beetles were collected from the experimental wetlands in three years at MAERC. The two genera of haliplids, four noterids, and 17 dytiscids represent the taxa list (i.e. regional pool) used in this study. See the BACKGROUND INFORMATION, Aquatic Coleoptera and Seasonal Wetlands section for details on the natural history of these beetles.

Phylogenetic Tree

The resulting consensus tree from the Bayesian analysis recovered all three families of aedepteran water beetles as monophyletic (Figure 7). The relationships among these families are well resolved and congruent with previously published phylogenies (Ribera et al 2002, Hunt et al 2007). The higher level relationships within Dytiscidae were not well resolved and the subfamily Hydroporinae (*Bidessini*, *Laccornis*, *Celina*, *Hydrovatus*, *Desmopachria*, and *Pachydrus*) was not recovered as monophyletic. Genus-level relationships were more consistent with previously published phylogenies: the clades of *Celina* + *Desmopachria*, *Copelatus* + *Coptotomus*, *Hydaticus* + *Thermonectus*, and the close relationship of *Hydrovatus* and *Laccophilus* are all congruent with Ribera et al (2008).

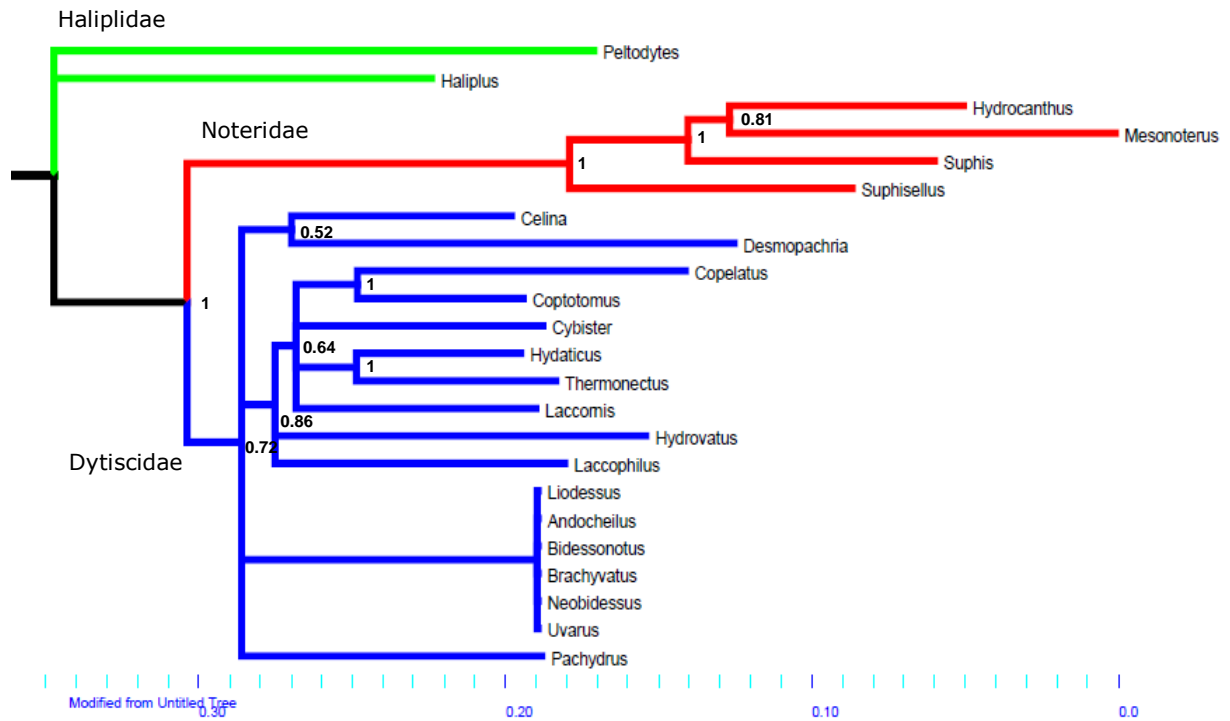


Figure 7: Phylogram of Adephagan Aquatic Beetles Showing Branch Length and Posterior Probabilities

A majority consensus tree obtained from Bayesian analysis of 18S, 16S, and COI sequences. Branch length corresponds to the legend at bottom and posterior probabilities are given for each clade. Branch color corresponds to family.

2006

All metrics with significant results in all years passed Levine's Test for homogeneity of variance ($p > 0.1$). By two related ecological measures (genera, PD, but not D), water beetle assemblages were significantly different among blocks and a marginal effect of pasture type was

observed (Table 4, Figures 8 & 9). In addition, near-significant pasture X burn interaction effects were found for genera and PD (Table 4), though burns were not conducted until 2007. Phylogenetic measures (NRI, NTI) did not detect significant or marginally significant effects of block or pasture, but a significant fence effect was observed for NTI in 2006, before fences were installed (Table 4, Figure 10). Additionally, wetlands in intensively-managed pastures and slated to be fenced and burned were significantly clustered in NTI ($t = 2.6466$, $df = 4$, $p\text{-value} = 0.02859$) as were the wetlands scheduled to be fenced ($t = 2.4611$, $df = 19$, $p\text{-value} = 0.01180$). Wetlands not scheduled to be fenced were found to be near-significantly overdispersed ($t = -1.4171$, $df = 18$, $p\text{-value} = 0.08677$). The significant effects of treatment yet to be applied indicate that randomized treatments and blocks did not fully account for the underlying variability among wetlands and supports the use of a BACI analytical approach for analyses of treatment effects in subsequent years.

Table 4
2006 ANOVA Results

Source	# genera	Jost (D)	PD	NRI	NTI
Blocks	p=0.002		p=0.002		
Pasture			p=0.094		
Fence					p=0.018
Burn					
Pasture x Fence					
Pasture x Burn	p=0.051		p=0.052		
Fence x Burn					
Pasture x Fence x Burn					

Blocks were found to be significantly different with both genera richness and phylogenetic diversity. No significant difference was found among pasture type. The significant effects of fence and near-significant pasture x burn interaction found pre-treatment indicate the BACI design was needed to account for this initial variation. Only p-values less than 0.1 are shown.

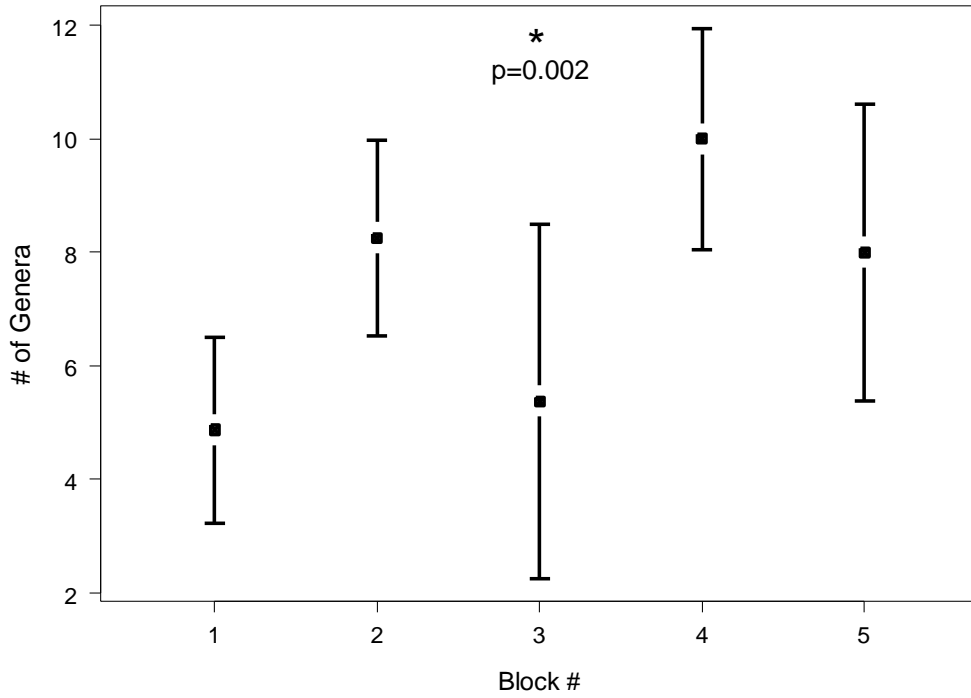


Figure 8: 2006 Mean + 95% CI for Differences Among Blocks in Number of Genera Wetlands in blocks 1 and 3 had fewer adepagan genera compared to blocks 2,4, and 5.

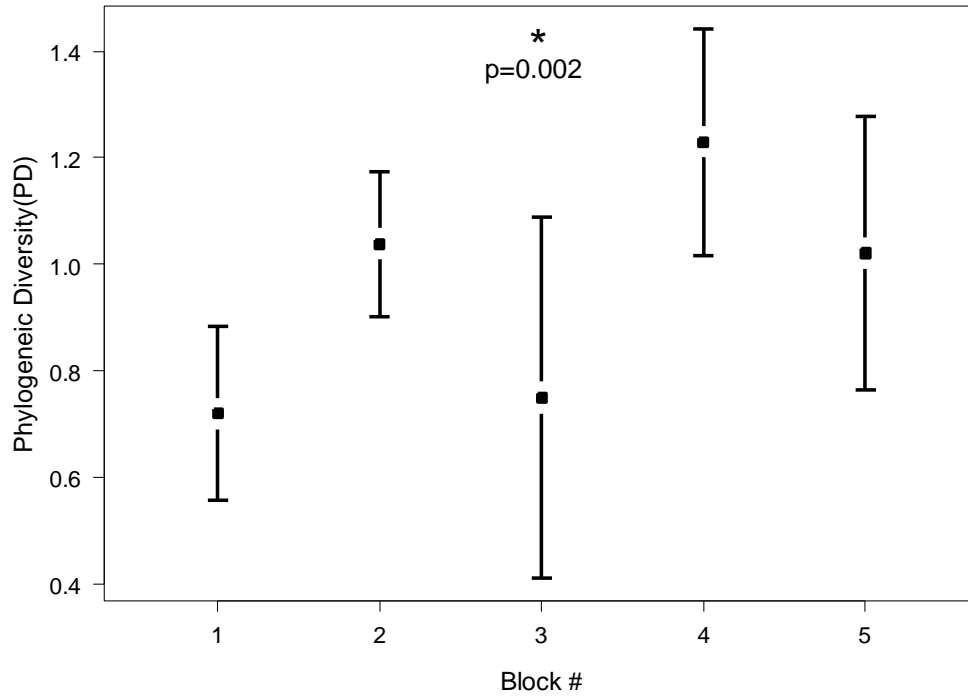


Figure 9: 2006 Mean + 95% CI for Differences Among Blocks in PD

Exhibiting the same pattern as with genera richness, wetlands in blocks 1 and 3 had reduced phylogenetic diversity of adephagan aquatic beetles compared to blocks 2,4, and 5.

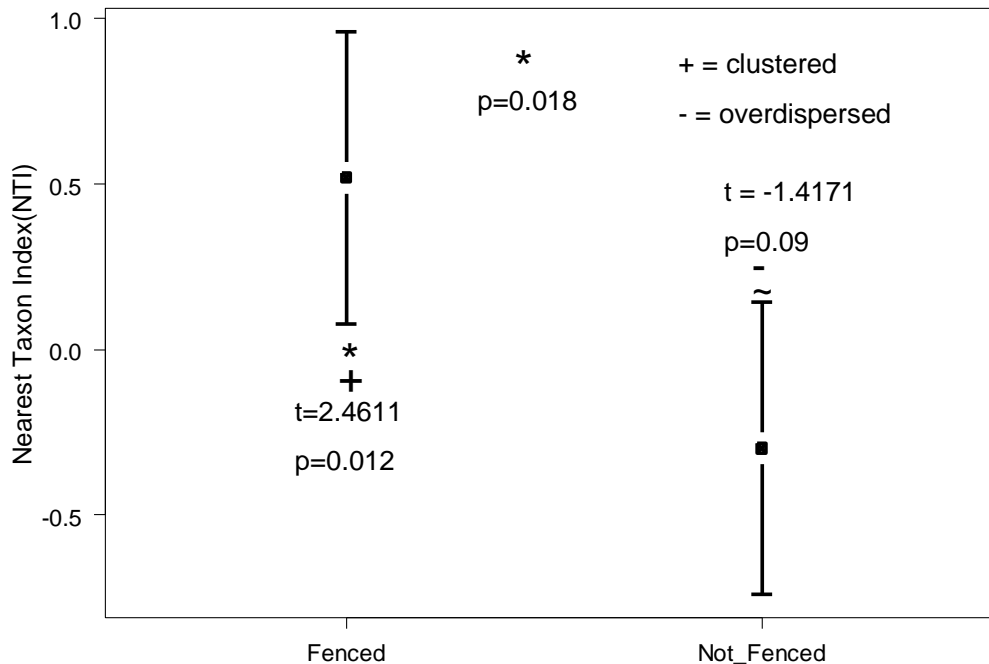


Figure 10: 2006 Mean + 95% CI for Differences Among Fenced/Not-Fenced Wetlands Pre-treatment, in NTI

Wetlands slated to be in the different fencing treatments were significantly different from each other as measured by NTI of aedeagid aquatic beetles. Wetlands that were scheduled to be fenced were significantly phylogenetically clustered, those scheduled to not be fenced were near-significantly overdispersed. Because this pattern was observed before fencing treatments were applied, the BACI design was implemented to account for this initial variation.

2008

The burn treatment applied in the dry season of 2007-2008 significantly reduced genera richness and PD of aquatic beetles in wetlands later that year (Table 5, Figures 11, 12). In contrast, non-burned wetlands did not significantly change for both of these metrics. Fencing (built in the dry season of 2006-2007) also significantly reduced (toward overdispersion) NTI by

2008 (Figure 13), whereas non-fenced wetlands had a slightly positive change (towards clustering) between 2006 and 2008. Beetle assemblages in wetlands that were scheduled to be fenced went from significantly clustered (NTI; $t = 2.4611$, $df = 19$, $p\text{-value} = 0.01180$) in 2006, to random (NTI; $t = -0.5129$, $df = 19$, $p\text{-value} = 0.3070$) after the fencing treatment in 2008, and non-fenced wetlands went from near-significantly overdispersed (NTI; $t = -1.4171$, $df = 18$, $p\text{-value} = 0.08677$) in 2006 to random (NTI; $t = 0.2607$, $df = 19$, $p\text{-value} = 0.3986$) in 2008. Additionally, the wetlands in intensively-managed pastures scheduled to be fenced and burned went from significantly clustered (NTI; $t = 2.6466$, $df = 4$, $p\text{-value} = 0.02859$) in 2006, to random (NTI; $t = -0.0262$, $df = 4$, $p\text{-value} = 0.4902$) in 2008. Similarly, in 2006 wetlands in both pasture types that were slated to be fenced but not burned went from random (NTI; intensively-managed: $t = 1.1514$, $df = 4$, $p\text{-value} = 0.1569$, semi-natural: $t = 0.4228$, $df = 4$, $p\text{-value} = 0.3471$) to significantly overdispersed (NTI; intensively-managed: $t = -2.2056$, $df = 4$, $p\text{-value} = 0.04604$, semi-natural: $t = -2.6079$, $df = 4$, $p\text{-value} = 0.02978$) in 2008 after fencing was installed.

Table 5
Change from 2006 to 2008 ANOVA Results

Source	# genera	Jost (D)	PD	NRI	NTI
Blocks					
Pasture					
Fence					p=0.042
Burn	p=0.027		p=0.031		
Pasture x Fence					
Pasture x Burn					
Fence x Burn					
Pasture x Fence x Burn					

Only p-values less than 0.1 are shown.

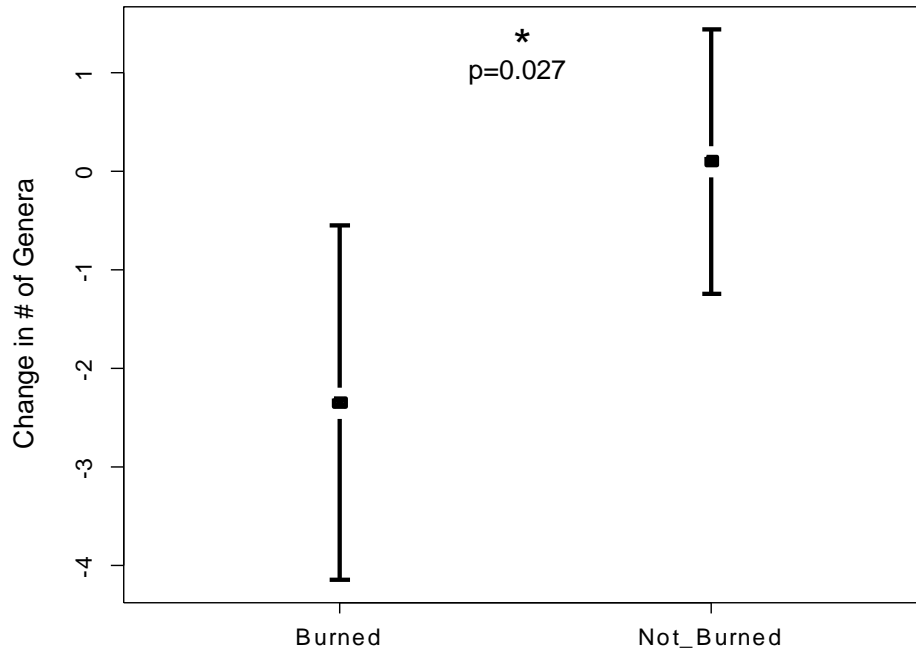


Figure 11: 2008 Mean + 95% CI for Differences Among Burn Treatments in Change in Genera Richness

Change in # of genera is the value obtained for each wetland by subtracting the adephagan aquatic beetle genera richness in 2008 from the genera richness in 2006, as implemented by the BACI design. Burned wetlands experienced a significant reduction in genera richness, as compared to non-burned wetlands.

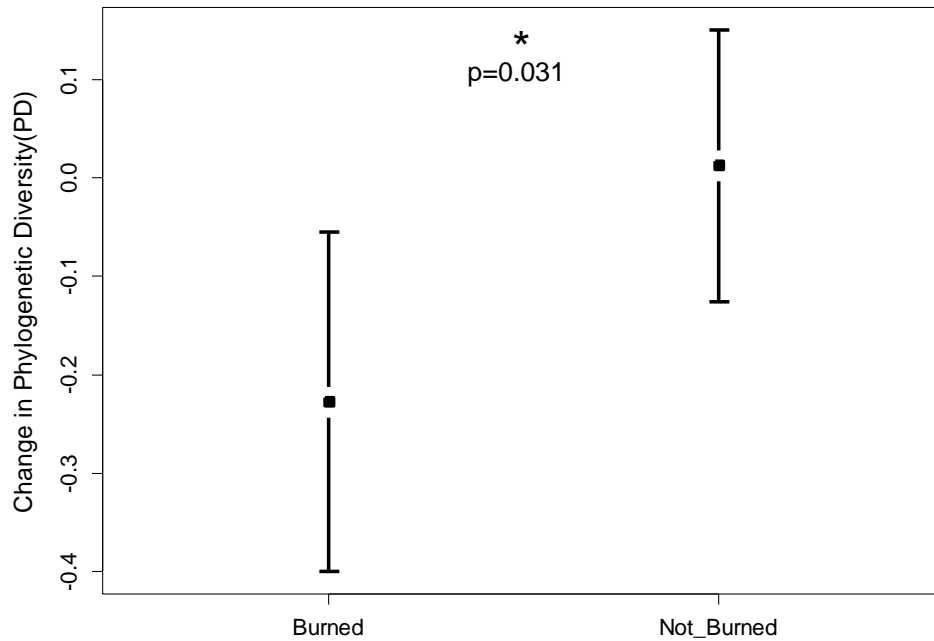


Figure 12: 2008 Mean + 95% CI for Differences Among Burn Treatments in Change in PD

Change in phylogenetic diversity is the value obtained for each wetland by subtracting adephagan aquatic beetle phylogenetic diversity in 2008 from the phylogenetic diversity in 2006, as implemented by the BACI design.

Burned wetlands experienced a significant reduction in phylogenetic diversity, as compared to non-burned wetlands.

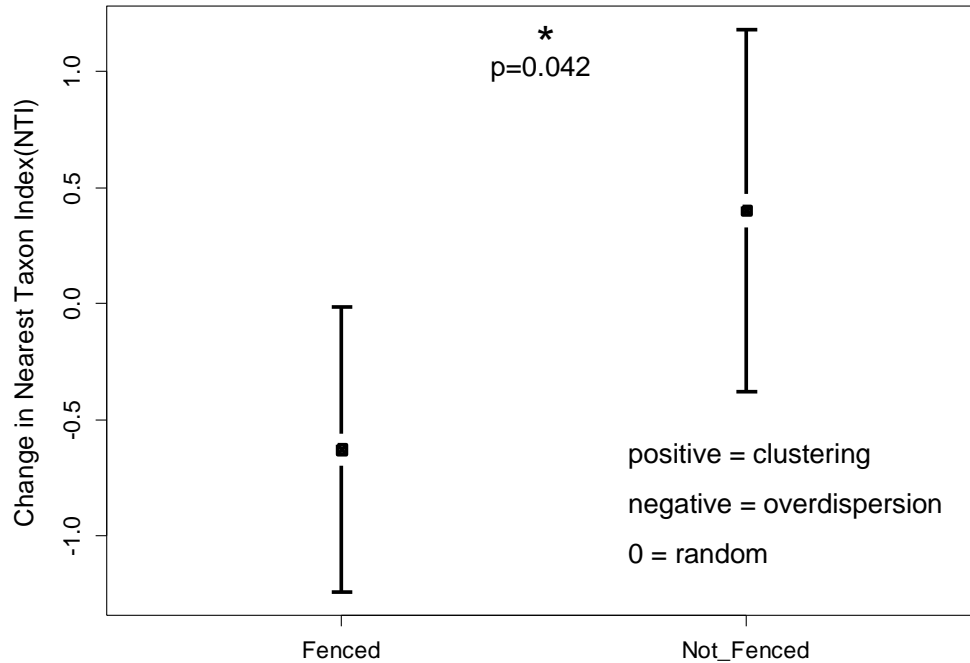


Figure 13: 2008 Mean + 95% CI for Differences Among Fence Treatments in Change in NTI

Change in nearest taxon index is the value obtained for each wetland by subtracting the NTI of adephagan aquatic beetles in 2008 from the NTI in 2006, as implemented by the BACI design. Fenced wetlands had significantly reduced NTI (became more overdispersed) of adephagans compared to non-fenced wetlands.

2009

Aquatic beetle assemblages in intensively-managed pastures changed from random in 2006 (NTI; $t = 0.6088$, $df = 19$, $p\text{-value} = 0.2749$) to overdispersed (NTI; $t = -2.1875$, $df = 19$, $p\text{-value} = 0.02070$) in 2009. Significant block effects re-appeared in 2009 for genera richness and PD (Table 6; Figures 14, 15). Two blocks (2 and 4) reduced in genera richness from 2006 to 2009, while the other three blocks did not change or changed positively (Figures 14, 15). Pasture x burn interaction significantly affected D ($p=0.01$) and marginally affected genera richness and

PD. Fire still reduced adaphagan diversity (D) in 2009 (two years after burn treatments) in intensively-managed pastures but had the opposite effect (increased D) in semi-natural wetlands (Figure 16). The opposite was true in non-burned wetlands: those in intensively-managed pastures increased D, but those in semi-natural pastures decreased D between 2006 and 2009.

A significant pasture x fence x burn interaction existed for the change in NRI of aquatic beetle assemblages between 2006 and 2009 (Figure 17), and this interaction was marginally significant for NTI. This significant interaction can be explained by the following: fenced and burned wetlands in semi-natural pastures became more clustered than those in intensively-managed pastures, while non-fenced and burned wetlands in semi-natural pastures became more overdispersed than those in intensively-managed ones. Fenced and non-burned wetlands in both pasture types had little change, while non-fenced and non-burned wetlands in semi-natural pastures became more clustered than those in intensively-managed pastures. Overall, the greatest clustering change occurred in semi-natural pastures that were fenced and burned, and in intensively-managed pastures that were not fenced and burned.

Table 6
Change from 2006 to 2009 ANOVA Results

Source	# genera	Jost (D)	PD	NRI	NTI
Blocks	p=0.005		p=0.005		
Pasture					p=0.098
Fence					
Burn				p=0.092	
Pasture x Fence			p=0.083		
Pasture x Burn	p=0.089	p=0.010	p=0.071		
Fence x Burn					
Pasture x Fence x Burn				p=0.016	p=0.078

Only p-values less than 0.1 are shown.

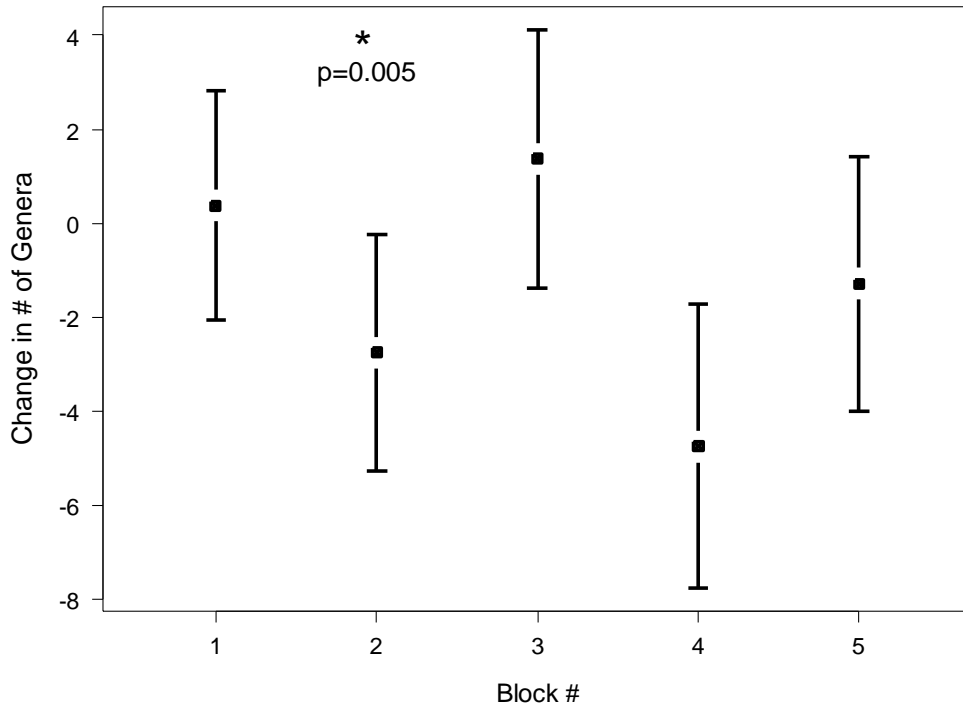


Figure 14: 2009 Mean + 95% CI for Differences Among Blocks in Change in Genera Richness

Change in # of genera is the value obtained for each wetland by subtracting the adephagan aquatic beetle genera richness in 2009 from the genera richness in 2006, as implemented by the BACI design. Wetlands in blocks 2 and 4 experienced a greater reduction in genera richness of adephagans compared to those in blocks 1, 3, and 5.

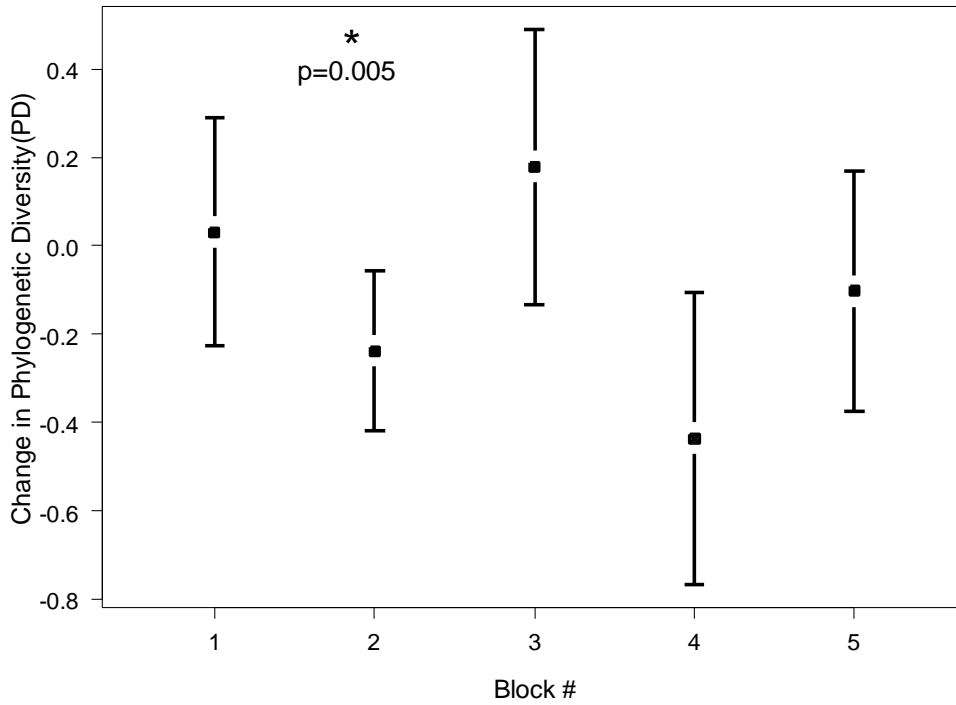


Figure 15: 2009 Mean + 95% CI for Differences Among Blocks in Change in PD

Change in phylogenetic diversity is the value obtained for each wetland by subtracting adepagan aquatic beetle phylogenetic diversity in 2009 from the phylogenetic diversity in 2006, as implemented by the BACI design. Wetlands in blocks 2 and 4 experienced a greater reduction in phylogenetic diversity of adepagans compared to those in blocks 1, 3, and 5.

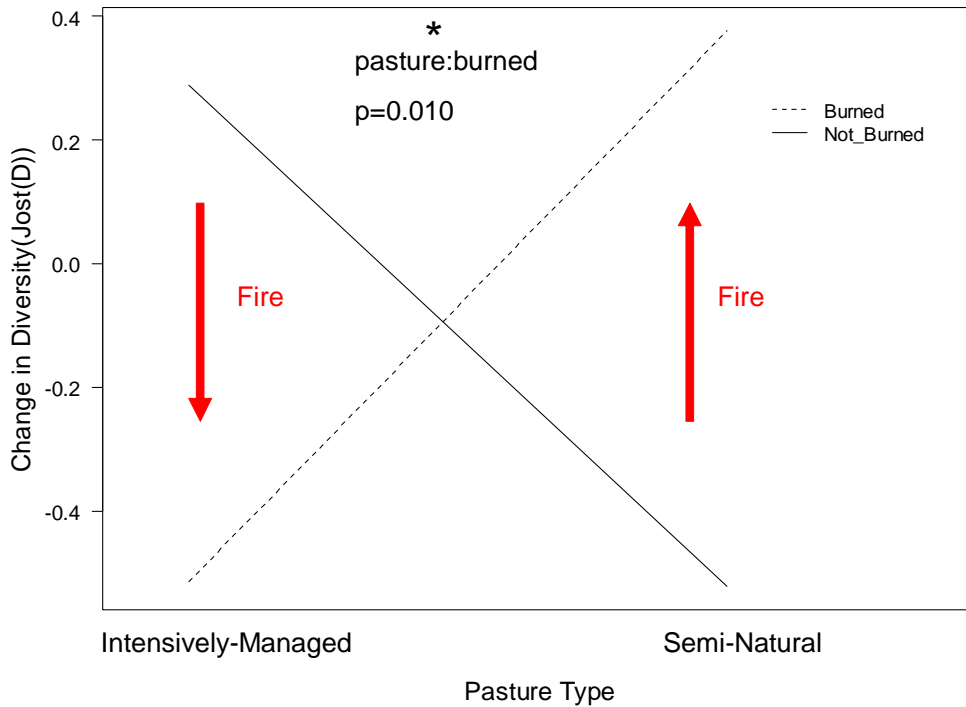


Figure 16: 2009 Pasture X Burn Interaction for Change in Jost (D)

Change in Diversity is the value obtained for each wetland by subtracting adephagan aquatic beetle Diversity in 2009 from the Diversity in 2006, as implemented by the BACI design. The dotted line connects the means of the burned wetlands in each pasture type. The solid line connects the means of the non-burned wetlands in each pasture type. The fire treatment decreased Diversity of wetlands in intensively-managed pastures, while increasing it in semi-natural pastures. The opposite was true in non-burned wetlands.

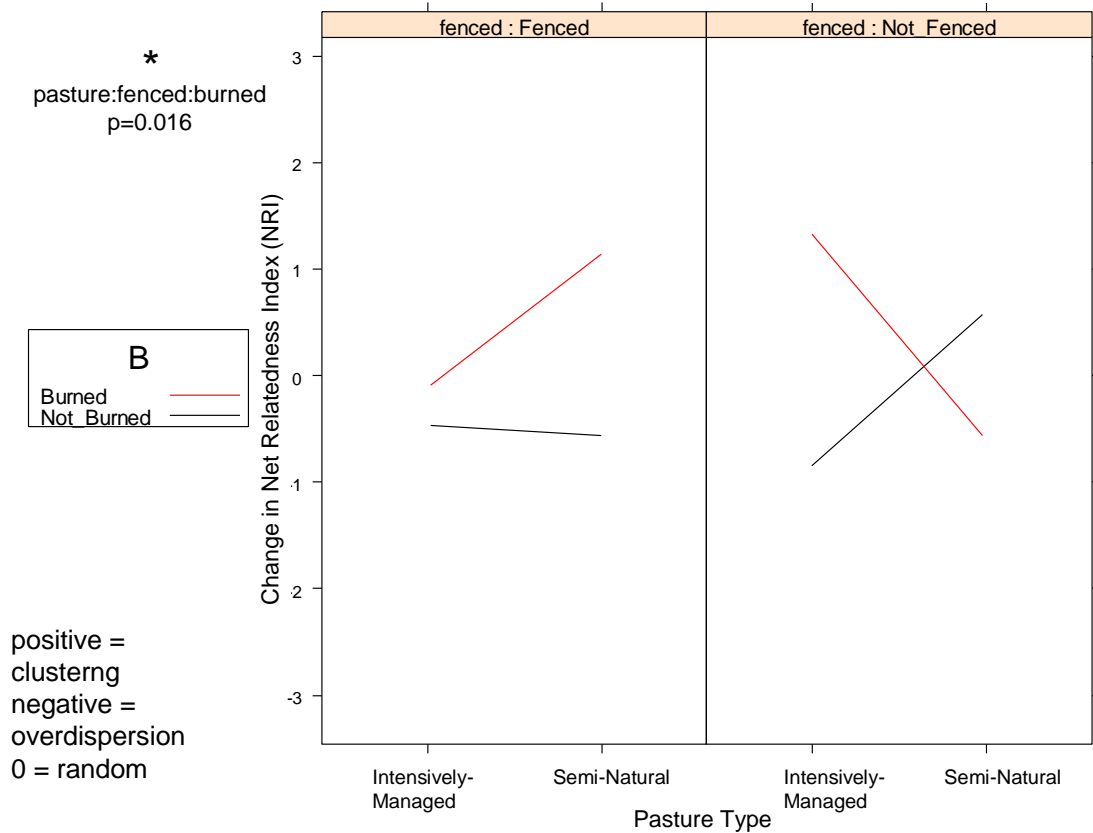


Figure 17: 2009 Pasture X Fence X Burn Interaction for Change in NRI

Change in net relatedness index is the value obtained for each wetland by subtracting the NRI of adepagan aquatic beetles in 2009 from the NRI in 2006, as implemented by the BACI design. The left side of the graph contains the fenced wetlands; the right side the non-fenced, with all combinations of burn and pasture treatment contained within. The red lines connect the means of the burned wetlands in each pasture type, for each fencing treatment. The black lines connect the means of the non-burned wetlands in each pasture type, for each fencing treatment. Aquatic adepagans in fenced and burned wetlands in semi-natural pasture became more clustered compared to those in intensively-managed pastures, while wetlands that were burned but not fenced in intensively-managed pastures became more clustered, as measured by change in NRI. Fenced but not burned wetlands in both pasture types were not different from each other; non-burned and non-fenced wetlands in intensively-managed pastures became more overdispersed compared to those in semi-natural pastures.

CHAPTER FIVE: DISCUSSION

These results generally support the hypothesis that different environmental treatments will lead to different phylogenetic structuring of aquatic beetle assemblages. Overall, burn treatments were more significant and consistent than expected given the single treatment, fencing treatments were significant but opposite of what was expected, and the pasture treatments less clearly affected beetle assemblages. Different indices yielded different results, and phylogenetic based measures provided results that differed from ecological measures.

Substantial variance existed among wetlands at the outset of the experiment despite careful site selection and a block design to account for spatial heterogeneity. In 2006, significant differences were found among beetle assemblages in wetlands for treatments that were not yet applied (fencing and pasture x burn interaction). Therefore the BACI approach was used for analyzing the results in subsequent years to test for treatment effects while accounting for this natural variation.

The significant block effects in analyses of 2006 and 2006-2009 indicate that adaphagan aquatic beetle assemblages in these wetlands were spatially auto-correlated, as was expected by blocked design. Aquatic beetle adults disperse readily (Larson et al 2000, personal observation) and individuals are likely to have moved among wetlands during the experiment. Significant block effects indicate that spatial substructure exists within the 4,170 ha ranch in the beetle assemblages, and that a regional species pool for any given wetland may, in part, be a subset of the total list of species found across the whole ranch. Subset regional species pools may exist

because of habitat filters already in place, including effects of pasture management, nearby canals, trees, and spatial variance in hydroperiod across the ranch.

Pasture type alone was not found to cause significant differences among beetle assemblages; only two marginally significant effects were found among five measures across three years. This runs contrary to initial predictions because of the differences already noted in wetland vegetation among intensively-managed and semi-natural pastures. However, adepagan aquatic beetle assemblages in intensively-managed pastures were converted from an overall random phylogenetic structure (measured by NTI) in 2006 to overdispersed in 2009. Combined with the marginally significant pasture x fence x burn interaction, it is inferred that the combined fencing and burning treatments improved the overall quality of wetlands on intensively-managed pastures by relaxing habitat filters, allowing competition to become the dominant ecological process.

Fire significantly reduced both number of genera and PD in 2008, whereas non-burned wetlands did not change. However, by 2009 the burn effects were no longer evident, with none of the metrics detecting significant differences in beetle assemblages between burned and non-burned wetlands. The strong but transient simple effect of fire on aquatic adepagan assemblages indicates that the re-assembled beetles (a) respond strongly to vegetation during site selection, (b) were directly affected by fire (e.g., eggs or larvae in soil were burned), or (c) some combination of both (a) and (b). Fire had remained as an interactive effect on beetle assemblages in 2009. For example, fire reduced beetle diversity (D) in intensively-managed pastures but increased D in semi-natural wetlands (Fig. 19) more than one year after fire was applied. This result is consistent with the intermediate disturbance hypothesis (Connell 1978),

given that semi-natural wetlands are relatively undisturbed (and so fire increases diversity) but intensively-managed wetlands are already disturbed, and so fire further decreases diversity.

Contrary to early expectations, fire had a delayed and complex effect on adepagan aquatic beetle assemblages; by simple count of significant and marginal outcomes, that effect was stronger than pasture or fence effects. Fire should be considered a potentially valuable tool for managing wetland biodiversity to mitigate effects of long term pasture management (fertilizer and ditching), but must be carefully applied to avoid further reducing diversity. Additional experiments and extension of analyses here to other taxa should show if this potential is consistent and general.

Cattle exclosure (fencing) appeared to reduce the habitat filter imposed by cattle grazing because adepagan aquatic beetle assemblages expanded their phylogenetic breadth (NTI) between 2006 and 2008. Beetle assemblages were significantly clustered in 2006 but became random in 2008 after cattle exclosure. At the same time, non-fenced wetlands changed from near-significantly overdispersed in 2006 to random in 2008. Thus, both fenced and non-fenced and non-fenced assemblages converged on random phylogenetic structure in 2008. The randomizing effect of fencing persisted in 2009, but non-fenced wetlands drifted back to overdispersed at the same time. Similarly, 2006 beetle assemblages in wetlands that were slated to be fenced but not burned were random, but became significantly overdispersed in 2008 after fencing was installed. These results run counter to the initial prediction that dog fennel blooms in 2007 after wetlands were fenced would create a habitat filter causing beetle assemblages to become clustered. Fenced wetlands tended to become more overdispersed, so releasing these wetlands from cattle grazing can be interpreted as benefiting them despite, or in conjunction with

dog fennel overgrowth. However, significant fence effects were limited to the changes discussed above, plus a significant pasture x fence x burn effect on NRI in 2009. Fencing effects did not carry over to other assemblage measures (e.g., number of genera, D, etc.). Thus fencing effects were subtle and would have been missed without phylogenetic community structure analyses.

Several interaction effects in 2009 indicate that aquatic adepagan beetle assemblage responses to treatments were context-dependent. Burned wetlands in intensively-managed pastures became less diverse (lower D), but those in semi-natural pastures became more diverse. Meanwhile, as measured by NRI, assemblages in fenced and burned wetlands in semi-natural pastures became more clustered than those in intensively-managed pastures, while wetlands that were burned but not fenced became more clustered in intensively-managed pastures. So, fire had contrasting effects on beetle assemblages depending on whether or not the wetlands were fenced, and in what pasture type they were located.

Although these results support the hypothesis that pasture management treatments affect aquatic beetle assemblages in experimental wetlands, which treatments have the strongest effects, and their directional impact, run contrary to the predictions. In the short-term, controlled burns decreased diversity in adepagan aquatic beetle assemblages, while fencing generally increased diversity. On the other hand, pasture type alone had little overall effect, although different combinations of fence and burn treatments differed within pasture type.

It is difficult to conclude whether phylogenetic community structure metrics are more sensitive than classic ecological metrics (richness, D). Across all years, six significant or marginally significant results were observed with genera richness and D, whereas 6 such outcomes were observed with NRI and NTI (ignoring PD here because it closely correlated with

richness). More important than the count of outcomes is the fact that phylogenetic community structure metrics found results that differed from, and complemented ecological metrics. Both NRI and NTI are standardized and thus more useful than richness or diversity for direct comparisons between sites or studies, but it is informative within a study to use a combination of phylogenetic community structure metrics and classical ones to compare assemblages or communities.

It should be noted that phylogenetic community structure methods should be used with caution, as they are based on a phylogenetic tree which is itself a hypothesis, and may not represent accurate relationships among taxa. Also, in this case, evidence was given for the assumption of phylogenetic conservatism of ecological traits for the three families of aquatic adephagans found in this study, but not directly tested for. A genus-level phylogenetic tree was used for this study, which could also create problems considering ecological processes such as habitat filtering and competition act on species, not genera. However, many of the genera had only one species represented at the study sight, and genus-level phylogenies have been used in previously published phylogenetic community structure studies (Lessard et al 2009). In addition, traits are more likely phylogenetically conserved at this taxonomic level (Cavender-Bares et al 2009, Vamosi et al 2009).

Although these results are from a multiple-year project, it should be remembered that this was a short-term study, only accounting for what happens to the wetlands after two seasons and one burning treatment. Evidence suggests controlled burns over a longer period of time are advantageous to the biodiversity of ecosystems (Myers and Ewell 1990, Clark and Wilson 2001), and so might be in these wetlands. The fencing effects on their own will be interesting, but their

interactions with pasture type and burn treatment will be even more noteworthy over many years, especially as non-burned-but-fenced wetlands become more dominated by woody vegetation. So, a long-term study, over many years and multiple burning treatments is needed to truly understand the full impact of these pasture management techniques.

APPENDIX A: GENBANK ACCESSION NUMBERS

Genus	COI	16S	18S
Celina	EF056597	EF056669	AJ318719
Copelatus	EF670049	EF670015	AJ850469
Coptotomus	AY071802	AY071776	AJ318686
Cybister	AJ850613	AJ850362	AJ318702
Desmopachria	AJ850643	AJ850394	EF670303
Haliphus	AY071804	AY071778	AJ318667
Hydaticus	AJ850616	AJ850365	AJ318707
Hydrocanthus	HQ383467	HQ381434	AF201415
Hydrovatus	AJ850652	AJ850404	AJ318717
Laccophilus	AY334246	AY334130	AJ318714
Laccornis	AF309298	AJ850419	AJ318715
Liodessus*	AJ850580	AJ850328	AJ318728
Mesonoterus	AY071814	AY071788	AF201416
Pachydrus	AJ850671	AJ850424	AJ318720
Peltodytes	AY071816	AY071790	AJ318668
Suphis	AY071817	AY071791	AF012523
Suphisellus	AY071818	AY071792	AJ318669
Thermonectus	AY334272	AY334156	AJ318712

* Used for all genera in Bidessini (*Andocheilus*, *Bidessonotus*, *Brachyvatus*, *Liodessus*, *Neobidessus*, *Uvarus*)

APPENDIX B: 2006 ANOVA TABLES

Number of Genera

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	144	36	5.683	0.001881**
Pasture	1	18.316	18.316	2.8914	0.10055
Fence	1	0.755	0.755	0.1191	0.73267
Burn	1	7.93	7.93	1.2518	0.27306
Pasture x Fence	1	9.75	9.75	1.5392	0.22541
Pasture x Burn	1	26.347	26.347	4.1591	0.051307
Fence x Burn	1	4.371	4.371	0.69	0.41346
Pasture x Fence x Burn	1	3.394	3.394	0.5357	0.47052
Within groups (residual)	27	171.036	6.335		

Jost diversity (D)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	28.918	7.229	4.5477	0.006148**
Pasture	1	0.12	0.12	0.0754	0.78569
Fence	1	1.951	1.951	1.2275	0.27766
Burn	1	0.259	0.259	0.1628	0.68976
Pasture x Fence	1	0.231	0.231	0.1451	0.70624
Pasture x Burn	1	4.536	4.536	2.8531	0.10272
Fence x Burn	1	0.601	0.601	0.3782	0.54372
Pasture x Fence x Burn	1	0.001	0.001	0.0008	0.97709
Within groups (residual)	27	42.922	1.59		

Phylogenetic Diversity (PD)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	28.918	7.229	4.5477	0.006148**
Pasture	1	0.12	0.12	0.0754	0.78569
Fence	1	1.951	1.951	1.2275	0.27766
Burn	1	0.259	0.259	0.1628	0.68976
Pasture x Fence	1	0.231	0.231	0.1451	0.70624
Pasture x Burn	1	4.536	4.536	2.8531	0.10272
Fence x Burn	1	0.601	0.601	0.3782	0.54372
Pasture x Fence x Burn	1	0.001	0.001	0.0008	0.97709
Within groups (residual)	27	42.922	1.59		

Net Relatedness Index (NRI)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	3.811	0.953	0.6028	0.6639
Pasture	1	0.114	0.114	0.0722	0.7902
Fence	1	1.167	1.167	0.7383	0.3978
Burn	1	0.282	0.282	0.1787	0.6758
Pasture x Fence	1	0.113	0.113	0.0714	0.7914
Pasture x Burn	1	0.03	0.03	0.0192	0.8909
Fence x Burn	1	0.139	0.139	0.0882	0.7688
Pasture x Fence x Burn	1	4.265	4.265	2.6983	0.1121
Within groups (residual)	27	42.674	1.581		

Nearest Taxon Index (NTI)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	0.4549	0.1137	0.1099	0.97801
Pasture	1	0.0089	0.0089	0.0086	0.92685
Fence	1	6.5492	6.5492	6.3289	0.01813*
Burn	1	1.0301	1.0301	0.9954	0.32727
Pasture x Fence	1	0.7501	0.7501	0.7248	0.40205
Pasture x Burn	1	0.03	0.03	0.029	0.86601
Fence x Burn	1	0.9905	0.9905	0.9572	0.33658
Pasture x Fence x Burn	1	0.9406	0.9406	0.909	0.34884
Within groups (residual)	27	27.9398	1.0348		

APPENDIX C: 2006-2008 CHANGE ANOVA TABLES

Number of Genera

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	84.8	21.2	1.9376	0.13296
Pasture	1	12.245	12.245	1.1192	0.29947
Fence	1	0.329	0.329	0.0301	0.86365
Burn	1	60.003	60.003	5.4839	0.02682 *
Pasture x Fence	1	0.079	0.079	0.0072	0.9329
Pasture x Burn	1	8.551	8.551	0.7815	0.38448
Fence x Burn	1	13.92	13.92	1.2722	0.26927
Pasture x Fence x Burn	1	3.729	3.729	0.3408	0.56423
Within groups (residual)	27	295.421	10.942		

Jost diversity (D)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	3.0338	0.75846	0.7385	0.5739
Pasture	1	0.024	0.02401	0.0234	0.8796
Fence	1	0.328	0.328	0.3194	0.5767
Burn	1	0.3784	0.37844	0.3685	0.5489
Pasture x Fence	1	0.0412	0.0412	0.0401	0.8428
Pasture x Burn	1	2.0681	2.06811	2.0137	0.1673
Fence x Burn	1	0.3897	0.38972	0.3795	0.543
Pasture x Fence x Burn	1	0.7172	0.71718	0.6983	0.4107
Within groups (residual)	27	27.7292	1.02701		

Phylogenetic Diversity (PD)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	0.79967	0.19992	1.8264	0.15285
Pasture	1	0.10882	0.10882	0.9942	0.32758
Fence	1	0.03386	0.03386	0.3093	0.58267
Burn	1	0.56918	0.56918	5.1999	0.03070 *
Pasture x Fence	1	0.00092	0.00092	0.0084	0.92764
Pasture x Burn	1	0.05713	0.05713	0.5219	0.47623
Fence x Burn	1	0.1065	0.1065	0.973	0.3327
Pasture x Fence x Burn	1	0.01423	0.01423	0.13	0.72126
Within groups (residual)	27	2.95546	0.10946		

Net Relatedness Index (NRI)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	11.467	2.8667	0.7865	0.544
Pasture	1	1.509	1.5095	0.4142	0.5253
Fence	1	0.059	0.059	0.0162	0.8997
Burn	1	0.002	0.0021	0.0006	0.9811
Pasture x Fence	1	0.973	0.9726	0.2669	0.6097
Pasture x Burn	1	1.875	1.8752	0.5145	0.4794
Fence x Burn	1	4.782	4.782	1.312	0.2621
Pasture x Fence x Burn	1	3.81	3.8098	1.0453	0.3157
Within groups (residual)	27	98.406	3.6447		

Nearest Taxon Index (NTI)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	5.431	1.3578	0.5835	0.67723
Pasture	1	2.365	2.365	1.0163	0.32234
Fence	1	10.575	10.5751	4.5446	.04227 *
Burn	1	1.141	1.1408	0.4902	0.48981
Pasture x Fence	1	0.023	0.0228	0.0098	0.92187
Pasture x Burn	1	1.276	1.2758	0.5483	0.46541
Fence x Burn	1	3.414	3.4142	1.4672	0.23628
Pasture x Fence x Burn	1	3.541	3.5412	1.5218	0.22798
Within groups (residual)	27	62.828	2.327		

APPENDIX D: 2006-2009 CHANGE ANOVA TABLES

Number of Genera

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	191.55	47.888	4.8273	0.004554 **
Pasture	1	6.236	6.236	0.6286	0.43478
Fence	1	0.411	0.411	0.0414	0.840272
Burn	1	10.167	10.167	1.0249	0.320353
Pasture x Fence	1	15.728	15.728	1.5855	0.218751
Pasture x Burn	1	30.777	30.777	3.1024	0.089498 .
Fence x Burn	1	10.693	10.693	1.0779	0.308388
Pasture x Fence x Burn	1	0.028	0.028	0.0028	0.95824
Within groups (residual)	27	267.846	9.92		

Jost diversity (D)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	7.9429	1.9857	2.2	0.095789 .
Pasture	1	0.0401	0.0401	0.0444	0.834654
Fence	1	0.1221	0.1221	0.1353	0.715849
Burn	1	0.0085	0.0085	0.0094	0.92357
Pasture x Fence	1	0.7831	0.7831	0.8676	0.359862
Pasture x Burn	1	6.9723	6.9723	7.7247	0.009796 **
Fence x Burn	1	0.3544	0.3544	0.3926	0.536202
Pasture x Fence x Burn	1	0.2407	0.2407	0.2667	0.609747
Within groups (residual)	27	24.3701	0.9026		

Phylogenetic Diversity (PD)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	1.81508	0.45377	4.7041	0.005194 **
Pasture	1	0.05132	0.05132	0.532	0.472047
Fence	1	0.00932	0.00932	0.0966	0.7583
Burn	1	0.09802	0.09802	1.0162	0.32238
Pasture x Fence	1	0.31203	0.31203	3.2347	0.083285 .
Pasture x Burn	1	0.34052	0.34052	3.53	0.071104 .
Fence x Burn	1	0.16194	0.16194	1.6788	0.206051
Pasture x Fence x Burn	1	0.0081	0.0081	0.084	0.774189
Within groups (residual)	27	2.60452	0.09646		

Net Relatedness Index (NRI)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	8.264	2.066	0.9487	0.45128
Pasture	1	0.336	0.3363	0.1544	0.69743
Fence	1	0.02	0.0201	0.0092	0.92417
Burn	1	6.645	6.6452	3.0514	.09203 .
Pasture x Fence	1	1.782	1.782	0.8183	0.37369
Pasture x Burn	1	2.915	2.9154	1.3387	0.2574
Fence x Burn	1	0.57	0.5703	0.2619	0.61301
Pasture x Fence x Burn	1	14.259	14.2591	6.5476	.01642 *
Within groups (residual)	27	58.799	2.1778		

Nearest Taxon Index (NTI)

Source	Df	Sum Sq	Mean Sq	F value	Pr(>F)
Blocks	4	1.039	0.2599	0.1577	0.95778
Pasture	1	4.828	4.8282	2.9309	.09837 .
Fence	1	0.163	0.1627	0.0987	0.75576
Burn	1	0.012	0.012	0.0073	0.93259
Pasture x Fence	1	4.562	4.5625	2.7695	0.10764
Pasture x Burn	1	0.536	0.5357	0.3252	0.57321
Fence x Burn	1	0.437	0.4374	0.2655	0.61056
Pasture x Fence x Burn	1	5.546	5.546	3.3666	.07757 .
Within groups (residual)	27	44.479	1.6474		

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