

Archives  
Closed  
LD  
175  
A40k  
Th  
449

GROUND BEETLES (COLEOPTERA: CARABIDAE) AS INDICATORS OF ENVIRONMENTAL CHANGE IN AN EASTERN U.S. TEMPERATE FOREST SUBJECTED TO LONG-TERM PRECIPITATION ALTERATIONS

A Thesis

By

BRYAN SCOTT MARBERT

Submitted to the Graduate School

Appalachian State University

In partial fulfillment of the requirements of the degree of

MASTER OF SCIENCE

**WILLIAM LEONARD EURY  
APPALACHIAN COLLECTION  
APPALACHIAN STATE UNIVERSITY  
BOONE, NORTH CAROLINA 28608**

May 2007

Major Department: Biology

GROUND BEETLES (COLEOPTERA: CARABIDAE) AS INDICATORS OF ENVIRONMENTAL CHANGE IN AN EASTERN US TEMPERATE FOREST SUBJECTED TO LONG-TERM PRECIPITATION ALTERATIONS

A Thesis

By

BRYAN SCOTT MARBERT

May 2007

APPROVED BY:

Ray S. Williams

Ray S. Williams  
Chairperson, Thesis Committee

Melany C. Fisk

Melany C. Fisk  
Member, Thesis Committee

Howard S. Neufeld

Howard S. Neufeld  
Member, Thesis Committee

Steven W. Seagle

Steven W. Seagle  
Chairperson, Department of Biology

Edelma D. Huntley

Edelma D. Huntley  
Dean, Research and Graduate Studies

Copyright © by Bryan Scott Marbert 2007  
All rights reserved.

## ABSTRACT

GROUND BEETLES (COLEOPTERA: CARABIDAE) AS INDICATORS OF  
ENVIRONMENTAL CHANGE IN AN EASTERN U.S. TEMPERATE FOREST  
SUBJECTED TO LONG-TERM PRECIPITATION ALTERATIONS

(MAY 2007)

Mr. Bryan S. Marbert, B.S. Appalachian State University

M.S., Appalachian State University

Thesis Chairperson: Ray S. Williams

To address how human-induced climate change could affect terrestrial ecosystem processes, I conducted an experiment at the Throughfall Displacement Experiment (TDE), Oak Ridge National Laboratory, TN, to examine how long-term precipitation alteration in an intact forest affected important ground-dwelling fauna. My primary goal was to examine potential effects of climate change on the community structure of ground beetles and to determine if abiotic and biotic factors affected by precipitation alteration were related to beetle responses. For the 2005 growing season over three time periods I collected arthropods and litter samples in plots at upper and lower elevation sites in each dry (33% precipitation interception), ambient (control), and wet (33% precipitation addition) treatments. Accounting for seasonality and landscape position (i.e. elevation) allowed me to also evaluate the role of naturally occurring factors that could shape ground beetle communities.

Beetle abundance and richness both declined in response to drought, depending on season and elevation. Overall, the abundance of carabid beetles was much higher in the wet

compared to the dry treatment, where Tribe Pterostchini, a hydrophilic beetle, was much more abundant. Wet and ambient treatment tribe similarity was greater compared to the dry plots. Carabid communities varied seasonally. During the summer collection wet and ambient treatments had greater abundance and tribe-level richness than the dry treatment. A shift to more individuals in dominant tribes in the wet plots resulted in lower evenness than in the dry plots, where tribes were more equally represented. Carabid abundance was inversely related to surface litter mass and this corresponded with treatment effects, where litter mass was 50% higher in the dry compared to wet plots. With respect to elevation, greater carabid abundance was associated with higher leaf litter mass, TAE, and C:N at upper elevation sites, suggesting that similar physical and chemical changes in the organic layer due to both precipitation and elevation have opposite effects on carabid communities. Soil water content positively predicted carabid abundance and richness, with overall lower values for each of these measures in the dry treatment. There were effects on landscape position with respect to soil water and the carabid community, with more water but lower abundance of ground beetles at the lower elevation in each treatment. I conclude from my experiment that the removal of natural precipitation in an intact forest can affect ground beetle communities on temporal and landscape scales, and that chemical and physical forest floor characteristics important for ground fauna are altered by drought. In addition, the strong positive relationships between carabid communities and prey availability demonstrated in this study, combined with the negative impact of drought on these relationships, suggest the need for closer examination of climate-induced effects on trophic level relationships important for shaping ground beetle community composition in temperate forests.

## ACKNOWLEDGMENTS

My gratitude and heartfelt appreciation need to be expressed first, and foremost, to all who supported me and contributed to the successful completion of this project, without whom, none of this would have been accomplished. My family deserves the greatest appreciation for their unconditional love and support throughout this process. I would also like to sincerely thank Ray Williams for his mentoring and guidance into the often frustrating and intimidating world of insect ecology. His high expectations for me have truly helped me to develop as a scientist and a person. A special thanks to my committee members Melany Fisk and Howie Neufeld who without their continued willingness to help, this project would not have succeeded. Dr. Paul Hanson, Don Todd, and staff from Oak Ridge National Laboratory provided unlimited support, resources, and insight for my research at their experimental site, the Throughfall Displacement Experiment, allowing my project to come to fruition. Shawn Villalpando, whose good-natured competition kept me going at times, was invaluable to my project, helping me to accomplish the impossible in the field and lab. I'm sincerely appreciative to Nathan Sanders at the University of Tennessee-Knoxville who advised our research group on NMDS and rarefaction, giving of his time when he had very little. I'll always be grateful for my interactions at Appalachian State University and in the Department of Biology with all of the people I'm not able to list here and who have helped with this project. This research was supported by funds from the Appalachian State University Office of Student Research, Cratis D. Williams Graduate School, the Appalachian

State University Biology Graduate Student Association (BGSA), and the Appalachian State  
University Graduate Student Association Senate (GSAS).

### **DEDICATION**

It is our task in our time and in our generation to hand down undiminished to those who  
come after us, as was handed down to us by those who went before, the natural wealth and  
beauty which is ours.

John F. Kennedy (1917-1963),  
Thirty-fifth President of the United States

This thesis is dedicated to my parents Robert Bruce Marbert and Kay English Marbert, who  
instilled in me a love of nature from a very early age and the values to help protect it.

## TABLE OF CONTENTS

	<u>Page</u>
List of Tables.....	ix
List of Figures.....	xi
Introduction.....	1
Methods and Materials.....	11
Results.....	20
Discussion.....	53
Literature Cited.....	65
Biographical Sketch.....	73

## LIST OF TABLES

	<u>Page</u>
1. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and $\pm$ SE of organic horizon mass from May-September 2005. <i>P</i> values and <i>df</i> (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT*ELEV interactions.....	22
2. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and $\pm$ SE of organic horizon litter moisture (%) from May-September 2005. <i>P</i> values and <i>df</i> (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT*ELEV interactions.....	23
3. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and $\pm$ SE of leaf litter nitrogen (%N) and carbon to nitrogen ratios (C:N) from May-September 2005. <i>P</i> values and <i>df</i> (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT*ELEV interactions.....	24
4. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and $\pm$ SE of leaf litter tannic acid equivalents (TAE %) from May-September 2005. <i>P</i> values and <i>df</i> (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT*ELEV interactions.....	25
5. Forest floor mean weekly minimum, maximum, and mean temperature ( $^{\circ}$ C) and $\pm$ SE for 2005. <i>P</i> values and <i>df</i> (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT*ELEV interactions.....	26
6. Beetle families collected in pitfall traps in the wet, ambient, and dry treatments in 2005.....	27
7. Significance values ( <i>P</i> ) and <i>df</i> for main effects of TRT, ELEV, and their interactions for beetle family community parameters using repeated measures ANOVA (Proc GLM).....	32
8. Cumulative abundance of Carabidae tribes in wet, ambient, and dry treatments at upper and lower sites at the TDE in 2005.....	32
9. Significance values ( <i>P</i> ) and <i>df</i> for main effects of TRT, ELEV, and their interactions for family Carabidae tribe community parameters using repeated measures ANOVA (Proc GLM).....	33
10. Significance values ( <i>P</i> ) and <i>df</i> for the effects of TRT, ELEV, and their interactions on summer carabidae community parameters using ANOVA (Proc GLM).....	33
11. Significance values ( <i>P</i> ) and <i>df</i> for main effects of TRT, ELEV, and their interactions on mite abundance using ANOVA (Proc GLM).....	44

12. Multiple regression analysis of habitat variables and Carabidae tribe abundance, richness, Shannon-Wiener Index (H'), and evenness (E) for cumulative (all seasons) and summer, 2005.....	45
---	----

## LIST OF FIGURES

	<u>Page</u>
1. Throughfall Displacement Experiment trough and pipe network used to transport precipitation from the dry to wet treatment. Each 80 m x 80 m treatment plot covers approximately 0.6 ha (ORNL, 2007b).....	12
2. Beetle abundance (all beetle families) ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	34
3. Beetle family richness ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	35
4. Beetle family Shannon-Wiener Index (H') ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	36
5. Beetle family evenness (E) ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	37
6. Carabid abundance ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	38
7. Carabidae tribe richness ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	39
8. Carabidae tribe Shannon-Wiener Index (H') ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	40
9. Carabidae tribe evenness (E) ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	41
10. Mite abundance ± SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.....	46
11. Relationship between soil water content and Carabid abundance across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.20$ , $P < 0.012$ ).....	48
12. Relationship between soil water content and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.15$ , $P < 0.037$ ).....	48
13. Relationship between soil water content and Carabidae tribe evenness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.20$ , $P < 0.014$ ).....	49

14. Relationship between litter mass and Carabid abundance across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.21, P < 0.010$ ).....49

15. Relationship between litter mass and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.11, P = 0.077$ ).....50

16. Relationship between mean weekly temperature maximum and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.16, P < 0.0463$ ).....50

17. Relationship between weekly mean temperature maximum and Shannon-Wiener Index ( $H'$ ) for Carabidae tribes across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.17, P < 0.030$ ).....51

18. Relationship between prey and mean Carabid abundance across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.49, P < 0.001$ ).....51

19. Relationship between prey and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.32, P < 0.001$ ).....52

20. Relationship between prey and Shannon-Wiener Index ( $H'$ ) for Carabidae tribes across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.26, P < 0.004$ )...52

### INTRODUCTION

Because climate is a primary factor shaping the geographic distribution of biota (Coope, 1994; Battisti, 2004), future alterations in temperature and precipitation patterns due to human activities may affect terrestrial ecosystems on broad scales. During the past century the burning of fossil fuels combined with large scale changes in land-use practices (e.g. deforestation), has lead to increases of atmospheric CO<sub>2</sub> from pre-industrial levels of 280 parts per million (ppm) to an estimated 385 ppm at present (NOAA, 2007). A result is the predicted increase in mean global temperature of 1.4° C to 5.8° C in this century (Houghton et al., 2001). In temperate forest, changes in precipitation regimes could be expected to accompany alterations in global temperature. Generally, precipitation alterations are expected to result in a greater number of hot days and less cold days, while simultaneously increasing the frequency of droughts and floods (Houghton et al., 2001). Average temperature has already increased 0.4 to 0.6 ° C over most of North America during the past century, while precipitation has increased 5% to 20% in certain regions of the US and decreased up to 20% in others (Hansen et al., 2001; Gitay et al., 2002). The examination of climate change effects on forest ecosystems is therefore timely.

Predicted alterations to the global hydrologic cycle have the potential to affect plant productivity, biogeochemical cycling, and water resource availability in forest ecosystems (Hanson and O'Hara, 2003). In addition, predicting the effects of future climate change on biodiversity and ecosystems is challenging. It is not exactly known how either precipitation and temperature or whether large-scale climate alterations will cause changes in biodiversity.

Performance of current bioclimatic models attempting to predict future climate and species distributions fall short of the confidence level required to make informed management decisions because there are no data against which results can be tested (Gitay et al., 2002; Araujo and Rahbek, 2006). Longer term and large-scale experiments clearly are essential for testing the effects of climate change on ecosystem processes and biodiversity. While effects on diversity are uncertain, it is known that the responses of individual species to climate changes such as drought are part of a complex cascade of reciprocal responses and feedback processes (Walther, 2007). This falls into the central hypothesis of biodiversity and ecosystem functioning described by Naeem et al. (2004), where changes in biodiversity reflect alterations to some ecosystem function or process due to strongly interweaved relationships. Past research to identify and evaluate species (or taxa) as reliable tools for monitoring and detecting changes in the environment caused by anthropogenic disturbance has proven useful (Bohac, 1999; Rainio and Niemela, 2003). The demonstrated effectiveness of biotic indicators in detecting change in a variety of disturbed habitats provides incentive to evaluate organisms that respond to habitat perturbations caused by climate change related precipitation alterations.

Ground beetles (Order Coleoptera: Family Carabidae) are an ideal model organism for examining the effects of climate change because of their high diversity, taxonomic familiarity, ubiquitous distribution, ease of sampling, and sensitivity to minor habitat modifications (Desender, 1996; Niemela et al., 1996; Rykken et al., 1997). Paleoecological data collected over the last few decades indicate that habitat fragmentation, isolation, and loss of habitat did not result in either a great reduction of beetle species through extinction or a subsequent speciation increase (Coope, 1994; Ashworth, 2001). Rather, beetles responded

to the past major climatic shifts in the Quaternary Period primarily through dispersal, which has ultimately led to their current biogeography (Elias, 1991; Coope, 1994; Ashworth, 2001). This suggests that ground beetles sensitive to climatic variation may respond to shifts in precipitation patterns. In addition, because ground beetles (especially) are known to quickly colonize areas where suitable habitat becomes available (Elias, 1991) habitat changes resulting from precipitation alteration may cause ground beetles to disperse in search of favorable habitat. Because carabids constitute a substantial fraction of the ground fauna in temperate forest (Magura, 2002) and are known to be affected by both drought (Yi and Moldenke, 2005) and the physical environment such as litter mass (Magura et al., 2004), ecosystem level effects on insect community structure could be observed via complex biotic-abiotic feedback mechanisms on the forest floor. Therefore, examination of beetle taxa (especially Carabidae) and their responses to changes in microhabitat caused by precipitation alterations would prove useful for monitoring climate change effects on temperate forests. To better understand the interrelationships between climate alteration, habitat and ground beetle community parameters, I sampled beetles and forest floor parameters over a single growing season to provide needed data for predicting how temperate forest may change as the earth warms and precipitation patterns change.

Climate can influence beetle diversity through physiological tolerances to moisture and temperature directly, as well through feedbacks via the forest floor environment. Previous studies have reported a strong influence of moisture availability on carabid community structure (Rykkken et al., 1997; Antvogel and Bonn, 2001; Koivula, 2002; Maudsley et al., 2002; Yi and Moldenke, 2005). In addition, several studies report distinct carabid community groupings in habitats characterized by hydric, mesic, and xeric habitats,

thus indicating taxon specific moisture requirements (Luff et al., 1989; Antvogel and Bonn, 2001; Maudsley et al., 2002). While the role of moisture seems clear, other factors such as habitat type and season of the year may exert influence on beetle communities. Suttle et al. (2007) observed dramatic declines of overall invertebrate richness in a California grassland resulting from precipitation manipulations, implying that changes in moisture may alter arthropod groups at finer taxonomic resolutions (e.g. Family Carabidae). With respect to seasons, Yi and Moldenke (2005) found a significant decline in mean ground beetle abundance during extended hot, dry seasons compared to milder, more favorable warm, wet seasons. Because moisture availability affects decomposition in the litter/soil environment (Salamanca et al., 2003) examination of the consequences of precipitation manipulation on important organic layer characteristics and beetle communities may help to address important questions with respect to climate change. Clearly an experimental approach that includes long-term monitoring of precipitation patterns to tease out direct and indirect effects would prove useful.

Climate-induced effects on forest floor biotic and abiotic components potentially change the environment for ground-dwelling beetles via effects on decomposition, litter architecture and litter/soil chemistry. It is also important to recognize that some processes are subject to complex feedbacks within the soil and litter. For example, the detrital pathway collects a major percentage of net primary production in temperate forests in the form of woody debris and foliage, acting as a storage pool for essential micro- and macronutrients and releasing these nutrients back into the soils for uptake by plants (Chen and Wise, 1999; Edwards, 2000; Knoepp et al., 2005; Madritch and Hunter, 2005). It seems likely that altered precipitation patterns could change chemical, physical, and microclimatic properties of the

forest floor that effects essential microhabitat for invertebrate inhabitants (Johnson et al., 2002; Taylor and Wolters, 2005; Chikoski et al., 2006). This is especially relevant because certain soil invertebrate groups mediate decomposition and nutrient cycling in the forest floor either through direct or indirect effects (Gist and Crossley, 1975; Hunter et al., 2003). Hunter et al. (2003) found that mass loss and nitrogen content of *Liriodendron tulipifera* foliage declined with macroinvertebrate exclusion. Ground beetles may indirectly influence decomposition through interactions with biota in lower trophic levels in the soil and litter and this may be subject to change via wet/dry periodicity. Microorganisms (i.e., microbes and fungi), responsible for the vast majority of organic material decomposition in terrestrial ecosystems, can become stressed in response to alterations of drying-rewetting cycles (Schimel et al., 1999; Fierer et al., 2003), potentially causing changes of leaf litter mass loss. Using soil respiration as a measure of microbial activity and litter decomposition, Chimner and Welker (2005) found slight increases in soil respiration under conditions of increased winter and summer precipitation. Recent studies manipulating precipitation throughfall reported 19-26% reductions in litter mass loss in drought treatments (Salamanca et al., 2003), with as much as 40% more organic material accumulation due to moisture reductions (Johnson et al., 2002). Alternatively, moisture increases may have an opposite effect on decomposition through increases in decomposition rate. Regardless of the direction of moisture alteration, potential changes in leaf litter mass may alter the structural complexity of the forest floor, impacting ground beetle community structure and other litter invertebrates.

Litter chemistry is known to exert a strong control on macroinvertebrate activity in forested ecosystems, strongly influencing the colonization of leaf litter by invertebrates and their comminution of the litter (Hunter et al., 2003). Plant secondary compounds such as

phenolics are effective inhibitors of decomposition processes and nutrient cycling in terrestrial ecosystems (Horner et al., 1988). Chemical analyses of numerous litter types have indicated significant concentrations of phenolic compounds in most plant species (Hoorens et al., 2003). Studies have shown a negative relationship between total phenolics and the rate of decomposition (Aerts and Caluwe, 1997; Bernhard-Reversat, 1998), where litter of high phenolic content decays slower. Precipitation can increase decomposition by leaching phenolics from leaf litter (Schadler and Brandl, 2005). It follows that reduced precipitation can thus slow decay because of the lack of removal of inhibitory phenolics, thereby altering the soil faunal community (Gist and Crossley, 1975).

The effects of precipitation on litter nutrient contents may also influence decay dynamics. Hanson et al. (2003b) observed significantly higher carbon: nitrogen (C:N) ratios in drought treatments compared to either wet or control treatments in a forest ecosystem. Though C:N ratio was shown to decrease over time for each treatment, drought treatment leaf litter C:N were significantly higher each time indicating poor quality leaf litter due to reduced moisture Hanson et al. (2003b). Carbon:nitrogen ratios have been found to be the good predictors of mass loss rates in organic layers (Taylor et al., 1989; Johnson et al., 2002), often showing a negative relationship between mass loss and C: N ratio. Such nutrient dynamics have the potential to affect ground-dwelling fauna. For example, increased nutrient availability may increase the colonization of litter by soil dwelling prey, and thus ground beetle abundance (Baker, 2006), while nutrient declines may render leaf litter as non-optimal for detritivores leading to a decline in carabid abundance due to reductions in prey availability.

Changes in leaf litter mass may directly affect the composition of ground beetle communities by altering the architecture of the forest floor. Studies on the effects of leaf litter addition to forest floor predators have shown mixed results. Bultman and Uetz (1984) observed a significant increase of dominant macroarthropod predators (Aranae) in response to increased litter structural heterogeneity, while other non-aranae predators showed weak or no response. In other studies, however, certain dominant ground beetle species responded to leaf litter addition with dramatic increases or decreases in abundance (Koivula et al., 1999; Magura et al., 2004; Magura et al., 2005). Magura et al. (2004) observed increased abundance of *Pterostichus oblongopunctatus* in leaf litter addition plots, while no response was elicited from other dominant ground beetle species. The significant affect of leaf litter addition on ground beetle communities is attributed to microhabitat changes that may influence the spatial distribution of species (Magura et al., 2004).

Forest floor temperature could also affect ground beetle communities via its indirect influence on litter moisture, mass, and ground architecture. Variation in thermal conditions caused by microhabitat features may directly affect ground beetle activity levels and colonization of habitat at fine scales (Mazia et al., 2006). A study in an arid Patagonian shrub steppe observed higher activity levels of carabids in shrub plots than in bare soil plots, where mean soil temperatures were significantly higher due to reduced ground cover (Mazia et al., 2006). Magura (2002) reported similar results for individual carabid species, finding a significant negative relationship between surface temperature and captures of *Carabus violaceus*. Changes in temperature and sporadic drought may result in altered soil fauna composition and local population extinction in temperate areas (Hodkinson, 2005). It seems

clear that the temperature of the litter/soil habitat could play a significant role in shaping the communities of significant ground fauna, especially beetles.

Finally, biotic feedbacks in the forest floor (such as predator-prey interactions) shape arthropod communities and are subject to change brought by precipitation effects on decomposition, litter chemistry and temperature. Perhaps most relevant would be factors responsible for determining microinvertebrate prey abundance. Mites (Order Acari) are the most abundant soil arthropod group in forested ecosystems and a potential prey source for ground beetles (Johnston, 2000). Because they are extremely sensitive to habitat disturbance (Lindberg, 2003), the examination of this group is useful in light of climate change. Several studies have found that precipitation has a strong control over mite population density (Heneghan et al., 1999; Ferguson and Joly, 2002; Lindberg, 2003). In a long-term moisture alteration experiment in Sweden, Lindberg et al. (2002) reported a significant decrease in mite abundance with drought and an increase in abundance with irrigation. Taylor and Wolters (2005) also observed a reduction in mite density and diversity under drought treatment, though this finding was influenced by litter type and quality. Part of the effect may stem from increases in litter C:N, which is known to strongly regulate mite communities in soil at the local scale (Hansen and Coleman, 1998; Taylor and Wolters, 2005). During a moisture addition experiment, Chikoski et al. (2006) found that mite abundance was negatively correlated with C:N ratio. In addition to litter chemistry, indirect effects of precipitation on forest floor structural complexity can affect mite populations. Many mite species, particularly suborder Oribatidae, vary in their distribution throughout the strata of the litter profile (Hansen, 2000). Any changes that occur in microhabitat, either through simplification (reduction) or augmentation (addition), may impact mite populations through

alterations of community structure. Because ground beetle activity and predation have a strong correlation with prey density (Winder et al., 2005), and because mites are known to be an important prey resource for invertebrate arthropod predators (Johnston, 2000; Wilson, 2005), altered mite populations may affect carabid distribution. In summary, altered resource availability in the form of prey may lead to changes in carabid spatial and temporal dynamics (Winder et al., 2005).

My study used three precipitation alteration treatments, dry, ambient, and wet, at the Oak Ridge National Laboratory Throughfall Displacement Experiment (TDE) during 2005 to examine both effects on beetle community structure and relationships between beetles and forest floor parameters changed by precipitation alterations. The study design allowed me to quantify effects of precipitation manipulation and seasonality on ground beetle communities relative to variation associated with landscape position. The duration of the larger experiment examining forest responses to climate change (13 years) allowed for a unique opportunity to investigate climate-induced effects on important ground fauna in an intact forest subjected to long-term drought.

I examined three questions:

- (1) How do beetle communities differ according to drought treatment, season and landscape position?
- (2) Does precipitation manipulation alter the chemical and physical characteristics (i.e., C: N, litter mass, and temperature) of the forest floor?
- (3) Are differences in physical and chemical characteristics of the forest floor related to ground beetle community parameters?

Data from my study are important for better understanding the effects of climate change-induced alterations of precipitations in temperate forest, which aids prediction of future change in terrestrial ecosystems.

## METHODS AND MATERIALS

### *TDE Site description and Experimental Design*

My study was part of a large scale experiment set up in 1993 to examine the long-term effects of precipitation alteration on ecosystem processes in an intact temperate forest. The Throughfall Displacement Experiment (TDE) field site is located on a south-facing slope in Walker Branch Watershed (35°58' N, 84°17' W), a part of the U.S. Department of Energy's (DOE) National Environmental Research Park near Oak Ridge, Tennessee (for a detailed site description of Walker Branch see Johnson and Van Hook, 1989). Walker Branch is a temperate zone forest with mean annual precipitation of 1358 mm and average temperature of 14.2°C (Hanson et al., 2003a). The area was chosen because of its uniform slope, consistent soils, and a reasonably uniform distribution of vegetation. Soils are classified as Fullerton series (fine, kaolinitic, thermic Typic Paleudult). Depth to bedrock at this location is approximately 30 m and situated at the upper divide of the watershed so that lateral flow of water into the soils at upper elevations would not confound attempts to create a reduced soil water treatment at lower elevations (Hanson and Wullschleger, 2003). A southern aspect was chosen, which was intended to accentuate the effects of reduced moisture. White oak (*Quercus alba* L.), chestnut oak (*Quercus montana* Willd.), and red maple (*Acer rubrum* L.) are the dominant tree species (Hanson et al., 2003a).

The details of the experimental design at the TDE have been described in detail by Hanson and Wullschleger (2003). Briefly, the site consisted of three (dry, ambient, and wet) adjacent 80 x 80 m plots. Each treatment plot was further subdivided into 100 8 x 8m plots.

Manipulation of hydrologic inputs was accomplished through a network of 2000 sub-canopy troughs (0.3 x 5 m) that divert an estimated 33% of available precipitation from the dry to the "wet" treatment plot (Figure 1). The ambient plot, with no precipitation alteration, served as a control.

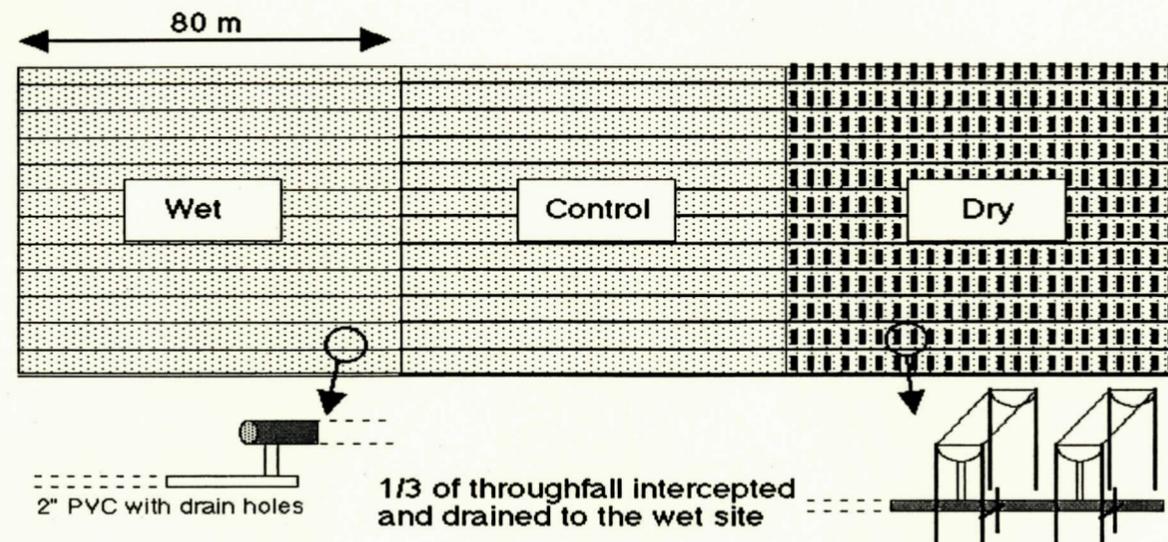


Figure 1. Throughfall Displacement Experiment trough and pipe network used to transport precipitation from the dry to wet treatment. Each 80 m x 80 m treatment plot covers approximately 0.6 ha (ORNL, 2007b).

#### Experimental Plots

To sample ground-dwelling arthropods and abiotic parameters, 10 8 x 8 m experimental plots in each of the three treatments were randomly selected from a gridmap of the site, providing a total of 30 plots. Potential plots were evaluated for suitability in early May 2005. Plots that contained obstacles, such as towers, exclusion cages, etc., that might impede arthropod movement or create artifacts in ground level moisture and litter accumulation were eliminated and another plot chosen. Of the 10 plots in each treatment, five plots were positioned at upper slope sites and five located at lower slope sites.

Hereafter, landscape position (upper or lower slope) will be referred to as elevation. Each experimental plot had at a minimum one 8 x 8 m unused plot as a buffer between other experimental plots on site boundary.

#### Biotic Measurements

##### *Macroarthropod Communities*

Standard pitfall trapping techniques were utilized to collect ground-dwelling arthropods during three sampling periods: spring (May), summer (July), and fall (September), 2005. Pitfall traps consisted of 250 ml Nalgene bottles attached to 10 cm diameter funnels. Bottles contained a 50% ethanol solution for preservation of arthropod specimens. Five traps were placed 1 m apart along a linear transect in the center of each plot. I collected arthropods beginning 11 May, 16 July, and 21 September 2005. Traps remained open for approximately 5 days.

Contents of all pitfall traps from each experimental plot were combined and dominant groups sorted into broad taxonomic categories: Aranae (Spiders), Opiliones (Harvestmen), Orthoptera (Grasshopper), Formicidae (Ants), Coleoptera (Beetles), Chilipoda/Diplopoda (Millipedes/Centipedes), and other, which consisted of Orders Collembola and Hymenoptera. Beetles (Order Coleoptera) were classified to the family level and ground beetles (Family Carabidae) classified to the level of tribe (following sources of Dillon and Dillon, 1972; White, 1983; Arnett and Thomas, 2001). Community level parameters were calculated using both total beetle families and Family Carabidae tribes as the taxonomic unit. I characterized the community using richness, evenness, and diversity indices.

Richness (R) represents the number of beetle families (or tribes) contained in a sample (Boulinier et al., 1998). I used equations for evenness (E) and Shannon-Wiener Index (H') from Rieske and Buss (2001):

$$E = H' / \log_e S$$

where S is the number of families (tribes) in the sample.

$$H' = \sum p_i \log_e p_i$$

where  $p_i$  is the number of beetles in family (Tribe) 'i' divided by the total number of beetles (carabids).

Sørensen Similarity Index was used to compare Carabidae tribe similarity between treatments following the equation from van Tongeren (1995):

$$S = A / (B + C) \times 200$$

where A is the total of the minimum number of individuals in a tribe between the two treatments compared divided by the sum of B and C (the total number of individuals from each treatment) multiplied by 200.

#### *Microarthropod Communities*

Microarthropods were collected from each plot in 5 cm diameter x 4 cm depth cores taken in conjunction with each pitfall trap collection. The 4 cm depth included Oe and Oa horizons in all treatments. Five cores were collected per plot and combined for one sample per plot (total 30 samples per treatment). Microarthropod samples were placed on ice, transported to ASU, and extracted using the methods of Crossley and Blair (1991). Briefly, core samples were weighed (g) and placed in 12.7 cm diameter x 20.3 inch high PVC extractor tubes equipped with a mesh screen on the bottom. Each extractor was fitted with a

5-watt bulb equipped with a rheostat to control light intensity. Microarthropods were extracted for seven days, increasing the intensity of light (heat) with each consecutive day.

Samples were analyzed specifically for mites (Order Acari). Mite suborders Oribatida, Prostigmata, and Mesostigmata were identified and abundance recorded (Krantz, 1970). Mite density was expressed on a  $m^2$  basis.

#### **Abiotic Measurements**

##### *Leaf Litter Mass and Moisture*

Leaf litter mass was sampled in both early summer (June 21) and early fall (September 22). In the early-summer sampling period, four 15  $cm^2$  board samples were obtained from the Oi and Oe layer of each experimental plot (i.e. 40/treatment). Samples were removed from each corner of the plot to minimize disturbance. Beneath the Oe layer in each sample, 5 cm diameter x 4 cm deep soil cores were removed to quantify Oa layer mass in each plot.

For the fall, leaf litter samples were obtained from only the Oi and Oe layers of the forest floor. Two 15  $cm^2$  board samples of the Oi and Oe layer were removed from each plot (one at the top of the plot and one at the bottom) for a total of 20 samples per treatment. Sampling of the Oa horizon was unnecessary due to the slow rates of change that occur annually in this layer.

I used the average mass and moisture from the two samples because these parameters were not expected to change substantially in a single growing season. Samples were weighed initially for fresh (wet) weight (g) and oven-dried to constant weight at 65°C. Dry-

weight, litter mass (g) and moisture content (%) were calculated. Litter samples were then stored for further chemical analyses.

#### *Litter Layer Temperature*

Litter layer temperature was recorded using iButton<sup>®</sup> continuous data loggers (Maxim Integrated Products). The iButtons were positioned in the center of each plot directly beneath the Oi layer of the organic horizon. iButtons<sup>®</sup> were programmed to record temperature at four hour intervals from 9 May to 28 September 2005. Temperature data were downloaded using iButton TMEX Application software and weekly minimum, maximum, and mean temperatures calculated.

#### *Nitrogen and Carbon Analysis*

Leaf litter samples collected for mass measurements during the first sampling period (i.e. May) were used to determine total carbon (C), total nitrogen (N), and carbon: nitrogen ratios (C: N) for the Oi, Oe, and Oa horizons in each plot. A standard protocol was followed for sample preparation (UGA, 2006). All samples collected in a plot were pooled and oven dried at 80° C for 24 hours. Samples were ground in a coffee mill followed by a ball mill (i.e. amalgamator) to talcum powder consistency. Ten 2-4 mg litter samples per treatment from each the Oi, Oe, and Oa horizons were sent to the University of Georgia's Institute of Ecology Stable Isotope Laboratory for plant tissue elemental analysis by Micro-Dumas Combustion Techniques.

#### *Total Phenolics Quantification*

Total phenolic content of leaf litter was assessed following the Folin-Ciocalteu (FC) reagent technique of Singleton and Rossi (1965). Approximately 40 mg of previously dried and ground leaf litter from the May collection for each the Oi, Oe, and Oa horizons in each plot were analyzed. Solution absorbance was read at 765 nm on a Shimadzu<sup>®</sup> UV-VIS Spectrophotometer. Total phenolics were expressed as tannic acid equivalents (%TAE).

#### *Data Analysis*

Three sampling periods representing spring (11-16 May), summer (16-21 July) and fall (21-26) were used to evaluate seasonal activity of ground-dwelling arthropods at the TDE in 2005. A two-factorial repeated measures ANOVA (SAS 9.1, SAS Institute, Cary, NC, USA) with sampling date as a repeated factor was used to determine the effects of treatment and elevation on all beetle families and Carabidae tribe community parameters (i.e., abundance, richness, H', and E), as well as mite abundance. Results are reported as significant at  $P \leq 0.05$ . All data were tested for normality using Shapiro-Wilk and non-normal data were log-transformed (ln). Tukey's honestly significant difference (HSD) was used for select pairwise comparisons of treatment means. I investigated potential change in beetle diversity measures within seasons (i.e., summer) using Proc GLM (a two-way factorial ANOVA) (SAS).

To account for potential effects of abundance on treatment effects on richness, I used rarefaction analysis (Gotelli and Entsminger, 2004; ECOSIM). Expected richness values were analyzed using Proc GLM using treatment and elevation as main effects.

Effects of treatment and elevation on leaf litter mass and moisture, nitrogen (%), carbon to nitrogen ratios (C:N), and total phenolic content from the Oi, Oe, and Oa horizons were tested with Proc GLM to determine the effects of treatment and elevation. Leaf litter mass and moisture content were averaged for two collection periods (e.g., May and September) prior to analysis, while samples from only the first collection (May) were used for analysis of nitrogen (%), carbon to nitrogen ratio (C:N), and total phenolic content (%TAE). Mean weekly temperature minimums, maximums, and means were analyzed by Proc GLM.

Proc CORR (SAS) was used to determine significant relationships between biotic and abiotic variables. Redundant independent variables were identified to reduce the number of variables entered into multiple regression models. Multiple regression analysis (Proc REG-Stepwise) (SAS) was used to determine the best models to describe my data. Predictor variables allowed to enter the model were significant at  $P \leq 0.15$ , however only variables significant at the  $P \leq 0.05$  level are discussed. Soil water content data for summer were obtained from the TDE data archive (ORNL, 2007a). The regression analyses were used to explain carabidae abundance, richness, diversity, and evenness for the combined data set (spring, summer, and fall) and for the summer data set only. Because season, treatment, and elevation were all discrete variables, dummy coded variables were used to assess the importance of each variable in our combined data set. For season, the summer was used as a baseline for comparison, where spring (i.e., Season 1) and fall (i.e., Season 2) were compared to the summer. For example, if Season 1 proved to be a negative predictor of abundance, then the interpretation follows that spring has less abundance than the summer. Likewise, wet (i.e., Treatment 1) and dry (i.e., Treatment 2) were compared to the ambient. Elevation

was dummy coded so that negative correlations indicated decreases at the lower elevations while positive correlations indicated increases at the upper elevation.

Simple linear regression (Proc REG) was used to analyze individual relationships based on the results of the multiple regression analyses. Regression analysis was used for those variables significant at  $P \leq 0.05$  and marginally significant at  $P \leq 0.10$ . In addition, I analyzed the relationship between arthropod abundance (excluding all beetles) and carabidae community parameters using linear regression.

## RESULTS

### Forest Floor Characteristics

#### *Leaf Litter Mass and Moisture*

Leaf litter mass was affected only by treatment (Table 1). There were significant effects of treatment on both total leaf litter mass and mass in the Oi and Oa horizons, each of which was highest in the dry treatment (Table 1). Total litter mass in the dry treatment was 106 % higher than in the ambient treatment, and 50 % higher than in the wet treatment. There was no effect of elevation on litter mass, however total litter mass was 16-17% higher at upper elevation sites than lower (Table 1).

Litter moisture was affected by both treatment and elevation (Table 2). Litter moisture (%) was generally higher in the dry treatment compared to ambient or wet. The % litter moisture in the Oa horizon and in all horizons combined was significantly different between treatments with moisture greater in the Oa horizon in the dry treatment compared to the ambient (Table 2). Treatment did not affect litter moisture content in the Oe or Oi horizons. Litter moisture content in the Oe horizon was higher at the lower slope sites than the upper slope sites (Table 2).

#### *Leaf Litter Chemistry*

Litter %N and C:N ratio were both affected by treatment in the Oi horizon and by elevation in the Oe (Table 3). At both elevations, Oi horizon %N was lower and C: N higher in the dry treatment (Table 3). No treatment or elevation effects on litter N and C: N were

found for the Oe and Oa horizons. In the Oe horizon, litter C: N ratios were higher in the upper elevation plots compared to the lower elevation (Table 3).

Total phenolics in leaf litter were higher in the Oi horizon of the dry treatment compared to both the ambient and wet. There was a significant effect of elevation on % TAE in the Oe horizon, where upper elevation sites had greater % TAE than lower sites (Table 4).

#### *Forest Floor Temperature*

Weekly average forest floor minimum, maximum, and mean temperatures showed no significant effects of treatment during any sampling period (Table 5). Elevation had no effects on forest floor temperature either.

### Forest Floor Biota

#### *Cumulative Beetle Family Community Parameters*

A total of 3261 beetles from 29 families were collected during 2005 at the TDE; 1301 from the wet treatment, 1050 from the ambient treatment, and 910 from the dry treatment (Table 6). Fourteen beetle families were collected in all treatments (Table 6). Fifteen out of the 29 families collected were not found in all treatments and were collected in low abundance (Table 6). Six beetle families comprised 93.4% of the total captures; Carabidae, Curculionidae, Nitulidae, Staphylinidae, Scolytidae, and Scarabidae (Table 6). In the two families comprising 55% of all beetles collected (i.e., Carabidae and Curculionidae) there were approximately 136% more individuals collected in the wet compared to the dry treatment (Table 6).

Table 2. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and standard errors ( $\pm$  SE) of organic horizon litter moisture (%) from May-September 2005. *P* values and *df* (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT\*ELEV interactions.

Horizon	Wet		Treatment Ambient		Dry		TRT	P Value	
	Mean	SE	Mean	SE	Mean	SE		ELEV	TRT*ELEV
			<u>Upper</u>						
Oi	25.7	$\pm$ 0.6	27.5	$\pm$ 1.6	26.5	$\pm$ 1.1	0.549	0.292	0.753
Oe	26.5	$\pm$ 1.0	27.3	$\pm$ 0.8	28.9	$\pm$ 1.1	0.599	<b>0.036</b>	0.315
Oa	22.7	$\pm$ 1.8	14.3	$\pm$ 4.0	32.0	$\pm$ 2.4	<b>0.005</b>	0.090	0.613
Total	25.0	$\pm$ 0.7	23	$\pm$ 1.9	29.1	$\pm$ 1.0	<b>0.015</b>	0.417	0.725
			<u>Lower</u>						
Oi	27.5	$\pm$ 1.0	27.8	$\pm$ 0.8	27.0	$\pm$ 0.9	a		
Oe	29.7	$\pm$ 0.4	29.1	$\pm$ 0.7	29.1	$\pm$ 1.5	a		
Oa	13.8	$\pm$ 7.5	13.0	$\pm$ 2.7	24.5	$\pm$ 3.3	a		
Total	23.7	$\pm$ 2.3	23.3	$\pm$ 1.1	26.9	$\pm$ 1.8	a		

Within each horizon and moisture, treatments not sharing the same letter are significantly different ( $p \leq 0.05$ ), Tukey's Honestly Significant post-hoc test. Oi, Oe, Oa, and Total moisture: *df* = 2, 24 for TRT and TRT\*ELEV, 1, 24 for ELEV. N=30

Table 1. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and standard errors ( $\pm$  SE) of organic horizon mass from May-September 2005. *P* values and *df* (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT\*ELEV interactions.

Horizon	Wet		Treatment Ambient		Dry		TRT	P Value	
	Mean	SE	Mean	SE	Mean	SE		ELEV	TRT*ELEV
			<u>Upper</u>						
Oi	339	$\pm$ 20.1	286	$\pm$ 15.2	414	$\pm$ 36.3	0.003	0.761	0.539
Oe	461	$\pm$ 27.6	533	$\pm$ 28.5	593	$\pm$ 35.4	0.355	0.768	0.076
Oa	2190	$\pm$ 469	1367	$\pm$ 506	3475	$\pm$ 362	<b>0.004</b>	0.325	0.987
Total	2990	$\pm$ 446	2186	$\pm$ 529	4481	$\pm$ 341	<b>0.003</b>	0.336	0.964
			<u>Lower</u>						
Oi	369	$\pm$ 28.6	305	$\pm$ 18.1	385	$\pm$ 37.2	a		
Oe	528	$\pm$ 46.0	542	$\pm$ 32.9	492	$\pm$ 39.6	a		
Oa	1678	$\pm$ 904	1020	$\pm$ 248	2989	$\pm$ 552	a		
Total	2574	$\pm$ 942	1867	$\pm$ 224	3865	$\pm$ 603	a		

Within each horizon and mass, treatments not sharing the same letter are significantly different ( $p \leq 0.05$ ), Tukey's Honestly Significant post-hoc test. Oi, Oe, Oa, and Total mass: *df* = 2, 24 for TRT and TRT\*ELEV, 1, 24 for ELEV. N=30

Table 4. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and standard errors ( $\pm$  SE) of leaf litter tannic acid equivalents (TAE %) from May-September 2005. *P* values and *df* (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT\*ELEV interactions.

Tannic Acid Equivalents (%)	Wet		Treatment Ambient		Dry		P Value					
	Mean	$\pm$ SE	Mean	$\pm$ SE	Mean	$\pm$ SE	TRT	ELEV	TRT*ELEV			
Horizon			Upper									
Oi	11.0	$\pm$ 0.80	a	10.7	$\pm$ 0.65	a	13.0	$\pm$ 1.22	a	<b>0.052</b>	0.681	0.921
Oe	6.74	$\pm$ 0.34	a	7.43	$\pm$ 0.78	a	7.35	$\pm$ 0.39	a	0.928	<b>0.010</b>	0.413
Oa	15.6	$\pm$ 1.65	a	8.32	$\pm$ 2.36	a	14.5	$\pm$ 3.17	a	0.133	0.160	0.624
				Lower								
Oi	10.9	$\pm$ 0.90	a	11.2	$\pm$ 1.20	a	13.7	$\pm$ 1.38	a			
Oe	6.24	$\pm$ 0.85	a	5.30	$\pm$ 0.64	a	5.85	$\pm$ 0.44	a			
Oa	11.2	$\pm$ 3.66	a	8.25	$\pm$ 1.36	a	10.2	$\pm$ 1.36	a			

Within each horizon and nutrient, treatments not sharing the same letter are significantly different ( $p \leq 0.05$ ), Tukey's Honestly Significant post-hoc test. Oi and Oe horizon TAE%: *df* = 2, 24 for TRT and TRT\*ELEV, 1.24 for ELEV, N=30. Oa horizon TAE%: *df* = 2, 18 for TRT and TRT\*ELEV, 1.18 for ELEV, N=24.

Table 3. Treatment (wet, ambient, and dry) and elevation (upper and lower) means and standard errors ( $\pm$  SE) of leaf litter nitrogen (%N) and carbon to nitrogen ratios (C:N) from May-September 2005. *P* values and *df* (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT\*ELEV interactions.

Forest Floor Chemistry	Wet		Treatment Ambient		Dry		P Value					
	Mean	$\pm$ SE	Mean	$\pm$ SE	Mean	$\pm$ SE	TRT	ELEV	TRT*ELEV			
Horizon			Upper									
Oi	1.30	$\pm$ 0.07	a	1.29	$\pm$ 0.06	a	1.09	$\pm$ 0.09	a	<b>0.039</b>	0.582	0.982
C:N	37.6	$\pm$ 2.41	a	37.4	$\pm$ 2.22	a	46.5	$\pm$ 3.58	a	<b>0.040</b>	0.405	0.760
				Lower								
Oi	1.34	$\pm$ 0.1	a	1.31	$\pm$ 0.04	a	1.14	$\pm$ 0.11	a			
C:N	36.7	$\pm$ 2.38	a	36.7	$\pm$ 1.17	a	42.0	$\pm$ 4.11	a			
Oe	1.55	$\pm$ 0.06	a	1.32	$\pm$ 0.08	a	1.42	$\pm$ 0.06	a	0.190	0.355	0.758
C:N	31.3	$\pm$ 1.80	a	33.7	$\pm$ 2.50	a	33.3	$\pm$ 1.71	a	0.811	<b>0.051</b>	0.676
				Lower								
Oe	1.57	$\pm$ 0.15	a	1.47	$\pm$ 0.08	a	1.48	$\pm$ 0.04	a			
C:N	29.6	$\pm$ 2.06	a	28.3	$\pm$ 1.76	a	30.3	$\pm$ 2.38	a			
Oa	1.15	$\pm$ 0.07	a	1.17	$\pm$ 0.02	a	1.30	$\pm$ 0.08	a	0.299	0.183	0.868
C:N	29.4	$\pm$ 1.77	a	26.3	$\pm$ 1.40	a	24.7	$\pm$ 0.79	a	0.445	0.363	0.187
				Lower								
Oa	1.15	$\pm$ 0.07	a	1.01	$\pm$ 0.10	a	1.18	$\pm$ 0.10	a			
C:N	24.6	$\pm$ 1.98	a	36.5	$\pm$ 8.78	a	28.4	$\pm$ 2.42	a			

Within each horizon and nutrient, treatments not sharing the same letter are significantly different ( $p \leq 0.05$ ), Tukey's Honestly Significant post-hoc test. Oi %N and C:N: *df* = 2, 22 for TRT and TRT\*ELEV, 1.22 for ELEV, N=28. Oe %N and C:N: *df* = 2, 24 for TRT and TRT\*ELEV, 1.24 for ELEV, N=30. Oa %N and C:N: *df* = 2, 18 for TRT and TRT\*ELEV, 1.18 for ELEV, N=24.

Table 6. Beetle families collected in pitfall traps at the TDE in the wet, ambient, and dry treatments in 2005.

Family	Total Captures/Treatment			Total	%of Total
	Wet	Ambient	Dry		
Carabidae	482	393	185	1060	32.51
Curculionidae	385	149	182	716	21.96
Nitulidae	127	132	135	394	12.08
Staphylinidae	143	136	186	465	14.26
Scolytidae	73	106	100	279	8.56
Scarabidae	31	43	58	132	4.05
Chrysomelidae	16	39	9	64	1.96
Elateridae	12	9	19	40	1.23
Leptodiridae	4	17	5	26	0.80
Mordellidae	5	5	11	21	0.64
Anthicidae	6	3	4	13	0.40
Phalacridae	2	4	3	9	0.28
Scaphididae	3	3	2	8	0.25
Tenebrionidae	5	1	1	7	0.21
Leiodidae	1	4	0	5	0.15
Cryptophagidae	0	1	3	4	0.12
Histeridae	0	2	2	4	0.12
Passalidae	1	1	0	2	0.06
Derodontidae	1	0	1	2	0.06
Lampyridae	1	0	0	1	0.03
Salpingidae	0	1	0	1	0.03
Silphidae	1	0	0	1	0.03
Cantharidae	0	0	1	1	0.03
Clambidae	0	1	0	1	0.03
Eucenetidae	0	0	1	1	0.03
Rhysodidae	0	0	1	1	0.03
Cerambycidae	1	0	0	1	0.03
Coccinellidae	1	0	0	1	0.03
Orsodacnidae	0	0	1	1	0.03
Treatment Total	1301	1050	910	3261	100%

Table 5. Forest floor mean weekly minimum, maximum, and mean temperature (°C) and standard errors (± SE) for 2005. P values and df (Proc GLM) for treatment (TRT), elevation (ELEV), and TRT\*ELEV interactions.

Season	Elevation	Temperature (°C)	Treatment			P Value		
			Wet Mean ± SE	Ambient Mean ± SE	Dry Mean ± SE	TRT	ELEV	TRT*ELEV
Spring	Upper	Minimum	14.0 + 0.35 a	13.0 + 0.29 a	13.9 + 0.43 a	0.357	0.711	0.090
		Maximum	18.4 + 0.13 a	20.5 + 1.02 a	20.7 + 2.23 a	0.389	0.247	0.632
		Mean	16.3 + 0.18 a	16.6 + 0.41 a	16.8 + 0.47 a	0.184	0.303	0.624
Summer	Lower	Minimum	12.1 + 1.27 a	14.1 + 0.43 a	14.1 + 0.19 a			
		Maximum	18.5 + 0.47 a	19.1 + 0.33 a	18.8 + 0.25 a			
		Mean	15.6 + 0.56 a	16.6 + 0.41 a	16.4 + 0.18 a			
Summer	Upper	Minimum	21.0 + 0.20 a	20.8 + 0.14 a	21.1 + 0.19 a	0.873	0.403	0.553
		Maximum	23.8 + 0.25 a	24.6 + 0.55 a	24.8 + 1.45 a	0.672	0.473	0.766
		Mean	22.1 + 0.16 a	22.2 + 0.18 a	22.2 + 0.29 a	0.655	0.807	0.759
Fall	Lower	Minimum	21.0 + 0.27 a	21.3 + 0.43 a	21.1 + 0.13 a			
		Maximum	23.8 + 0.34 a	24.3 + 0.32 a	23.8 + 0.14 a			
		Mean	22.1 + 0.26 a	22.4 + 0.39 a	22.0 + 0.1 a			
Fall	Upper	Minimum	19.1 + 0.24 a	18.6 + 0.13 a	19.3 + 0.37 a	0.634	0.239	0.402
		Maximum	23.1 + 0.13 a	25.6 + 0.83 a	24.4 + 1.11 a	0.066	0.898	0.696
		Mean	21.2 + 0.10 a	21.7 + 0.20 a	21.6 + 0.31 a	0.189	0.915	0.824
Fall	Lower	Minimum	19.3 + 0.20 a	19.4 + 0.43 a	19.3 + 0.25 a			
		Maximum	23.4 + 0.40 a	24.8 + 0.60 a	24.8 + 1.01 a			
		Mean	21.3 + 0.30 a	21.9 + 0.38 a	21.5 + 0.23 a			

Spring collection = 10-16 May, Summer Collection = 16-22 July, and Fall Collection = 21-27 September, 2005  
Treatments not sharing the same letter are significantly different ( $p \leq 0.05$ ), Tukey's Honestly Significant post-hoc test. Spring collection:  $df = 2, 22$  for TRT and TRT\* ELEV, 1,22 for ELEV, N=28. Summer and fall collection:  $df = 2, 20$  for TRT and TRT\* ELEV, 1,20 for ELEV, N=26.

Significantly more beetles were collected during the summer than in spring or fall (Table 7, Figure 2). Treatment effects on beetle abundance were significant only during the summer, which was higher in wet and ambient than dry plots ( $F_{2, 23} = 6.50, P < 0.006$ ) (Figure 2). Only elevation had a significant effect on beetle abundance across collection dates (Table 7). Elevation effects were significant in spring ( $F_{1, 23} = 4.33, P < 0.049$ ) and summer ( $F_{1, 23} = 25.41, P < 0.0001$ ), with higher beetle numbers in upper than lower elevation sites (Figure 2).

Beetle family richness differed significantly among sampling dates, with richness highest in the summer collection (Table 7, Figure 3). There was a significant Date x ELEV interaction, with richness more similar between spring and fall in lower compared to the upper elevation (Figure 3). Elevation effects were only significant during the summer ( $F_{1, 23} = 4.92, P < 0.037$ ), with higher richness in upper than lower sites (Figure 3).

Shannon-Wiener Index ( $H'$ ) differed significantly among sampling dates, with spring and summer having higher  $H'$  than fall (Table 7, Figure 4). There was a significant treatment and Date x TRT interaction, when  $H'$  was generally higher in the dry plots in the summer compared to the spring or fall (Table 7). Within dates treatment had a significant effect on  $H'$  during the summer, with  $H'$  higher in the dry treatment than either the wet or ambient ( $F_{2, 23} = 7.54, P < 0.003$ ) and in the fall when diversity was greater in the ambient treatment than the wet ( $F_{2, 23} = 3.78, P < 0.038$ ) (Figure 4).

Depending on the treatment, E was greater in the spring than either the summer or fall (Table 7, Figure 5). Treatment was significant only during the summer sampling period, when E was highest in the dry treatment than the ambient or wet ( $F_{2, 23} = 12.49, P < 0.002$ )

(Figure 5). Elevation effects were also only significant during the summer season, when E was highest at the lower sites ( $F_{1, 23} = 5.79, P < 0.025$ ) (Figure 5).

#### *Cumulative Carabidae Tribe Community Parameter*

A total of 1060 ground beetles (Family Carabidae) were collected in the experiment representing 33% of the total abundance of beetles. Carabids were 160% more abundant in the wet compared to the dry treatment (Table 6). All carabids were members of nine tribes (Table 8). Each tribe was represented in all treatments, although not at each elevation (Table 8).

Tribes Harpalini and Pterostichini constituted 72% of all carabids collected. When averaged across elevation, beetles in Tribes Harpalini and Pterostichini were 600% and 100% more abundant (respectively) than in the dry treatment, but were generally comparable between wet and ambient treatments (Table 8). These tribes also differed substantially between elevation. For Harpalini, there were 700% more beetles collected in the wet treatment compared to the dry at the upper elevation and 420% at the lower (Table 8). Differences between wet and dry treatments were also seen for Tribe Pterostichini with 110% and 27% more in wet than dry treatments at the upper and lower elevation respectively.

Sørensen similarity indices showed that carabid tribe communities in the dry treatment were 56% similar to those found in the wet, while only 64% similar to those in the ambient. Wet and ambient treatment carabid communities were 90% similar.

Ground beetle abundance was significantly affected by season (Table 9), with abundance higher during the summer collection than any other date. Within dates treatment significantly affected abundance in summer ( $F_{2, 14} = 8.87, P < 0.003$ ), when ambient and wet

treatments had higher abundance than the dry (Figure 6). Elevation significantly affected abundance during the summer collection, with greater abundance in the upper than lower sites ( $F_{1, 14} = 10.34, P < 0.006$ ) (Figure 6). Differences in abundance at the upper and lower sites between seasons resulted in a significant Date x ELEV interaction (Table 9).

Ground beetle tribe richness differed significantly among sampling dates in the order summer > spring > fall (Table 9, Figure 7). Neither treatment nor elevation had an effect on richness across sampling dates, nor was there any difference within seasons (Table 9). Rarefaction analysis, which accounts for abundance effects, found tribe richness using combined collections showed no differences due to treatment ( $F_{2, 14} = 0.02, P = 0.981$ ) or elevation ( $F_{1, 14} = 1.86, P = 0.185$ ).

Tribe Shannon-Wiener Index ( $H'$ ) differed significantly by season, being highest in the spring and summer collections (Table 9, Figure 8). Neither treatment nor elevation effects were significant across collection periods (Table 9). The effect of treatment was only significant in the fall season where  $H'$  was lower in the dry treatment than the wet or ambient ( $F_{2, 13} = 5.65, P < 0.017$ , Figure 8).

There was no effect of sampling date on carabid tribe evenness (Table 9, Figure 9). Within seasons, treatment effects were significant in the summer ( $F_{2, 6} = 6.61, P < 0.037$ ), when evenness was higher in the dry and ambient treatments than the wet (Figure 9). The fall sampling period had higher evenness in the wet treatment than the ambient or dry ( $F_{2, 6} = 5.37, P < 0.046$ ) (Figure 9). Differences in evenness caused by treatment effects between seasons represent a significant Date x TRT interaction (Table 9).

W. L. EURY APPALACHIAN COLLECTION  
BELK LIBRARY  
APPALACHIAN STATE UNIVERSITY  
BOONE, NC 28608

### *Carabidae Tribe Community Parameters (Summer)*

When only the summer sample was considered, treatment and elevation had significant effects on ground beetle abundance (Table 10, Figure 6). Abundance was approximately 200% greater in both the wet and ambient treatments compared to the dry in this season. Carabid abundance was significantly higher in the upper sites than the lower sites (Table 10, Figure 6). There were significant effects of treatment and elevation on tribe richness in the summer (Table 10, Figure 7). Wet and ambient treatment sites contained greater tribe richness than the dry treatment and the upper elevation sites had greater tribe richness than the lower elevation sites (Table 10, Figure 7). Rarefaction analysis of summer carabid tribe richness detected no significant effect of treatment ( $F_{2, 24} = 0.29, P = 0.754$ ) or elevation ( $F_{1, 24} = 2.56, P = 0.123$ ). Therefore, observed effects of treatment and elevation can be attributed to individuals. Carabid tribe  $H'$  was solely affected by elevation (Table 10, Figure 8). Consistent with abundance and richness,  $H'$  was significantly greater at upper elevation sites than lower elevations. Differences in tribe evenness were due to treatment (Table 10, Figure 9), where the dry treatment had greater tribe evenness than the wet at both elevations.

Table 7. Significance values ( $P$ ) and  $df$  for main effects of TRT, ELEV, and their interactions on beetle family community parameters using repeated measures ANOVA (Proc GLM).

	Abundance	Richness	Shannon-Wiener (H')	Evenness
<b>Between-Subjects</b>				
TRT	0.263	0.404	<b>0.027</b>	0.516
ELEV	<b>0.009</b>	0.610	0.525	0.469
TRT*ELEV	0.459	0.424	0.458	0.603
<b>Within-Subjects</b>				
Date	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.007</b>
Date*TRT	0.154	0.646	<b>0.007</b>	<b>0.013</b>
Date*ELEV	0.269	<b>0.050</b>	0.796	0.422
Date*TRT*ELEV	0.166	<b>0.052</b>	<b>0.043</b>	0.574

Between-subjects abundance, richness, diversity, and evenness:  $df = 2, 23$  for treatment and treatment \* elevation, and  $df = 1, 23$  for elevation. Within-subjects abundance, richness, diversity, and evenness:  $df = 2, 46$  for date and date \* elevation, and  $df = 4, 46$  for date \* treatment and date \* treatment \* elevation.  $N = 29$ , Differences significant at ( $P \leq 0.05$ ).

Table 8. Cumulative abundance of carabidae tribes in wet, ambient, and dry treatments at upper and lower sites at the TDE in 2005.

Carabidae Tribe	Upper			Lower		
	Wet	Ambient	Dry	Wet	Ambient	Dry
Harpalini	174	86	22	52	65	10
Callistini	10	20	2	24	13	6
Cydrini	8	15	9	8	2	6
Scaritini	7	1	0	4	1	3
Pterostichini	81	71	38	61	63	48
Licinini	24	17	10	8	1	1
Galeritini	5	14	12	9	7	4
Notiophilini	2	3	4	9	3	1
Cicindelid	2	8	8	4	4	0
Total	313	235	105	179	159	79

Table 9. Significance values ( $P$ ) and  $df$  for main effects of TRT, ELEV, and their interactions on family Carabidae tribe community parameters using repeated measures ANOVA (Proc GLM).

	Abundance	Richness	Shannon-Wiener (H')	Evenness
<b>Between-Subjects</b>				
TRT	0.067	0.521	0.355	0.251
ELEV	0.323	0.539	0.943	0.509
TRT*ELEV	0.533	0.226	0.156	0.062
<b>Within-Subjects</b>				
Date	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.673
Date*TRT	0.195	0.779	0.205	<b>0.015</b>
Date*ELEV	0.055	0.072	0.469	0.126
Date*TRT*ELEV	0.349	0.320	0.188	0.246

Between-subjects:

- Abundance and richness:  $df = 2, 14$  for TRT and TRT \* ELEV, and  $df = 1, 14$  for ELEV.
- Diversity:  $df = 2, 13$  for TRT and TRT \* ELEV, and  $df = 1, 13$  for ELEV.
- Evenness:  $df = 2, 6$  for TRT, and  $df = 1, 6$  for ELEV and TRT \* ELEV.

Within-subjects:

- Abundance and richness:  $df = 2, 28$  for Date and Date \* ELEV, and  $df = 4, 28$  for Date \* TRT and Date \* TRT \* ELEV.
- Diversity:  $df = 2, 26$  for Date and Date \* ELEV, and  $df = 4, 26$  for Date \* TRT and Date \* TRT \* ELEV.
- Evenness:  $df = 2, 12$  for Date, Date \* ELEV, Date \* TRT \* ELEV, and  $df = 4, 12$  for Date \* TRT.
- Abundance and Richness  $N = 20$ ,  $H' N = 19$ , and Evenness  $N = 11$ , Differences significant ( $P \leq 0.05$ ).

Table 10. Significance values ( $P$ ) and  $df$  for the effects of TRT, ELEV, and their interactions on summer carabidae community parameters using ANOVA (Proc GLM).

	Abundance	Richness	Shannon-Wiener (H')	Evenness
<b>Between-Subjects</b>				
TRT	<b>0.002</b>	<b>0.049</b>	0.411	<b>0.028</b>
ELEV	<b>0.002</b>	<b>0.014</b>	<b>0.034</b>	0.663
TRT*ELEV	0.976	0.193	0.127	0.544

Abundance, richness, diversity, and evenness:  $df = 2, 24$  for treatment and treatment \* elevation,  $df = 1, 24$  for elevation.  $N = 30$ , Differences significant at ( $P < 0.05$ )

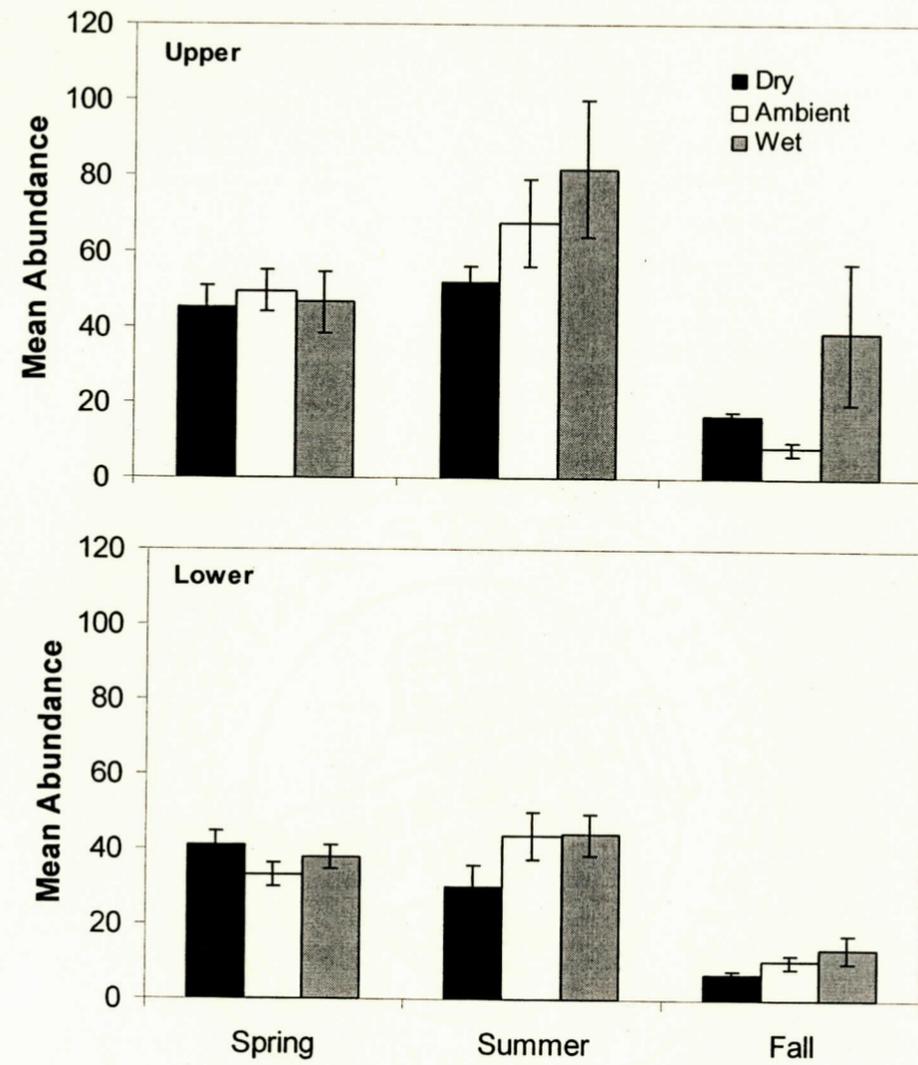


Figure 2. Beetle abundance (all beetle families)  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

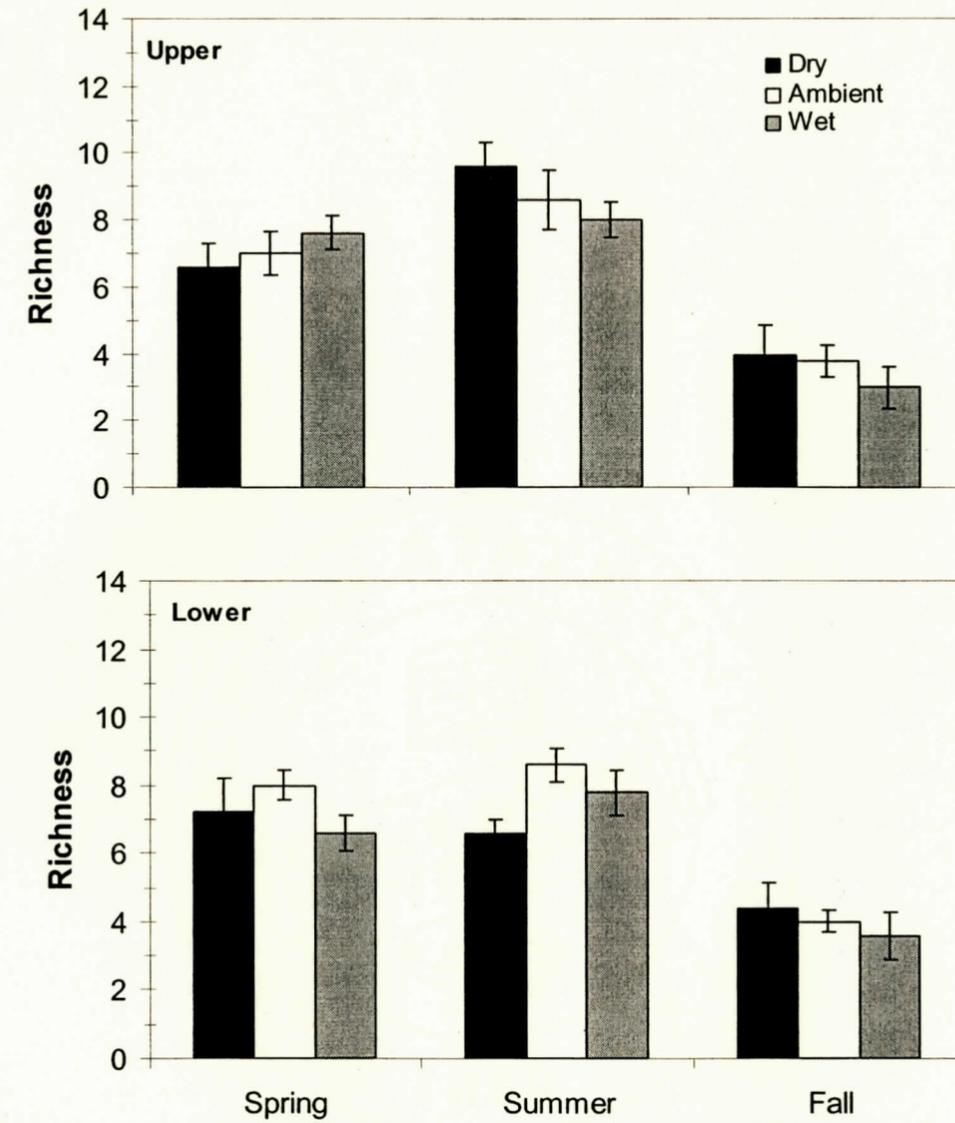


Figure 3. Beetle family richness  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

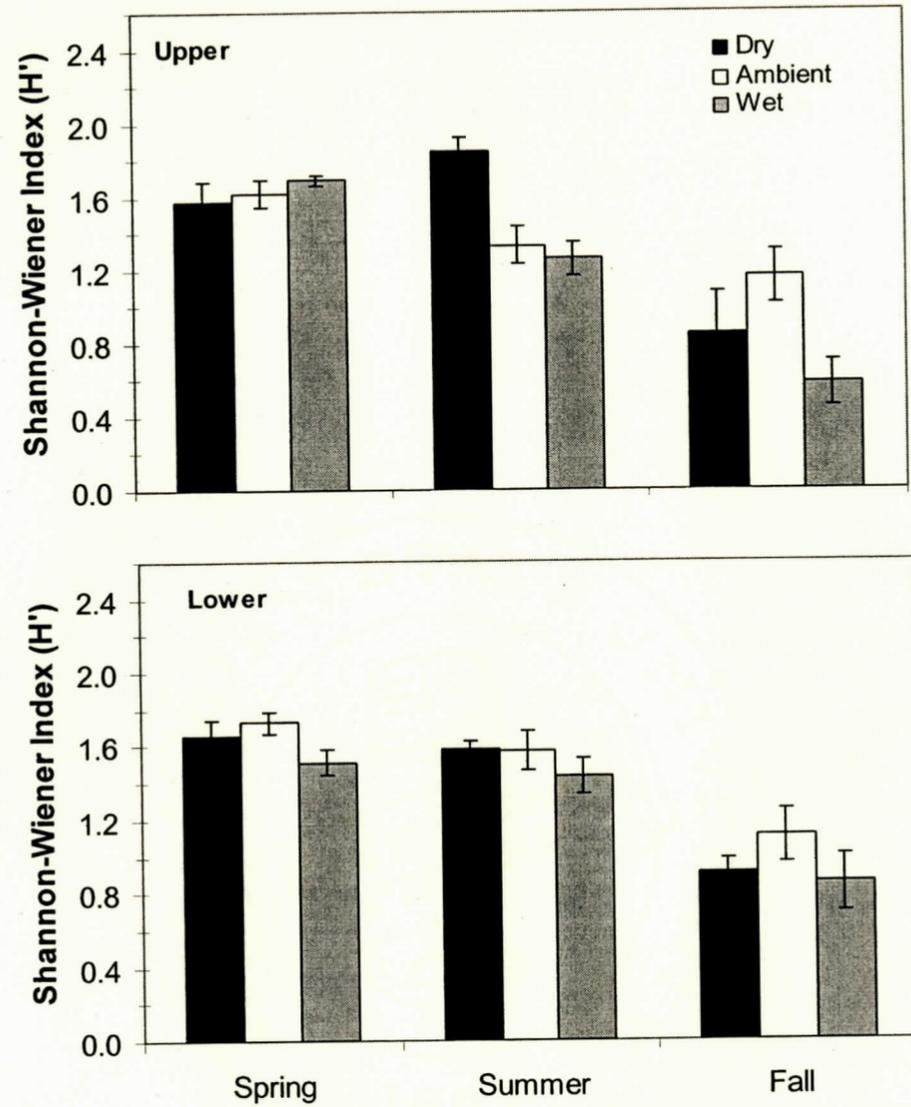


Figure 4. Beetle family Shannon-Wiener Index (H')  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

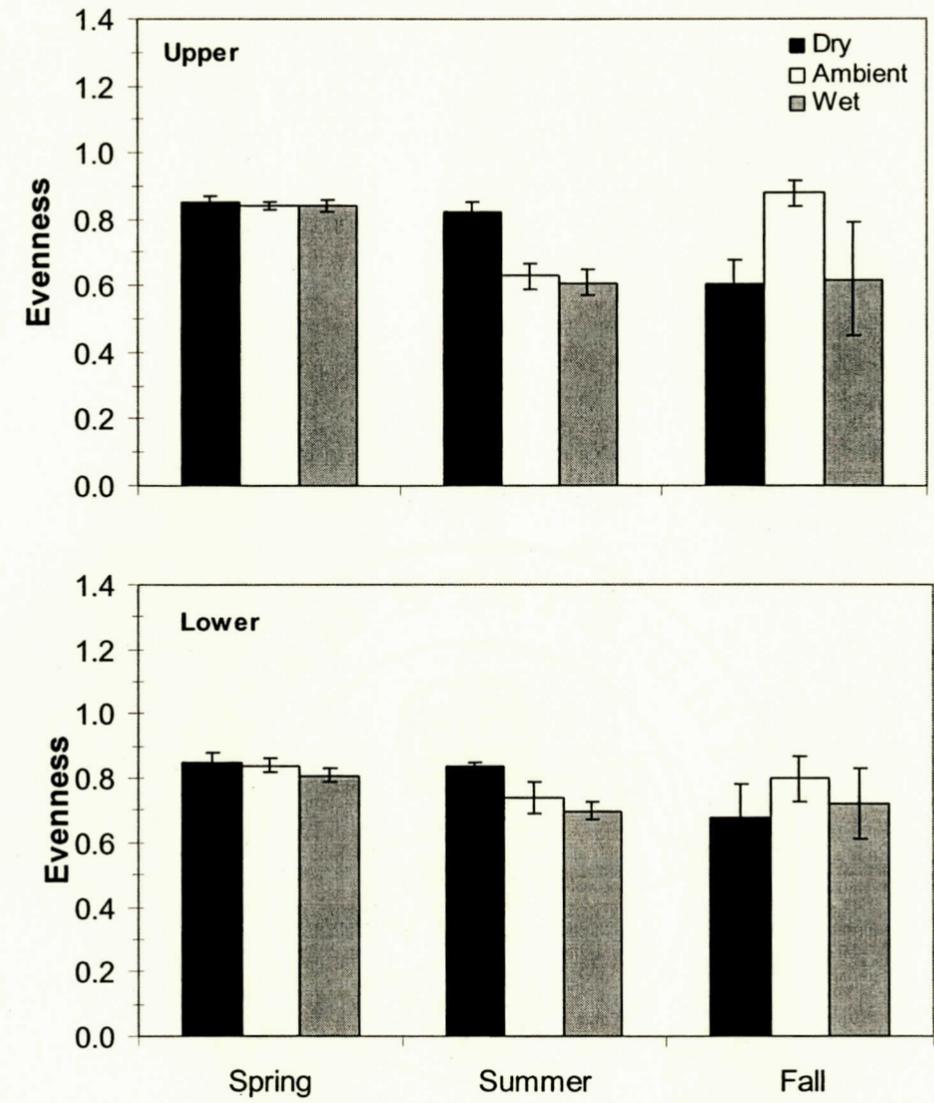


Figure 5. Beetle family evenness  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

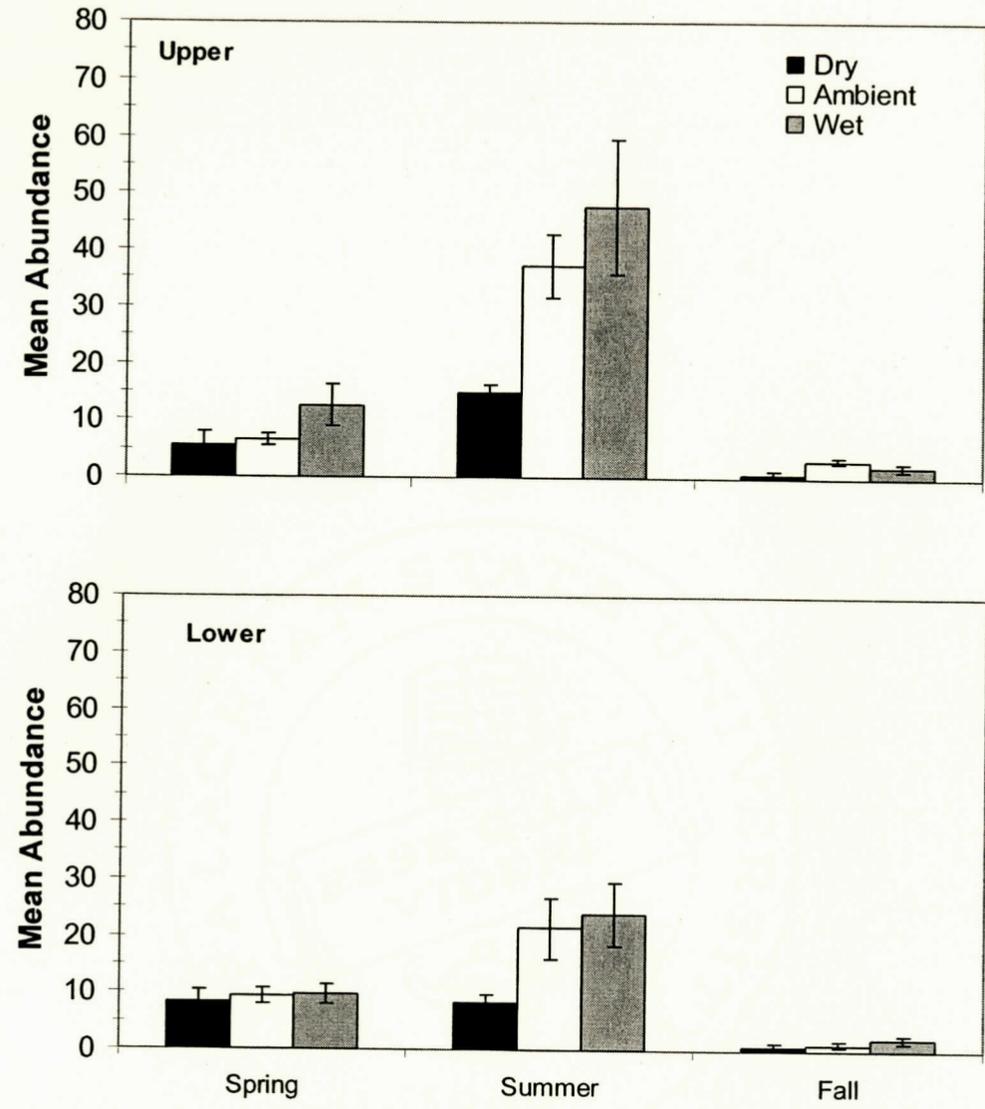


Figure 6. Carabid abundance  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

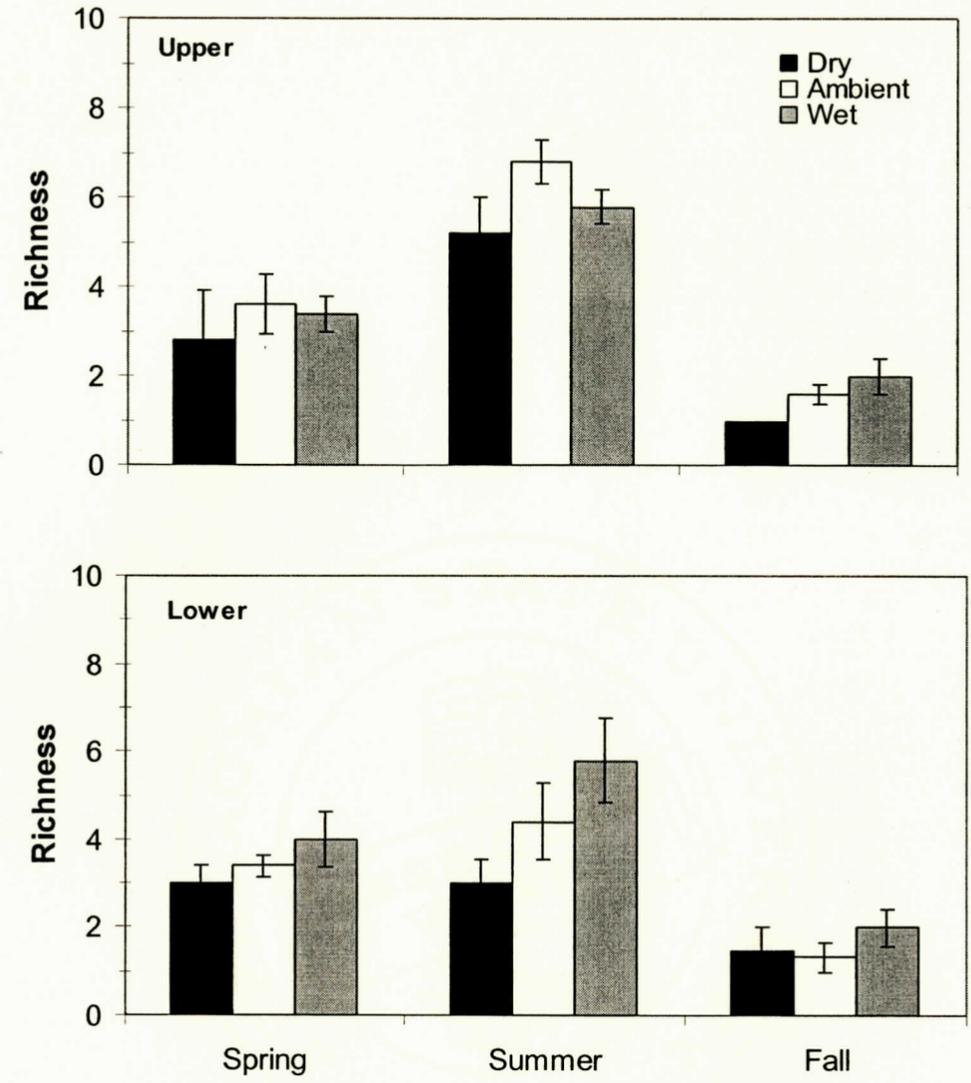


Figure 7. Carabidae tribe richness  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

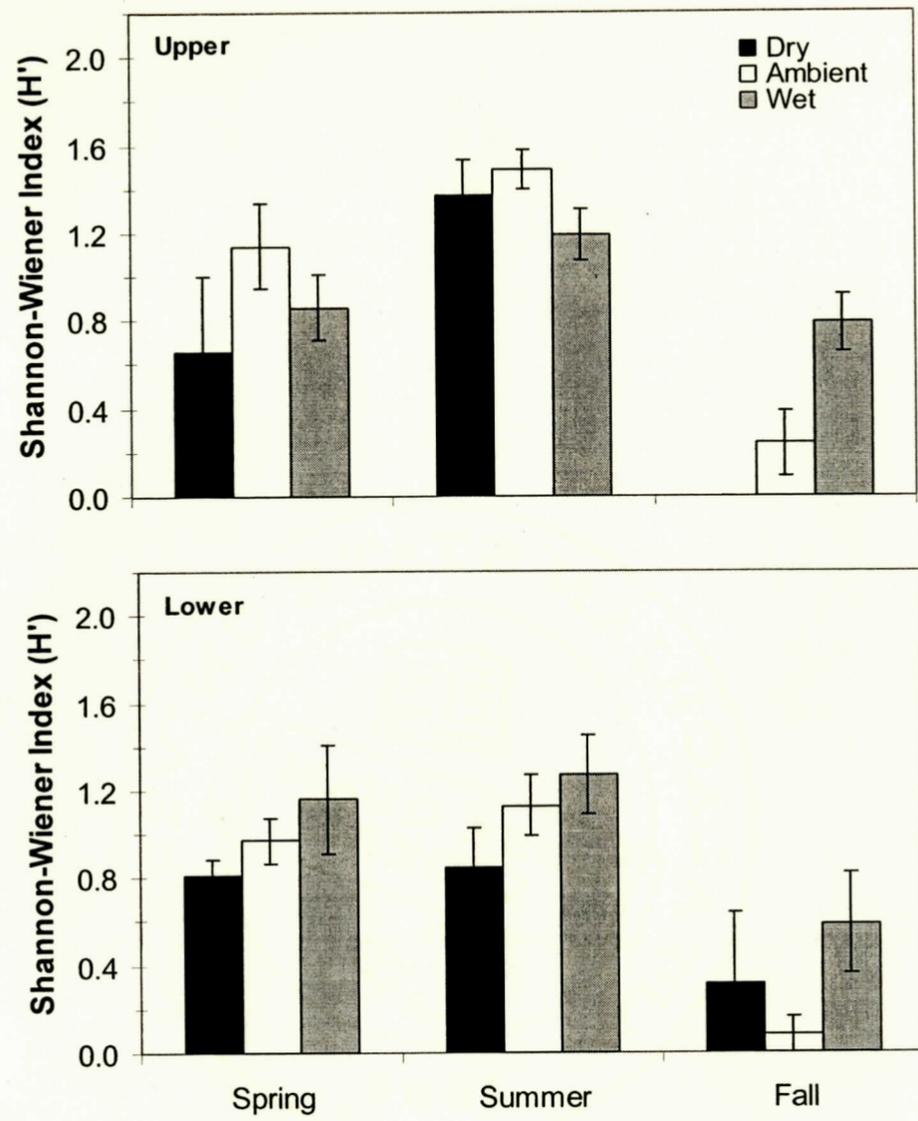


Figure 8. Carabidae tribe Shannon-Wiener Index (H') at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

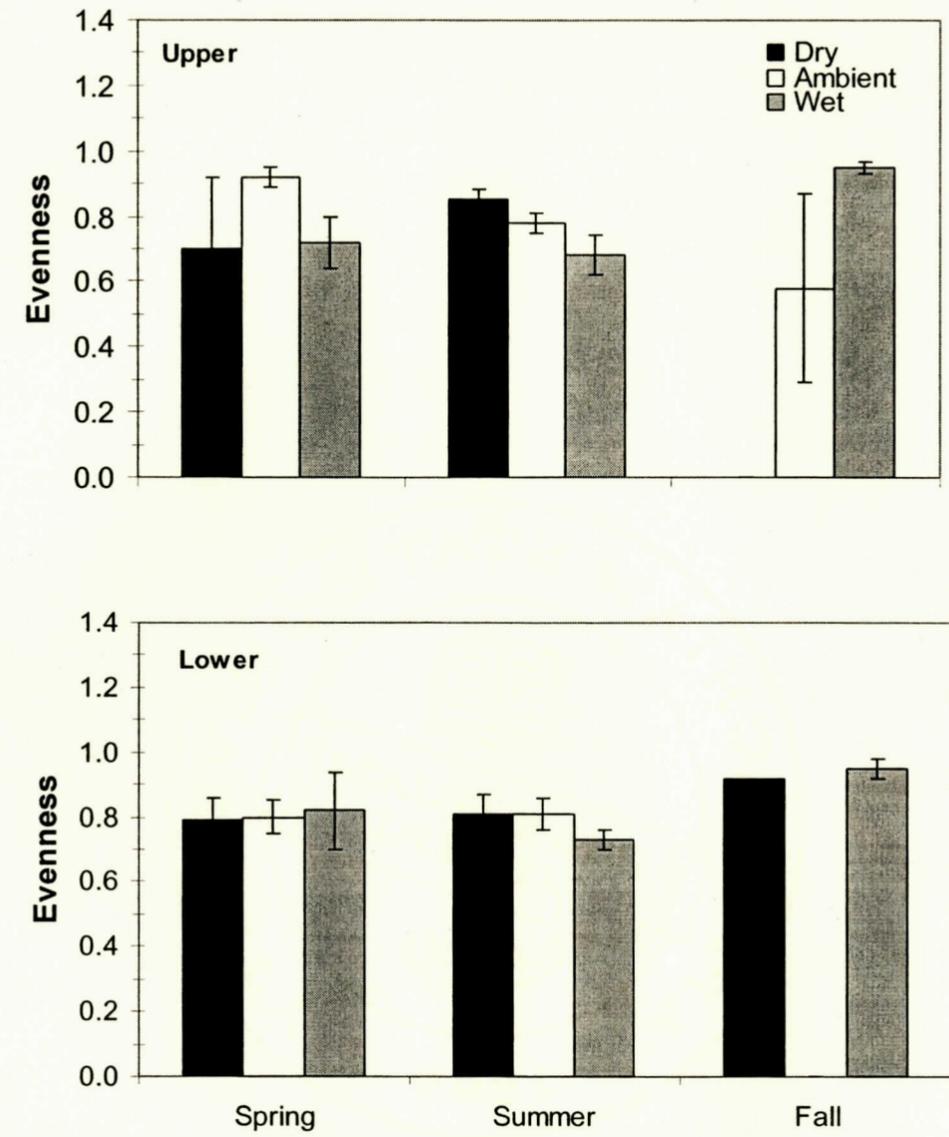


Figure 9. Carabidae tribe evenness  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

### Prey Availability

Mite abundance was affected by season; highest in the spring and fall collection and lowest during the summer (Table 11, Figure 10). Also, treatment effects were significant for mite abundance across all collection dates (Table 11, Figure 10). Mites were more abundant in the dry than ambient treatment in spring ( $F_{2, 21} = 5.05, P < 0.016$ ), whereas they were more abundant in the dry and ambient treatments than the wet in the fall ( $F_{2, 21} = 7.70, P < 0.003$ , Table 11, Figure 10). The only effect of elevation on mite abundance was in the fall when abundance was higher at upper than lower elevation sites ( $F_{1, 21} = 5.91, P < 0.024$ ). Both treatment and elevation interacted with season (Table 11), especially with differences between the dry and wet treatment in spring versus fall at the upper elevation (Figure 10).

Prey abundance, calculated from remaining pitfall trap contents less beetles, was affected by season when abundance was highest in the summer ( $F_{2, 46} = 63.53, P < 0.0001$ ). Elevation was the only factor that had significant effects on prey abundance across collection periods ( $F_{1, 23} = 5.34, P < 0.030$ ). Within seasons, prey abundance was greatest at upper than lower sites ( $F_{1, 23} = 8.71, P < 0.007$ ) during the summer collection.

### Stepwise Multiple Linear Regression Analysis

The multiple regression analysis for the cumulative data set (spring, summer, and fall) showed season and treatment were the best fit predictors for mean carabidae abundance (Table 12). Using dummy coding, the analysis demonstrated less abundance in the spring ( $P < 0.0001, R^2 = 0.44$ ) and fall ( $P < 0.0001, R^2 = 0.17$ ) compared to summer and in the dry treatment compared to ambient ( $P < 0.0001, R^2 = 0.09$ ). For the summer only, five habitat variables were useful predictors of summer ground beetle abundance (Table 12). Litter mass

( $P < 0.027, R^2 = 0.22$ ) and soil water content ( $P = 0.074, R^2 = 0.11$ ) contributed to more than 33% of the total model variation (Table 12).

Carabidae tribe richness was best explained by season, treatment, and weekly temperature maxima in multiple regression analysis of the combined data set (Table 12). The analysis indicated that there was less richness in the fall compared to the summer ( $P < 0.0001, R^2 = 0.31$ ) and in the dry treatment compared to the ambient ( $P < 0.0001, R^2 = 0.09$ ). Weekly temperature maximum was also a good predictor of richness in the combined data set ( $P < 0.0001, R^2 = 0.24$ ) (Table 12). For the summer, five variables were selected by the model as significant predictors of carabidae tribe richness. Three variables Oe horizon C: N ( $P < 0.009, R^2 = 0.29$ ), soil water content ( $P < 0.022, R^2 = 0.17$ ), and mean weekly temperature maximum ( $P < 0.010, R^2 = 0.17$ ) explained 63% of the total model variation (Table 12).

Season and treatment accounted for 43% of the total variation of carabidae tribe diversity in multiple regression analysis of the combined data set (Table 12). Shannon-Wiener Index ( $H'$ ) declined in the fall compared to the summer ( $P < 0.0001, R^2 = 0.35$ ) and in the dry treatment compared to the ambient ( $P < 0.002, R^2 = 0.08$ ) (Table 12). Carabid tribe  $H'$  from the summer collection was moderately explained by four variables, with Oe horizon C: N ( $P < 0.018, R^2 = 0.25$ ) and mean weekly temperature maximum ( $P = 0.071, R^2 = 0.12$ ) explaining 37% of model variation (Table 12).

Carabid tribe evenness was significantly explained by season in the combined analysis, though the relationship was weak (Table 12). Soil water content was the only variable selected in the summer analysis ( $P = 0.108, R^2 = 0.12$ ) (Table 12).

Table 12. Multiple regression analysis of habitat variables and carabidae tribe abundance, richness, diversity ( $H'$ ), and evenness for cumulative (all seasons) and summer, 2005.

	Model $R^2$	P
<b>Carabidae Abundance</b>		
Cumulative Carabidae Abundance = 1.013 - (0.779 X Treatment 2) - (0.736 X Season 1) - (2.309 X Season 2) + (0.061 X Temperature Maximum) + (0.024 X Oe Horizon C:N)	0.73	<0.001
Summer Carabidae Abundance = 114.674 + (2.728 X Temperature Maximum) - (9.741 X Temperature Minimum) - (0.005 X Litter Mass) + (1.214 X Oe Horizon C:N) + (2.295 X Soil Water Content)	0.61	0.007
<b>Carabidae Tribe Richness</b>		
Cumulative Carabidae Richness 2005 = -6.101 + (0.535 X Treatment 1) - (1.222 X Treatment 2) - (3.934 X Season 2) + (0.384 X Temperature Maximum) + (0.074 X Oe Horizon C:N)	0.68	<0.001
Summer Carabidae Richness = -27.218 + (0.665 X Temperature Maximum) + (0.106 X Oi Horizon C:N) + (0.204 X Oe Horizon C:N) + (0.554 X Soil Water Content) - (0.067 X Mites)	0.75	0.002
<b>Carabidae Tribe Diversity (<math>H'</math>)</b>		
Cumulative Carabidae $H'$ = -0.184 - (0.318 X Treatment 2) - (0.937 X Season 2) + (0.064 X Temperature Maximum)	0.53	<0.001
Summer Carabidae $H'$ = -4.601 + (0.137 X Temperature Maximum) + (0.020 X Oi Horizon C:N) + (0.035 X Oe Horizon C:N) + (0.068 X Soil Water Content)	0.54	0.008
<b>Carabidae Tribe Evenness</b>		
Cumulative Carabidae Evenness = -0.259 + (0.180 X Season 2)	0.07	0.046
Summer Carabidae Evenness = 0.948 - (0.016 X Soil Water Content)	0.12	0.108

Dummy coding scheme: Season 1 = Spring compared to the summer, Season 2 = Fall compared to summer, Treatment 1 = Wet compared to ambient, Treatment 2 = Dry compared to ambient, Positive relationships of elevation indicate an increase ascending lower to upper elevations, while negative relationships indicate a decline descending from upper to lower elevations.

Table 11. Significance values ( $P$ ) and  $df$  for main effects of TRT, ELEV, and their interactions on mite abundance using ANOVA (Proc GLM).

	Abundance
<b>Between-Subjects</b>	
TRT	0.029
ELEV	0.378
TRT*ELEV	0.254
<b>Within-Subjects</b>	
Date	<0.001
Date*TRT	0.018
Date*ELEV	0.012
Date*TRT*ELEV	0.248

Between-subjects abundance:  $df = 2, 21$  for treatment and treatment \* elevation,  $df = 1, 21$  for elevation. Within-subject abundance:  $df = 2, 42$  for date and date \* elevation,  $df = 4, 42$  for date \* treatment and date \* treatment \* elevation. N= 27, Differences significant at ( $P \leq 0.05$ )

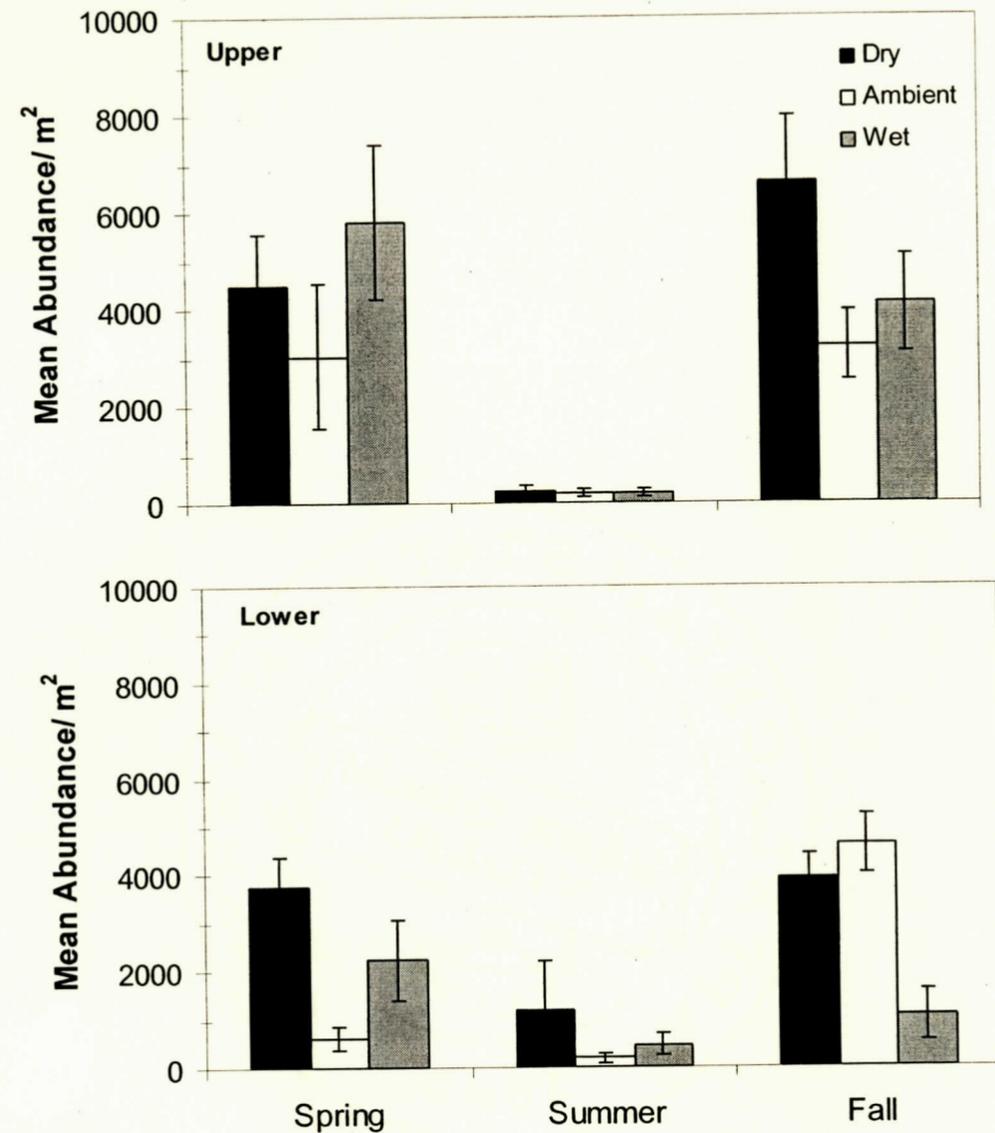


Figure 10. Mite abundance  $\pm$  SE at upper elevation (top) and lower elevation (bottom) sites for spring, summer, and fall 2005.

### Simple Linear Regression

Significant predictors selected in the summer multiple regression model were individually analyzed using simple linear regression. Mean carabidae abundance and tribe richness were positively related to soil water content ( $P < 0.012$ ,  $r^2 = 0.20$ ,  $P < 0.037$ ,  $r^2 = 0.15$ , respectively; Figures 11, 12), while tribe evenness was negatively related to soil water ( $P < 0.014$ ,  $r^2 = 0.20$ ; Figure 13). Reductions in carabidae abundance and tribe richness were associated with increasing litter mass ( $P < 0.010$ ,  $r^2 = 0.21$ ,  $P = 0.077$ ,  $r^2 = 0.11$ ; Figure 14, 15). Mean weekly temperature maximum was a positive predictor of both carabidae tribe richness ( $P < 0.050$ ,  $r^2 = 0.16$ ; Figure 16) and Shannon-Wiener Index ( $H'$ ) ( $P < 0.031$ ,  $r^2 = 0.17$ ; Figure 17) with each measure increasing with increased temperature. In order to account for all non-beetle potential prey items in the traps, pitfall trap content was analyzed with simple linear regression. Pitfall trap contents had highly significant positive relationships with mean carabidae abundance ( $P < 0.001$ ,  $r^2 = 0.49$ ; Figure 18), carabidae tribe richness ( $P < 0.010$ ,  $r^2 = 0.32$ ; Figure 19), and  $H'$  ( $P < 0.004$ ,  $r^2 = 0.26$ ; Figure 20). Dry treatment carabidae community parameters, especially abundance, had a tendency to group with low pitfall trap contents.

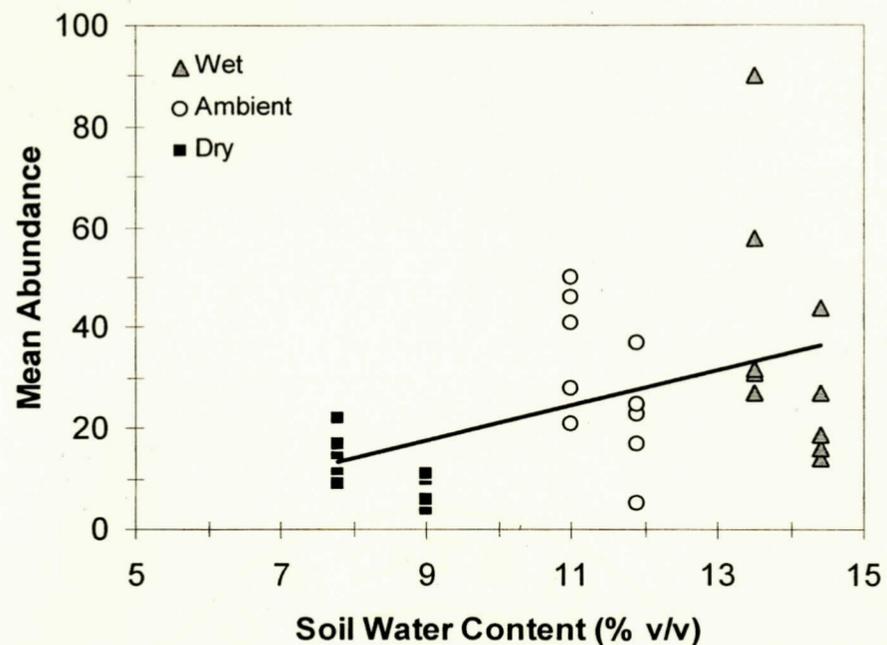


Figure 11. Relationship between soil water content and ground beetle abundance across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.20$ ,  $P < 0.012$ ).

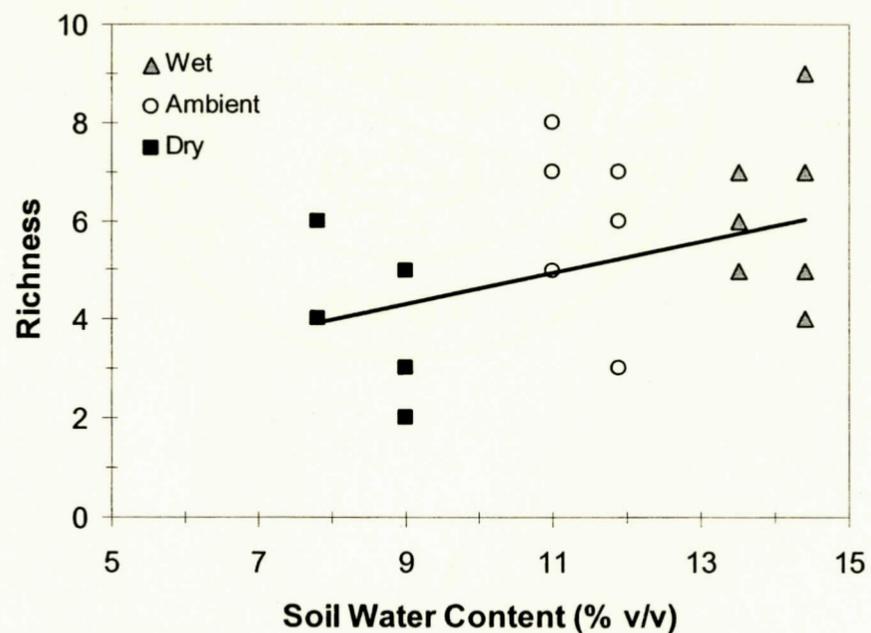


Figure 12. Relationship between soil water content and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.15$ ,  $P < 0.037$ ).

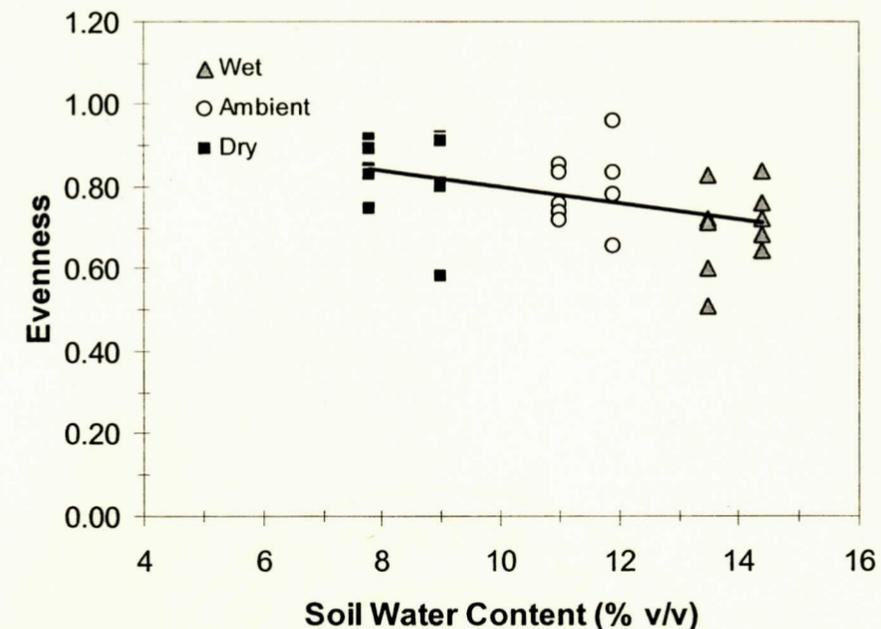


Figure 13. Relationship between soil water content and Carabidae tribe evenness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.20$ ,  $P < 0.014$ ).

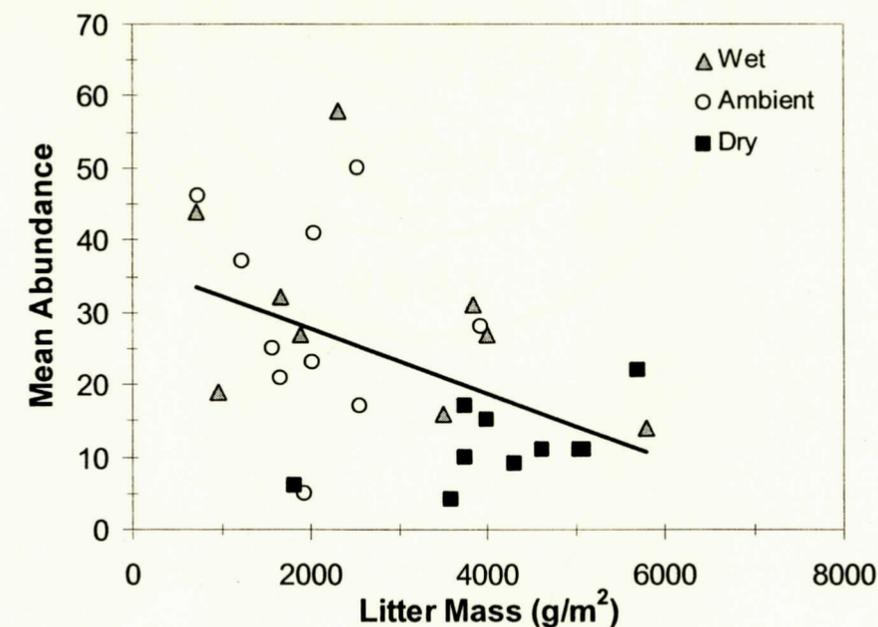


Figure 14. Relationship between litter mass and ground beetle abundance across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.21$ ,  $P < 0.010$ ).

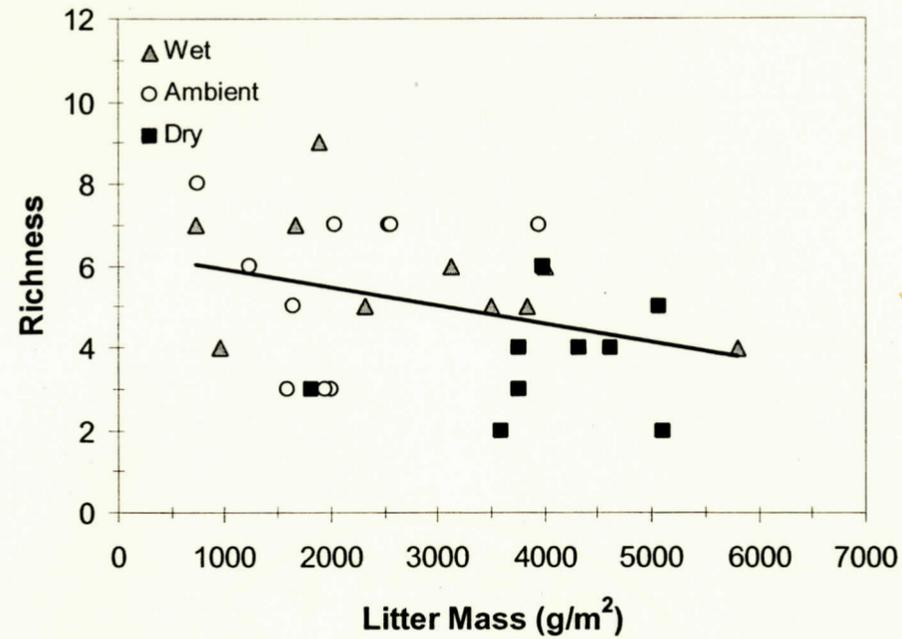


Figure 15. Relationship between litter mass and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.11$ ,  $p = 0.077$ ).

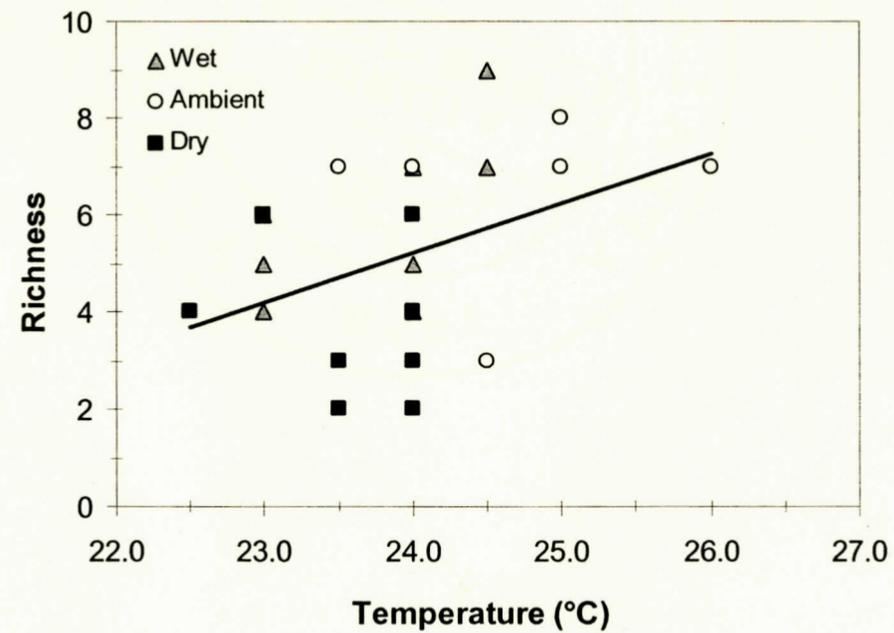


Figure 16. Relationship between mean weekly temperature maximum and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.16$ ,  $P < 0.0463$ ).

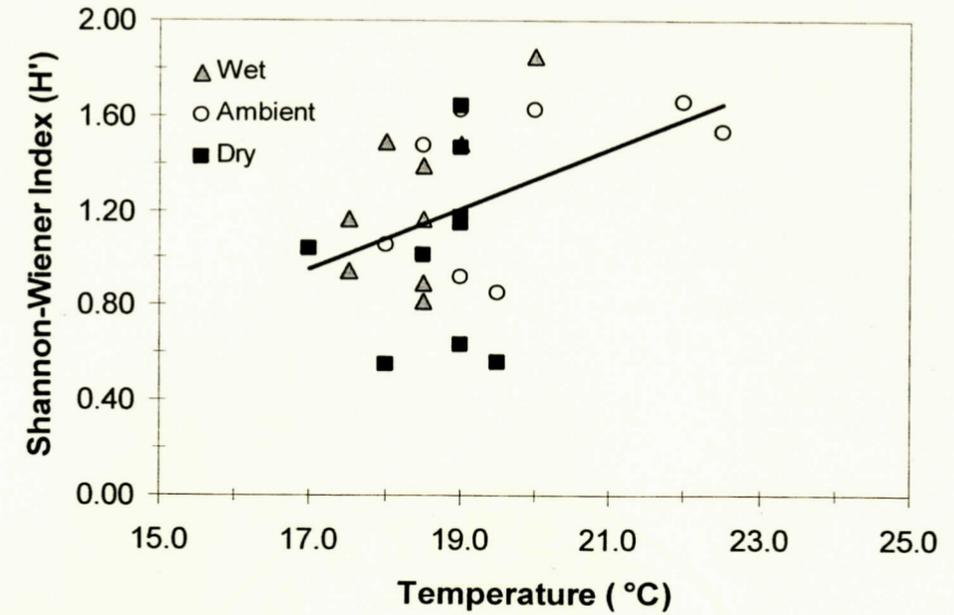


Figure 17. Relationship between weekly mean temperature maximum and Shannon-Wiener Index ( $H'$ ) for Carabidae tribes across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.17$ ,  $P < 0.030$ ).

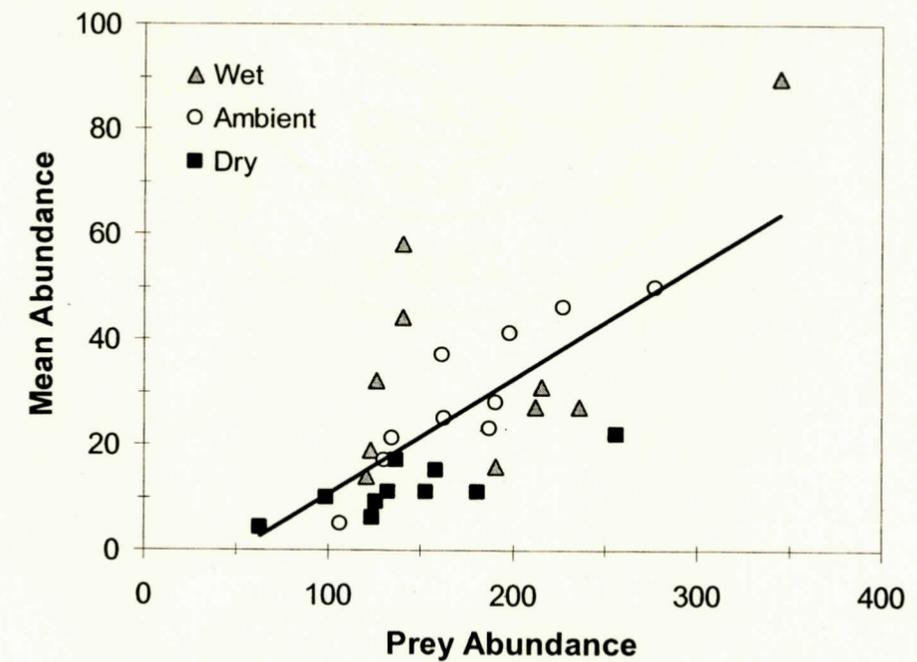


Figure 18. Relationship between prey abundance and ground beetle abundance across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.49$ ,  $P < 0.001$ ).

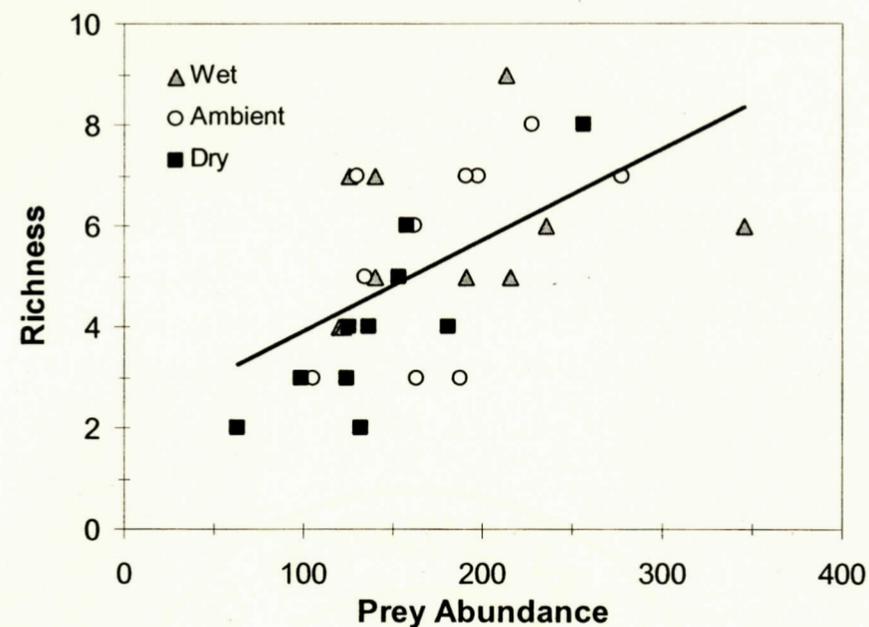


Figure 19. Relationship between prey abundance and Carabidae tribe richness across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.32$ ,  $P < 0.0001$ ).

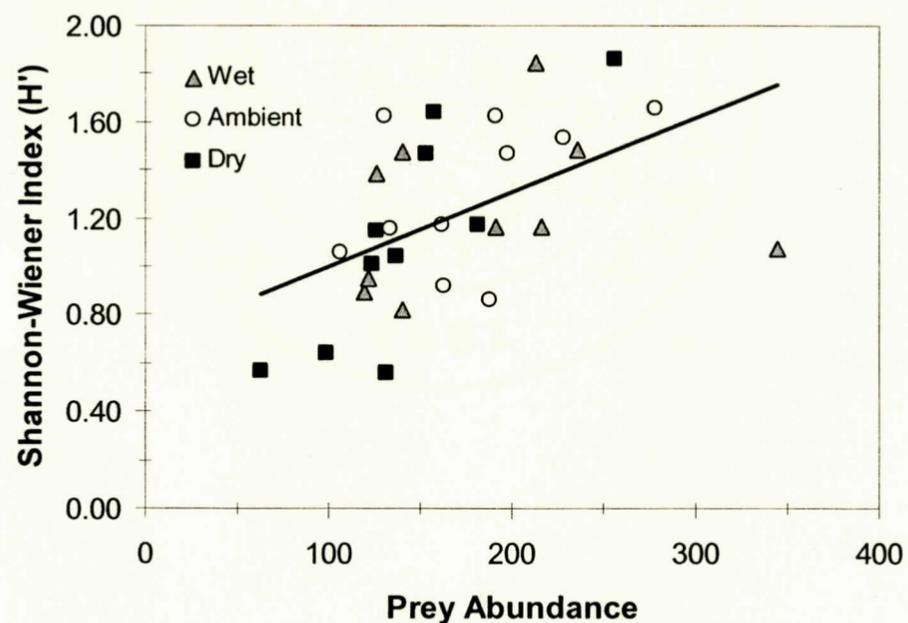


Figure 20. Relationship between prey abundance and Shannon-Wiener Index ( $H'$ ) for carabidae tribes across wet, ambient, and dry treatments in the summer collection ( $r^2 = 0.26$ ,  $P < 0.004$ ).

## DISCUSSION

My study was conducted at one of the first experimental sites of its kind, where a temperate forest ecosystem was subjected to long-term precipitation additions and reductions. The advantages of the duration (13 years) and scale (1.92 ha) of this larger experiment allowed me to examine the impact of altered precipitation, seasonality and elevation on forest floor characteristics important to ground-dwelling fauna such as ground beetles, Family Carabidae. I found that beetle abundance and richness both declined in response to drought, depending on season and elevation. The abundance of carabid beetles was much higher in the wet compared to dry treatment, due to the combined effects of a decrease in dominant tribes (Harpalini and Pterostichini) in the dry treatment and a proliferation of these same tribes in the wet treatment. An abundance-based similarity index showed great similarity in carabid tribes between wet and ambient treatments, while dry plot similarity was much lower than in the other two treatments. Seasonality had a strong effect on carabid community parameters. During the summer collection abundance and tribe-level richness were higher in wet and ambient treatments than the dry treatment. A shift to more abundant tribes in the wet plots increased evenness relative to dry plots. Of the physical and chemical forest floor characteristics I examined, leaf litter mass was the best predictor of carabid abundance, with higher mass resulting in less beetles collected, corresponding to observed treatment effects; averaged across the collection period litter mass was 50% higher in the dry compared to wet plots. Soil water content positively predicted carabid abundance

and richness, with overall lower values for each of these measures in the dry treatment. Soil contained more water but lower abundance of ground beetles at the lower elevation in each treatment, suggesting landscape-level constraints on the effects of water, probably via effects on litter mass. I conclude from my experiment that precipitation manipulations can affect the temporal and spatial distribution of ground beetle communities in temperate forests. However, similar changes in forest floor characteristics (e.g., higher leaf litter in drought treatment and upper elevation sites) caused by treatment and elevation produced contradictory responses of ground beetle communities, which suggest idiosyncratic relationships occur between ground beetles and their habitat depending upon precipitation and landscape position.

A primary goal of my experiment was to determine if beetle communities responded to precipitation alteration, especially drought. For climate change studies this is very relevant because moisture is known to exert strong influence over beetle community demographics as certain beetles have specific moisture requirements (Rykken et al., 1997; Kiovula, 2002; Maudsley et al., 2002). In my study drought reduced the abundance and tribe-level richness (summer season), which is somewhat consistent with others who found reductions in beetle abundance and specific carabid taxa due to dry conditions (Kiovula, 1999; Yi and Moldenke, 2005). I examined tribes to tease out potential treatment effects on ground beetles with specific habitat preferences. I found that Carabidae tribe Harpalini was much less abundant in the drought treatment (Table 8). The greater abundance of Harpalini in wet compared to dry treatment is supported by studies that found this tribe to be constrained by moisture deficits (Noonan, 1990). At the TDE available moisture in the litter was not, however, a good indicator of Harpalini abundance, since this measure was not

affected by precipitation treatments (Table 2). It appears that indirect effects and feedbacks of higher soil water content consistently demonstrated in the wet treatment over the numerous years of this study (Hanson et al., 2003a) are contributing to a preferential shift in this tribe towards a wet environment. A greater similarity between the beetle community in wet and ambient versus the dry treatment (Sørensen Index) clearly reflects community-level effects due to drought, suggesting future changes in forest floor faunal communities as precipitation patterns shift due to climate change.

Because seasonality is known to contribute to the temporal and spatial variability of ground dwelling arthropods (Rieske and Buss, 2001), I assessed whether treatment responses by beetles differed depending on the collection date. I found seasonality to have a strong effect on beetle abundance, which was greatest in the summer in agreement with other studies examining temperate forest (Wolda, 1988; Rieske and Buss, 2001). Lower carabid abundance and richness primarily in the summer due to drought demonstrates a need to consider temporal variation in communities across a growing season. In addition to abundance and richness, higher evenness in the drought treatment compared to the wet (Figures 5, 9) suggests a shift away from more dominant tribes found in the wet treatment. For beetle communities, climate change effects are best detected during times of maximum abundance, which for temperate regions occur during mid-summer.

In addition to seasonality I addressed the effect of landscape position at the TDE with respect to treatment and season of the year. Elevation is recognized as a frequently occurring ecological pattern affecting community demographics of biota (Janzen et al., 1976; Gentry, 1988; Olson, 1994; Sanders, 2002). In my study, elevation refers to landscape position in terms of upper and lower slopes rather than to more widely varying elevation gradients over

which temperature and precipitation vary markedly. The summer collection provided the best resolution for examining elevation effects and their relationship to treatment. Beetle family abundance and richness were highest at the upper elevation, while evenness was higher at lower sites (Figures 2-3, 5). Reductions of dominant family abundance may have led to higher evenness in the downslope sites. For ground beetles the higher abundance, richness, and Shannon-Wiener Index at upper elevation sites (Figures 6-8) demonstrates that treatment effects on the community were dependent on variation within the landscape. Additionally, within the summer season, where most treatment and elevation responses on the carabid community were observed, there were no interactive effects, suggesting responses of the beetles to drought were driven by factors at a specific landscape position. The findings of my study regarding the effects of elevation on beetle communities are in accord with other studies that found increased carabid community measures at upland sites (Epstein and Kulman, 1990), although the scale of my landscape position makes comparisons difficult.

A second goal of my study was to examine possible chemical, physical, and biotic changes to forest floor habitat caused by precipitation alterations and elevation that might directly or indirectly affect beetle communities. A number of habitat variables responded as expected. For example, differences in soil water content due to treatment have been established from long-term data sets at the TDE (Hanson et al., 2003a). In years without excessive rainfall, analysis of soil water showed a separation of treatment means, where the wet plot soil water content was elevated more than dry plots in the top 0.35-m soil depth. This has implications for important forest floor processes as the frequency and intensity of drying-rewetting cycles are known to affect microorganisms responsible for the vast majority

of decomposition in natural systems (Schimel et al., 1999; Fierer et al., 2003). In my study, reduced soil moisture likely contributed to greater total litter mass found in the dry treatment compared to the ambient and wet (Table 1). Previous studies at the TDE found litter mass to be significantly greater in the dry treatment compared to both the wet and ambient (Johnson et al., 2002), thereby largely supporting the results from this study at the conclusion of this long-term experiment. Despite reduced soil moisture in the dry treatment, I observed increased litter moisture in the dry plots litter, possibly resulting from the buffering capacity of greater litter mass, which thereby reduced evapotranspiration. The effects of drought on litter architecture are therefore important to elucidate in terms of explaining insect community responses. In addition to drought effects, total litter mass in all treatments was higher at upper sites than lower (Table 1), likely resulting from increased decomposition due to higher soil moisture at downslope sites. I can conclude from my study that both water limitation and effects of landscape on soil water content contributed to an important physical variable (litter mass) for shaping ground-fauna communities, including ground beetles.

In many studies litter quality (especially C:N) has been shown to be a critical factor influencing the rate of litter decomposition (Taylor et al., 1989; Gallardo and Merino, 1993). Depending on the litter horizon, several litter quality differences in my study provided a useful framework for characterizing habitats exposed to moisture manipulations. For example, significantly less N and higher C:N ratios were characteristic of dry treatment Oi horizon leaf litter. Hanson et al. (2003b) also observed significantly higher C:N ratios and lower N in drought treatments at the TDE. My study also found that moisture manipulations could reduce the leaching of secondary compounds (i.e., phenolics), rendering leaf litter less

desirable to decomposer organisms (see Aerts and Caluwe, 1997; Bernhard-Reversat, 1998). This has implications for future shifts in precipitation patterns in forest, as more or less leaching of secondary compounds important for decomposers may affect the nutrient flow in this system. My study also suggests that the effects of elevation on leaf litter quality are similar to the effects of treatment. Oe horizon C:N ratios and TAE were higher at upper than lower sites. Again, increased moisture at lower elevation sites may provide favorable conditions (i.e., moisture) for decomposer organisms leading to less, high quality leaf litter. Elevation and treatment effects altered resource quantity and quality in my study resulting in greater amounts of lower quality litter at upper elevation sites and in drought treatments. According to resource addition studies, I might expect increased abundance of ground beetles in response to detrital subsidies (Kiovula et al., 1999; Halaj and Wise, 2002). Because beetle and carabid abundance declined in the drought treatment and increased at upper elevation sites in my study, beetle communities might be differentially affected by litter quality according to landscape position and precipitation availability.

The effect of altered prey resources on beetle communities via precipitation alterations is relatively unknown. My study found differing prey availability (i.e., mites and trap contents) due to treatment, season, and elevation. Mites were more abundant in the spring and fall than summer (Table 11, Figure 10), in contrast with my ground beetle response to season. Mite populations may have been lowest during the summer collection as the result of increased predator activity though it is likely mites were least abundant during this period due to life cycle strategy or climatic constraints (i.e., aestivation due to high temperatures). Depending on the season, mites were more abundant in dry plots, in contrast with studies that found fewer mites in drought treatments (Lindberg, 2003; Taylor and

Wolters, 2005). This is relevant because it demonstrates that the dry plots at the TDE may have provided ideal habitat and forage resources for mites during extreme climatic conditions. Greater litter mass in the dry treatment may not only have been a favorable resource base for mites, but may also have served as a stable refuge during climate extremes (i.e., wet spring, dry fall). Because mite populations were lowest in the summer and did not explain carabid community variation during this period, I used the remainder of pitfall trap captures (less beetles) to determine how precipitation affects relationships between carabids and prey. This method has proved useful in similar studies (Magura, 2002). Prey from pitfall captures was greatest during the summer collection, corresponding with the largest population peaks of carabids in my study. Though there were no effects of treatment on prey abundance, more prey were found at upper than lower sites in the summer, consistent with greater carabid abundance at upper sites during the summer collection. Thus population-level effects in a predator-prey trophic interaction could be acting in my study system, although this was not observed for mites. Therefore, landscape position may be of greater importance than precipitation in temperate forests for shaping predator-prey trophic interactions, though the potential effects of precipitation alterations should not be neglected.

The final goal of my study was to examine potential relationships between carabid communities and habitat variables subject to change via precipitation manipulations. Soil water content was the most important abiotic predictor of carabid communities in agreement with a number of studies that found this an important factor in shaping beetle communities (Luff et al., 1989; Rykken et al., 1997; Maudsley et al., 2002). Increasing soil water content increased both carabid abundance and tribe richness, suggesting important feedbacks with soil/litter processes important to beetles. Because soil water was reduced in dry plots, this

study suggests that potential future reductions in precipitation could lead to declining carabid abundance and tribe richness. Also, because soil water was a negative predictor of evenness, a shift away from dominant tribes in the dry treatment and a tendency for more dominant carabid tribes in the wet treatment demonstrates a possible shift in certain beetles as habitat preferences change due to climate change. However, a distinct pattern likely due to elevation emerged in my analysis depicting a negative relationship between soil water content and both carabid abundance and richness in each treatment. This trend was characterized by a decrease in abundance and richness from upper to lower elevation sites where soil water increased from top to bottom of the elevation gradient. These findings suggest that future moisture alterations will likely affect beetle communities in temperate zone forests (i.e., less beetles in droughted areas) through intensifying the effects of landscape position and inherent moisture gradients that shape beetle communities and habitat.

Changes in leaf litter mass due to precipitation alterations corresponded to changes in carabid communities in this study. Past litter or resource addition studies have shown a positive response of arthropod communities to increased litter depth and architecture (Bultman and Uetz, 1984). My study, however, found a negative correlation between litter mass and both carabid abundance and tribe richness (Figures 14-15). Regression analysis found a pattern where greater litter mass, characteristic of dry plots, clusters with lower abundance and richness, while less litter mass, typical of wet and ambient plots, clusters with higher carabid abundance and tribe richness. These findings suggest that precipitation manipulations indirectly affect carabid communities through alterations of forest floor litter mass, possibly hindering the mobility of carabids through changes in structural complexity of

the organic layer. In addition to physical changes in the habitat, at a microclimate level litter temperature could influence carabid abundance and distribution. My study found no differences in forest floor temperature due to treatment or elevation effects, while regression analysis found weak positive correlations between weekly mean temperature maximums and carabid tribe richness and  $H'$  (Figures 16-17). Though I found no clear patterns for treatment or elevation effects on litter temperature, my study does suggest that precipitation alteration on broad scales could affect the microclimate of the litter layer and that effects on ground-dwelling beetles could result.

Ground beetle communities in this study responded in contradictory ways to the effects of elevation and treatment on litter mass and soil water content. Ground beetle abundance and richness decreased in the drought treatment where leaf litter mass was highest and soil water content lowest. In contrast, carabid abundance and richness were greatest at upper elevation sites where leaf litter mass was highest and soil water content lowest. Multiple regression analysis showed no covariation between leaf litter mass and soil water content (data not shown) when predicting carabid communities. However, a simple linear regression did show that as soil water content increased, leaf litter mass decreased (data not shown). With respect to elevation, this suggests that moisture does indirectly affect carabid communities through modification of resource availability (i.e., litter mass), but carabids are directly limited by leaf litter at the landscape level. In contrast, treatment effects were associated with a divergent trend when a switch from resource limitation (i.e., leaf litter) to moisture limitation caused deleterious effects on carabid communities. This is likely due to extended large-scale precipitation deficits that disrupt decomposition processes, causing higher litter mass (e.g., increased resource availability) and less soil water content. This

suggests that at the landscape level carabid communities are primarily limited by resource availability (i.e., leaf litter), while extended, large-scale precipitation alterations (i.e., drought) may deterministically alter this relationship permitting moisture to become the foremost limiting factor for carabid communities intensifying elevation effects.

Prey availability in this study had a strong relationship with several carabid community parameters. Though others have cited mites as an important prey source for carabids (Johnston, 2000), I found no relationship between mites and carabid communities during the summer. This suggests that ground beetles were not primarily using mites as a prey source in my system. However, prey collected from pitfall traps (i.e., crickets, ants, etc.) had strong positive relationships with carabid abundance and tribe level richness and  $H'$  (Figures 18-20). Because dry plots were typically associated with lower prey and carabid abundance, richness, and  $H'$ , it appears that altering precipitation in this forest affected trophic level responses between predators to their prey. Some caution is needed in the interpretation of this result because all arthropods besides beetles collected were not likely prey (example, spiders) and no treatment effects on prey abundance were observed. Nonetheless, my data are suggestive of treatment-induced effects on prey abundance that may be dependent on the same habitat variables (i.e., soil water content, litter mass, etc.) acting to shape the carabid community.

### **Conclusion**

My study found that precipitation alteration, seasonality, and elevation altered beetle community parameters and that key habitat variables were related to the insect responses. The two most abundant beetle families were lower in abundance in the dry compared to the

wet treatment. Abundance-based community comparisons for ground beetle tribes demonstrated dissimilarity between the dry treatment compared to the wet and ambient. Dominant carabid tribes accounting for the vast majority of individuals were much less abundant in the drought treatment and at lower elevation sites, while carabid abundance, richness, and  $H'$  were higher in upper plots suggesting the importance of both moisture and landscape position in shaping carabid communities. Seasonality had a strong effect on beetle abundance, which was greatest in the summer. Total beetle and carabid abundance during the summer collection declined significantly in response to drought, coinciding with a decrease in carabid tribe richness. Evenness was lower in wet plots due to the presence of more dominant tribes than in dry plots.

I found 50% greater litter mass in the dry compared to the wet treatment coupled with reduced leaf litter quality in the dry treatment Oi horizon (i.e., higher TAE and C:N, and lower N). Additionally, patterns of less litter mass at lower elevation sites, along with significantly lower TAE and C:N in certain organic horizons (i.e., Oe), suggest increased decomposition and therefore less available habitat for beetles due to elevation. Treatment and elevation had similar effects on litter mass and moisture, though the responses of carabid communities were contradictory. Overall, litter mass was a significant negative predictor of both carabid abundance and richness. However, carabid abundance and tribe richness were greater in upper elevation sites where there was 16-17% higher litter mass than at lower sites. Also, there was a significant positive relationship between soil water content and carabid abundance and tribe level richness characterized by lower soil water in the dry compared to the wet treatment. In contrast, an underlying pattern of decreasing carabid abundance and richness from upper to lower elevation sites corresponded with increased soil water content

from upper to lower elevation plots. Lack of interactive effects between treatment and elevation, suggests that both block effects act independently to influence limiting factors that determine carabid communities. For example, with regard to elevation, there was an association of higher litter mass, lower soil water content, and increases of carabid community parameters at upper elevation sites, while in treatment-wise comparisons, leaf litter increases and lower soil water were associated with declining carabid community parameters. Even though I was unable to fully examine predator-prey relationships in my study, I did find some evidence that carabid communities were related to prey availability, where dry treatment and lower elevation community parameters were generally associated with less prey.

In summary, my study provides valuable insight into the role precipitation alteration, season, and landscape have on abiotic and biotic components of the forest floor in temperate hardwood forests, and as such makes a valuable contribution to predicting future climate change impacts on terrestrial ecosystems. In addition to examining effects on important habitat variables, my study also demonstrates the need for more examination of climate-induced effects on trophic level relationships important for shaping ground beetle community composition in temperate forests.

### LITERATURE CITED

- Aerts, R., Caluwe, H., 1997. Nutritional and plant mediated controls on leaf litter decomposition of carex species. *Ecology* 78, 244-260.
- Antvogel, H., and Bonn, A., 2001. Environmental parameters and microspatial distribution of insects: A case study of carabids in an alluvial forests. *Ecography* 24, 470-482.
- Araujo, M.B., Rahbek, C., 2006. How does climate change affect biodiversity? *Science* 313: 1396-1397.
- Arnett, Jr., H.G., Thomas, M.C., 2001. *American Beetles: Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*. CRC Press, New York.
- Ashworth, A.C., 2001. Perspectives on quaternary beetles and climate change. In: Gerhard, L.C., Harrison, W.E., Hanson, B.M., (Eds.) *Geological Perspectives of Global Climate Change*. American Association of Petroleum Geologists Studies in Geology 47, 153-168.
- Baker, S., 2006. A comparison of litter beetle assemblages (Coleoptera) in mature and recently clearfelled Eucalyptus oblique forest. *Australian Journal of Entomology* 45, 130-136.
- Battisti, A., 2004. Forests and climate change- lessons from insects. *Forest@* 1, 17-24. URL: <http://www.sisef.it/>
- Bernhard-Reversat, F., 1998. Changes in relationships between initial litter quality and CO<sub>2</sub> release during early laboratory decomposition of tropical leaf litter. *European Journal of Soil Biology* 34, 117-122.
- Bohac, J., 1999. Staphylinid beetles as bioindicators. *Agriculture, Ecosystems, and Environment* 74, 357-372.
- Boulinier, T., Nichols, J.D., Sauer, J.R., Hines, J.E., Pollock, K.H., 1998. Estimating species richness: The importance of heterogeneity in species detectability. *Ecology* 79, 1018-1028.
- Bultman, T.L., Uetz, G.W., 1984. Effect of structure and nutritional quality of litter on the abundance of litter-dwelling arthropods. *American Midland Naturalists* 111, 165-172.

- Chen, B., Wise, D.H., 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. *Ecology* 3, 761-772.
- Chikoski, J.M., Ferguson, S.H., Meyer L., 2006. Effects of water addition on soil arthropods and soil characteristics in a precipitation limited environment. *Acta Oecologia* 30, 203-211.
- Chimner, R.A., Welker, J.M., 2005. Ecosystem respiration responses to experimental manipulations of winter and summer precipitation in a Mixedgrass Prairie, WY, USA. *Biogeochemistry* 73, 257-270.
- Coope, R.G., 1994. The Response of Insect Faunas to Glacial-Interglacial Climatic Fluctuations [and Discussion]. *Philosophical Transactions: Biological Sciences* 344, 19-26.
- Crossley, D.A., Blair, J.M., 1991. A high-efficiency, "low-technology" Tullgren-type extractor for soil microarthropods. *Agriculture, Ecosystems and Environment* 34, 87-192.
- Desender, K.R., 1996. Diversity and dynamics of coastal dune carabids. *Ann. Zool. Fennici* 33, 65-75.
- Dillon, E.S., Dillon, L.S., 1972. *A Manual of Common Beetles of Eastern North America*. Dover Publications, Inc. New York.
- Edwards, C.A., 2000. Soil invertebrate controls and microbial interactions in nutrient and organic matter dynamics in natural and agroecosystems. IN: Coleman, D.C., Hendrix, P.F., (eds.). *Invertebrates As Webmasters in Ecosystems*. CAB Publishing, NY.
- Elias, S.A., 1991. Insects and Climate Change. *Biosciences* 41, 552-559.
- Epstein, M.E., Kulman, H.M., 1990. Habitat distribution and seasonal occurrence of carabid beetles in east-central Minnesota. *American Midland Naturalist* 123, 209-225.
- Ferguson, S.H., Joly, D.O., 2002. Dynamics of springtail and mite populations: the role of density dependence, predation, and weather. *Ecological Entomology* 27, 565-573.
- Fierer, N., Schimel, J.P., Holden, P.A., 2003. Influence of drying-rewetting frequency on soil bacterial community structure. *Microbial Ecology* 45, 63-71.
- Gallardo, A., Merino, J., 1993. Leaf decomposition in two Mediterranean ecosystems of southwest Spain: Influence of substrate quality. *Ecology* 74, 152-161.

- Gentry, A.H., 1988. Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Annals of the Missouri Botanical Garden* 75, 1-34.
- Gist, C.S., Crossley, D.A., 1975. The litter arthropod community in a southern Appalachian hardwood forest: Numbers, biomass, and mineral element content. *American Midland Naturalist* 93, 107-122.
- Gitay, H., Suarez, A., Dokken, D.J., Watson, R. T., (Eds.), 2002. Intergovernmental Panel On Climate Change, 2002. Climate change and biodiversity. IPCC Technical Paper V.
- Gotelli, N.J., G.L. Entsminger., 2004. EcoSim: Null models software for ecology. Version 7. Acquired Intelligence Inc. & Kesey-Bear. Jericho, VT 05465. <http://garyentsminger.com/ecosim/index.htm>.
- Halaj, J., Wise, D.H., 2002. Impact of a detrital subsidy on trophic cascades in a terrestrial grazing food web. *Ecology* 83, 3141-3151.
- Hansen, R.A., 2000. Effects of habitat complexity and composition on a diverse litter microarthropod assemblage. *Ecology* 81, 1120-1132.
- Hansen, R.A., Coleman, D.C., 1998. Litter complexity and composition are determinants of the diversity and composition of oribatid mites (Acari: Oribatida) in litterbags. *Applied Soil Ecology* 9, 17-23.
- Hansen, A.J., Neilson, R.P., Dale, V.H., Flather, C.H., Iverson, L.R., Currie, D.J., Shafer, S., Cook, R., and Bartlein, P.J., 2001. Global change in forests: responses of species, communities, and biomes. *Bioscience* 51, 765-779.
- Hanson, P.J., O'Hara, F.M., 2003. Introduction. IN: Hanson, P.J., and Wullschleger, S.D., (eds). *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes*. Springer, New York, 8-31.
- Hanson, P.J., Wullschleger, S.D., 2003. *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes*. Springer, New York.
- Hanson, P.J., Huston, M.A., Todd, D.E., 2003a. Walker Branch Throughfall Displacement Experiment. IN: Hanson, P.J., and Wullschleger, S.D., (eds). *North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes*. Springer, New York, 3-7.

- Hanson, P.J., O'Neill, E.G., Chambers, M.L., Riggs, J.S., Joslin, J.D., Wolfe, M.H., 2003b. Soil respiration and litter decomposition. IN: Hanson, P.J., and Wullschlegel, S.D., (eds). North American Temperate Deciduous Forest Responses to Changing Precipitation Regimes. Springer, New York, 163-189.
- Heneghan, L., Coleman, D.C., Zou, X., Crossley, D.A., Haines, B.L., 1999. Soil microarthropod community structure and litter decomposition dynamics: A study of tropical and temperate sites. *Applied Soil Ecology* 9, 33-38.
- Hodkinson, I.D., 2005. Terrestrial insects along elevation gradient: Species and community responses to altitudes. *Biological Review* 80, 489-513.
- Hoorens, B., Aerts, R., Stroetenga, M., 2003. Does initial litter chemistry explain litter mixture effects on decomposition? *Oecologia* 137, 578-586.
- Horner, J.D., Gosz, J.R., Cates, R.G., 1988. The role of carbon-based secondary metabolites in decomposition in terrestrial ecosystems. *The American Naturalist* 132, 869-883.
- Houghton, J.T., Ding, Y., Griggs, D.J., Noguera, M., van der Linden, P.J., Xiaosu, D., (Eds), 2001. *Climate Change 2001: The Scientific Basis: Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change (IPCC)*. Cambridge University Press, Cambridge, England.
- Hunter, M.D., Adl, S., Pringle, C.M., Coleman, D.C., 2003. Relative effects of macroinvertebrates and habitat on the chemistry of litter during decomposition. *Pedobiologia* 47, 101-115.
- Janzen, D.H., Ataroff, M., Farinas, M., Reyes, N., Rincon, N., Soler, A., Soriano, P., Vera, M., 1976. Changes in the arthropod community along an elevational transect in the Venezuelan Andes. *Biotropica* 8, 193-203.
- Johnson D.W., VanHook, R.I., 1989. *Analysis of biogeochemical cycling processes in Walker Branch Watershed*. Springer-Verlag, New York.
- Johnson, D.W., Hanson, P.J., Todd, D.E., 2002. The effects of throughfall manipulation on soil solution chemistry and leaching in a deciduous forest. *Journal of Environmental Quality* 31, 204-216.
- Johnston, J.M., 2000. The contribution of microarthropods to aboveground food webs: A review and model of belowground transfer in a coniferous forest. *American Midland Naturalist* 143, 226-238.

- Knoepp, J.D., Reynolds, B.C., Crossley, D.A., Swank, W.T., 2005. Long-term changes in forest floor processes in southern Appalachian forests. *Forest Ecology and Management* 220, 300-312.
- Koivula, M., 2002. Alternative harvesting methods and boreal carabid beetles. *Forest Ecology and Management* 167, 103-121.
- Koivula, M., Punttila, P., Haila, Y., Niemela, J., 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* 22, 424-435.
- Krantz, G.W., 1970. *A Manual of Acarology*. Oregon State University Bookstores, Inc., Corvallis, OR.
- Lindberg, N., 2003. Soil fauna and global change- responses to experimental drought, irrigation, fertilization, and soil warming. Ph.D. Thesis. Swedish University of Agricultural Sciences, Uppsala, Sweden.
- Lindberg, N., Engtsson, J.B., Persson, T., 2002. Effects of experimental irrigation and drought on the composition and diversity of soil fauna in a coniferous stand. *Journal of Applied Ecology* 39, 924-936.
- Luff, M.D., Eyre, M.D., Rushton, S.P., 1989. Classification and ordination of habitats of ground beetles (Coleoptera, Carabidae) in north-east England. *Journal of Biogeography* 16, 121-130.
- Madritch, M.D., Hunter, M.D., 2005. Phenotypic variation in oak litter influences short- and long-term nutrient cycling through litter chemistry. *Soil Biology and Biochemistry* 37, 319-327.
- Magura, T., 2002. Carabids and forest edge: spatial pattern and edge effect. *Forest Ecology and Management* 157, 23-37.
- Magura, T., Tothmeresz, B., Elek, Z., 2004. Effects of leaf litter addition on carabid beetles in a non-native Norway spruce plantation. *Acta Zoologica Academiae Scientiarum Hungaricae* 50, 9-23.
- Magura, T., Tothmeresz, B., Elek Z., 2005. Impacts of leaf-litter addition on carabids in a conifer plantation. *Biodiversity and Conservation* 14, 475-491.
- Maudsley, M., Seeley, B., Lewis, O., 2002. Spatial distribution patterns of predatory arthropods within an English hedgerow in early winter in relation to habitat variables. *Agriculture, Ecosystems, and Environment* 89, 77-89.

- Mazia, C., Chaneton, E.J., Kitzberger, T., 2006. Small-scale habitat use and assemblage structure of ground-dwelling beetles in a Patagonian shrub steppe. *Journal of Arid Environments* 67, 177-194.
- Naeem, S., Loreau, M., Inchausti, P., 2004. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. Loreau, M., Naeem, S., and Inchausti (eds.). *Biodiversity and Ecosystem Functioning: Synthesis and Perspectives*. Oxford University Press, New York, 3-11.
- National Oceanic and Atmospheric Administration (NOAA), 2007. Information available on the Internet at: [www.esrl.noaa.gov/gmd/ccgg/trends](http://www.esrl.noaa.gov/gmd/ccgg/trends).
- Niemela, J., Haila, Y., Punttila, P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity of forest-floor invertebrates across the succession gradient. *Ecography* 19, 352-368.
- Noonan, G.R., 1990. Biogeographical patterns of North American *Harpalus* Latreille (Insecta: Coleoptera: Carabidae). *Journal of Biogeography* 17, 583-614.
- Olson, D.M., 1994. The distribution of leaf litter invertebrates along a neotropical altitudinal gradient. *Journal of Tropical Ecology* 10, 129-150.
- Oak Ridge National Laboratory (ORNL), 2007a. Information available on the Internet at: <http://tde.ornl.gov/nine.html>
- Oak Ridge National Laboratory (ORNL), 2007b. Information available on the Internet at: <http://tde.ornl.gov/TDEDESIG.GIF>
- Rainio, J., Niemela, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. *Biodiversity and Conservation* 12, 487-506.
- Reiske, L.K., Buss, L.J., 2001. Influence of site on diversity and abundance of ground- and litter-dwelling coleoptera in Appalachian oak-hickory forests. *Environmental Entomology* 30, 484-494.
- Rykken, J.J., Capen, D.E., Mahabir, S.P., 1997. Ground beetles as indicators of land type diversity in the Green Mountains of Vermont. *Conservation Biology* 11, 522-530.
- Salamanca, E.F., Kaneko, N., Katagiri, S., 2003. Rainfall manipulation effects on litter decomposition and microbial biomass of the forest floor. *Applied Soil Ecology* 22, 271-281.
- Sanders, N.J., 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. *Ecography* 25, 25-32.

- SAS Institute., 2002. SAS/STAT software: changes and enhancements through release 9.1. SAS Institute, Cary, NC.
- Schadler, M., Brandl, R., 2005. Do invertebrate decomposers affect the disappearance rate of litter mixtures? *Soil Biology and Biochemistry* 37, 329-337.
- Schimel, J.P., Gullledge, J.M., Clein-Curley, J.S., Lindstrom, J.E., Braddock, J.F., 1999. Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology and Biochemistry* 31, 831-838.
- Singleton, V.L., Rossi, J.A., 1965. Colorimetry of total phenolics with phosphomolybdic-phosphotungstic acids reagents. *American Journal of Enology and Viticulture*, 16, 144-158.
- Suttle, K.B., Thomsen, M.A., Power, M.E., 2007. Species interactions reverse grassland responses to climate change. *Science* 315, 640-642.
- Taylor, B.R., Parkinson, D., Parsons, W.J., 1989. Nitrogen and lignin content as predictors of litter decay rates: A microcosm test. *Ecology* 70, 97-104.
- Taylor, A.R., Wolters, V., 2005. Responses of oribatid mite communities to summer drought: The influence of litter type and quality. *Soil Biology and Biochemistry* XX, 1-14.
- University of Georgia (UGA) Institute of Ecology Stable Isotope Laboratory, Information available on the Internet at: <http://www.uga.edu/~sisbl/sampling.html#erba>
- van Tongeren, O.F.R., 1995. Cluster analysis. IN: Jongman, R.H.G., ter Braak, C.J.F., and van Tongeren, O.F.R., (eds.) *Data analysis in community and landscape ecology*. New edition. Cambridge University Press, New York, 174-212
- Walther, G.R., 2007. Tackling ecological complexity in climate impact research. *Science* 315, 606-607.
- White, R.E., 1983. *A Field Guide to the Beetles of North America*. Houghton Mifflin Company, New York.
- Wilson, E.O., 2005. Oribatid mite predation by small ants of the genus *Pheidole*. *Insect Society* 52, 263-265.
- Winder, L., Alexander, C.A., Holland, J.M., Symondson, W.O., Perry, J.N., Woolley, C., 2005. Predatory activity and spatial pattern: The response of generalist carabids to their aphid prey. *Journal of Animal Ecology* 74, 443-454.

Wolda, H., 1988. Insect seasonality: Why? *Annual Review of Ecology and Systematics* 19, 1-18.

Yi, H., Moldenke A., 2005. Response of ground-dwelling arthropods to different thinning intensities in young Douglas Fir forests of western Oregon. *Environmental Entomology* 34, 1071-1080.

### **BIOGRAPHICAL SKETCH**

Bryan Scott Marbert was born on May 11, 1977 in Fayetteville, North Carolina to parents Robert and Kay Marbert. Bryan attended Appalachian State University in Boone, North Carolina graduating with a Bachelor of Science in Business Administration in August 2000. Deciding to pursue a career in the sciences, Bryan matriculated into Western Carolina University's Department of Natural Resource Management in Cullowhee, North Carolina graduating in May 2003 with his Bachelor of Science. While in attendance, Bryan was employed by both the Mountain Aquaculture Research Center and the United States Forest Service. In fall 2004, Bryan continued his pursuit of scientific training beginning work on his Master of Science degree in Biology under the tutelage of Dr. Ray Williams at Appalachian State University completing all requirements for the degree in May 2007. Bryan will be entering the Department of Entomology at the University of Kentucky in summer 2007 to begin work on his Ph.D.