Impacts of tamarisk biocontrol (Diorhabda elongata) on the trophic dynamics of terrestrial insects in monotypic tamarisk stands

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Impacts of tamarisk biocontrol (*Diorhabda elongata*) on the trophic dynamics of terrestrial insects in monotypic tamarisk stands

A Thesis

Presented to

the Faculty of Natural Sciences and Mathematics

University of Denver

In Partial Fulfillment

of the Requirements for the Degree

Master of Science

by

Stephanie Strudley

August 2009

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TITLE: Impacts of tamarisk biocontrol (*Diorhabda elongata*) on the trophic dynamics of terrestrial insects in monotypic tamarisk stands.
ADVISOR: Anna A. Sher
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ABSTRACT

Combating tamarisk (*Tamarix* spp.), an exotic tree species that has invaded 1-1.6 million hectares of riparian land in the Midwestern United States, with the introduced leaf beetle *Diorhabda elongata* provides an opportunity to evaluate how the trophic spectra of terrestrial insects respond to a herbivorous biocontrol. To evaluate this restoration approach and the interaction biocontrol may have with terrestrial insect populations, I quantified trophic unit richness and abundance and common family abundance of resident insect populations while also measuring biocontrol abundance and status during the previous season (present or not present). These measurements were taken four times throughout one season in monotypic tamarisk at two locations in Grand County, Utah. Biocontrol abundance was lower when biocontrol had been present in the previous season. Predator, omnivore and herbivore richness and omnivore, Histeridae, Lygaeidae and Formicidae abundance showed a relationship with biocontrol abundance. When biocontrol had been present in the previous season, predator richness and, Histeridae abundance was higher while when biocontrol had not been present in the previous season herbivore richness and detritivore, Lygaeidae and Elateridae abundance was higher. The results suggest relationships exist between *D.elongata* and multiple members of the trophic spectra of terrestrial insects that changes when biocontrol have been present for more than one season. If *D. elongata* are adding connections and complexity to the trophic spectra through these relationships with terrestrial insects than the use of
biocontrol in monotypic tamarisk stands may help preserve what is left of the trophic web in the invaded ecosystem. Understanding the side effects of a biocontrol on the trophic structure of an ecosystem is essential to land management. At the same time, this work provides a more thorough understanding of the effect of herbivorous biocontrol on the trophic ecology of disturbed ecosystems.
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INTRODUCTION

By exploring the intersection of trophic dynamics, exotic plant disturbance, and biocontrol we can achieve a better understanding of biocontrol as a restorative approach and the trophic impact in these ecosystems. Trophic dynamic theory has evolved to include myriad ecological concepts (e.g. biodiversity, life history, population dynamics, environmental conditions, resource availability) in an attempt to describe the true complexity and connectivity among species in an ecosystem (Darnell 1961, Polis and Strong 1996, Boror et al. 2005, Polis 1999, Montoya et al. 2006). Current literature suggests that ecosystems with high spatial heterogeneity provide conditions for high biodiversity, which increases food web complexity and weakens the potential for cascades in trophic structure (Polis 1999). This is particularly important to the current study of biocontrol introduction in altered ecosystems because it implies that strong trophic cascades may be found in ecosystems that have lower complexity and thus lower biodiversity with less spatial heterogeneity. It has also been suggested that monoculture vegetation leads to stronger trophic interactions (as evident in agricultural biocontrol systems, Polis 1999) because of the simplified trophic web. Terrestrial ecosystems that have low spatial heterogeneity and biodiversity because of single species dominance, such as an introduced invasive, would therefore be expected to have reduced biodiversity and food web complexity (this string of logic has been vaguely suggested by Kagata and
Ohgushi (2006) and Polis et al. (2000), Mack et al. (2000)). However, studies that assess trophic structures within invaded ecosystems are limited, rendering this thought progression plausible, but unsubstantiated. Furthermore, few have explored how non-invasive species introductions, such as introduced biocontrol agents, affect trophic structures in natural (or altered) ecosystems.

Although tamarisk (Tamarix spp., there are 4 species per Gaskin and Schaal 2002) was introduced to the United States in the 1820’s (Robinson 1965) as an ornamental, windbreak, and stream stabilizer species, it was not until the 1920’s that it was recognized as a problem for riparian habitat (Botherson and Field 1987). Vast expanses of the riparian corridors in the Midwestern United States are infested with tamarisk. As of 1965 tamarisk had invaded 600,000 hectare (United States Geological Survey 1965). Tamarisk, in some cases in conjunction with controlled water regime, overgrazing, and other geomorphic changes, has brought many negative impacts to the once lush riparian fringes in the Midwest, including: 1) a change to the biodiversity of native wildlife (Ellis et al. 2000, Bailey and Schweitzer 2001), 2) an increase in surface soil salinity (Ladenburger et al. 2006, Ohrtman 2009), and 3) changes in forest structure and spatial heterogeneity (Bess et al. 2002). In addition to these problems, the only known herbivores that feed on tamarisk in the United States are the exotic tamarisk leafhopper Opsius stactogalus and the scale, Chionespis spp., and potentially a few generalist herbivores (Liesner 1971, Lewis et al. 2003).

In an effort to combat the damaging environmental effects of tamarisk, a biocontrol beetle, Diorhabda elongata (Family: Chrysomelidae), has been introduced
from Eurasia. *D. elongata* consumes the foliage of tamarisk in both the adult and larval stages. When the day length shortens, the leaf beetle goes into diapause through the winter in the leaf litter beneath the tamarisk, then, resumes consumption, reproduction, and dispersal when tamarisk is foliated and flowering again in the spring (Lewis et al. 2003, Bean et al. 2007). They use two detectable aggregation pheromones to direct the population onto foliated tamarisk shrubs (Cosse et al. 2005). Potentially two to three generations are produced each season (Cosse et al. 2005, Bean et al. 2007, Dudley and Kazmer 2005, Lewis et al. 2003). When the beetle consumes leaf matter from tamarisk, the plant is unable to maintain the necessary photosynthesis to proliferate, however, tamarisk can re-foliate (with less foliage) within three to six weeks after biocontrol damage (Dudley 2005). Studies suggest that 3-5 years of biocontrol usage on tamarisk in the United States are necessary to successfully kill tamarisk (Tom Dudley, personal communication). Although the ecological effects of *D. elongata* have been investigated with regard to non-target plant consumption and success in tamarisk in the United States (Lewis et al. 2003, Milbrath and DeLoach 2005), to date there are no published works on the impact of this introduced species on the faunal community, with the exception of birds (Dudley 2004, Owens et al. 2005). Researchers have reported that *D. elongata* may be impacting the trophic structure by supplementing prey to the ants, birds, and small mammals in monotypic tamarisk stands (Dudley and Kazmer 2005), but this hypothesis has yet to be scientifically tested.
Considering the influences of tamarisk on once native ecosystems, the introduction of the biocontrol *D. elongata* in this system could be enzymatic for a strong trophic cascade. The addition of biocontrol to the trophic web of terrestrial insects in tamarisk stands could impact trophic dynamics by altering vegetation, detritus, and prey availability. Biodiversity and abundance of terrestrial insects that depend on these resources may change to such an extent that other connected trophic units may also be affected. The work done here seeks to determine if the impact of the *Diorhabda elongata* in riparian corridors is strong enough to alter the trophic structure (abundance and richness) of terrestrial insects in monotypic tamarisk ecosystems. My research seeks to test the following specific predictions:

1. Predator richness and abundance will increase with biocontrol abundance because of the increase in food supply (biocontrol).
2. Detritivore richness and abundance will decrease when biocontrol abundance increases because the mass of green matter that once fell from tamarisk, which served as habitat and as a food source for detritivores, will change in quality and quantity as biocontrol abundance increases.
3. Omnivore abundance will increase when biocontrol are more abundant and because of the increased food supply. Richness will slightly decrease because omnivores that require edible foliage will not benefit with the addition of biocontrol.
4. Herbivore richness and abundance will decrease when biocontrol abundance increases because of competition with biocontrol for a
shrinking supply of tamarisk foliage. Even for herbivores that do not
directly compete for the green leaves of the tamarisk but feed on other
parts (flowers, sap, etc), the increased density of biocontrol will have
negative effects on the entire tamarisk plant and indirectly affect these
populations.

Elucidating the trophic interactions resulting from the introduction of
biocontrol in tamarisk-dominated ecosystems aids in understanding ecosystem
behavior, and how restoration ecologists may apply biocontrol in managed
ecosystems. Critics of biocontrol have emphasized the value of understanding the
full impact that biocontrol imparts to ecosystems (Simberloff and Stiling 1996,
Zavaleta et al. 2001, Hoodle 2004, Raghu and Dhileepan 2005) because of the
importance of trophic interactions to ecosystem health and the preservation of
biodiversity. This work addresses this concern, acknowledging that trophic
interactions can invoke influential changes in ecosystems, and also seeks to provide
information that could potentially influence the decisions restoration and conservation
ecologists make to control tamarisk and restore riparian corridors.
LITERATURE REVIEW

My research seeks to marry a theoretical understanding of how herbivorous biocontrol affect trophic dynamics with a practical understanding of the response of a tamarisk-invaded riparian corridor to the introduction of biocontrol in the Southwest. In this chapter I describe the background literature on trophic dynamic theory in an effort to determine whether the introduction of an herbivorous biocontrol would be expected to affect trophic dynamics in an ecosystem dominated by an invasive plant, and why this information is critical to making long-term resource management decisions.

Trophic structures were originally thought to exist, conceptually, as a trophic pyramid with three levels, where energy flows from primary producers (bottom level) to herbivores to predators (top level), with the abundance decreasing inversely with trophic level (Elton 1927, Lindeman 1942). The bottom-up concept followed, describing a system regulated by the producers control over herbivores which regulate predators. After the observation that herbivores rarely exhaust their resources (vegetation), the top-down concept was developed in which the predators controlled herbivores and prevented the exploitation of primary producers (green world hypothesis: Hairston et al. 1960, Hairston and Hairston 1993). The combination of the top-down, bottom-up concepts was described in the exploitation ecosystem hypothesis in which the relative productivity of the producer determined the controlling trophic level (Oksanan et al. 1981, Fretwell 1987). A fourth level was
added to the conceptual trophic pyramid to describe the role of omnivores, which expanded the type relationships between each trophic level (Carpenter and Kitchell 1987). In a more recent synthesis of trophic dynamic theory it was suggested that perhaps neither bottom-up nor top-down fully describes what manipulates trophic dynamics and that in real world trophic dynamics the relationships are much more complex than these simple models suggest (Strong 1993, Polis and Strong 1996, Montoya et al. 2006, Polis et al. 1999).

In the latest efforts to model trophic behavior, a ‘trophic spectrum” (Polis and Strong 1996, Darnell 1961) was described as a gradient between primary producers and apex predators. In this paradigm, species slide between what were previously defined as discrete trophic levels (Elton 1927, Lindeman 1942, Hairston et al. 1960), depending on life history, environmental conditions, resource availability, and trophic complexity. Unlike the original model, which was linear, this revised version describes systems as an ever-changing reticulate trophic web in which each organism is dependent on resource availability and multiple other trophic units for survival. Although the term ‘trophic level’ overly simplifies a complex set of interactions (Paine 1980, Polis 1999), our current knowledge of trophic habits and organism life histories limits our ability to correctly construct a trophic spectra, especially for terrestrial insects. For this reason, the term trophic unit is used in my research to describe all organisms that consume the same type of food (detritus, prey, vegetation), to the best of our knowledge, at the stage at which we have caught them, in an attempt to correctly place them in the trophic spectra. The true connectivity and
complexity of each individual ecosystem cannot be easily modeled. Stability, effects of complexity, resource availability, and other related topics continue to be debated and tested by trophic ecologists.

Trophic dynamic theory also includes the concept of ‘trophic cascades’, which occur when an event causes a change in population size or biomass of one trophic unit, leading to a “ripple effect” through the connected and dependent trophic units and temporary (Boyer et al. 2003) or permanent changes in the trophic web (Polis et al. 2000). This effect is not necessarily linear and may vary in strength and length, and may be caused by both trophic and environmental factors (Polis 1999, Montoya et al. 2006, Pace et al. 1999). Not all changes in the trophic web, however, have a strong enough effect to lead to a cascade. By some definitions, cascades are limited to community level interactions, while others think strong species interactions should also be called a cascade (Polis 1999, Schmitz et al. 2000, Pace et al. 1999). Generally cascades have been assessed at the species level and evaluated for top-down (natural enemy manipulations) cascades (Schmitz et al. 2000 and Boror et al. 2005 offer a meta-analysis of these types of cascades) or bottom-up cascades (Kagata and Ohgushi (2000) provided a meta-analysis of bottom-up cascades). But it has been suggested that species level cascades will not necessarily lead to community-wide effects (Polis et al. 2000). Boror et al. (2005) cites five primary hypotheses to explain what causes cascades, one of which (proposed by Polis (1999)) is high herbivore efficiency (especially in invertebrates) and another is spatial heterogeneity. In addition Strong and Polis (1992) argue that community level cascades are limited to ecosystems with lower diversity where a change in a species populations can have a bigger impact.
Therefore, *D. elongata* (an efficient herbivore) and monotypic tamarisk stands yield conditions that would be considered likely to cause a cascade. My research considers effects from herbivores on trophic and family levels. The need for this type of study has been highlighted by trophic ecologists that recognize that the complexity of trophic structures exceed simple (linear) food chains described in top-down and bottom-up experiments (Polis et al. 2000, Hunter and Price 1992).

Despite the discrepancy in definitions of trophic cascades, agricultural scientists have expended much effort in performing experiments that have shown multi-link relationships (top-down cascade) among biocontrols, herbivores, and crops. These relationships consist of a ‘natural enemy’ (referring to a predator or parasitoid) whose abundance or richness was manipulated, causing an effect in crop productivity and usually suggesting that herbivorous ‘pest’ control was achieved by the ‘natural enemy’ abundance and richness (e.g. Moran et al. 1996, Moran and Hurd 1998, Halaj and Wise 2002, Matsumoto 2003, Cardinale et al. 2003, Straub and Snyder 2006). In these biocontrol experiments, the production of a ‘trophic cascade’ has often been determined by a measurement of plant performance; however, Polis (1999) implies that few natural terrestrial trophic cascades have been observed to impact plant populations. In the case of tamarisk ecosystems, biocontrol by *D. elongata* does impact plant performance (Dudley 2005). The main difference between the agricultural biocontrol and tamarisk biocontrol is that the objective of the control measure for the tamarisk case is to reduce and eventually remove the primary producer from the system via herbivorous consumption, not increase its productivity. In addition, agricultural biocontrol experiments are generally performed in
greenhouses or agricultural fields. Under these conditions researchers can control and simplify their experiments with low terrestrial insect biodiversity and/or homogeneous plants, something that is difficult to do in natural ecosystems (Polis 1999). Thus, the agricultural literature does provide information that cascades can be induced by adding a predatory biocontrol to the simplified agro-ecosystems but it may not aid in understanding how herbivorous biocontrol impact natural ecosystems. Research on trophic interactions of animals caused by herbivorous biocontrol in natural systems is lacking and critical to adequately determine the long-term impact of biocontrol.

Although several papers have noted the necessity to test the impact of biocontrol on trophic dynamics in the natural settings (Simberloff and Stiling 1996, Pearson and Callaway 2003, Hoodle 2004, Raghu and Dhileepan 2005), few such natural ecosystem experiments can be found in the published literature. In a study by Pearson et al. (2006), an herbivorous biocontrol agent (*Urophora* spp.) for knapweed, an introduced species, led to an increase in abundance of deer mice (*Peromyscus maniculatus*). It is suggested that this response is due to the mice feeding on the pupae of the biocontrol. This is an example of biocontrol causing a bottom-up trophic cascade that increased predators. Similarly, scientists have hypothesized that mice, birds and ants in tamarisk stands may be feeding on biocontrol (Dudley 2005, C. J. DeLoach February 2009). Although this trophic interaction may add connectivity to the trophic structure, high levels of predation may also be the reason that biocontrol does not successfully establish in all tamarisk stands. However, where biocontrol has succeeded in tamarisk, the findings from the experiment discussed
above would make it conceivable that a bottom-up cascade could be occurring where predators depend on biocontrol as a food source and increase with their presence and abundance. In another study by Louda et al. (1997) a biocontrol agent (*Rhinocyllus conicus* Froeh) for thistle was used but was found that it also damaged native thistle seeds and indirectly reduced the abundance of *Paracantha culta* (Family: Tephritidae) that frequent such thistles. In this case the trophic impact of the biocontrol was negative even though it was efficient at consuming its target. This study is an example of why knowing the side effects of biocontrol on the trophic structure is necessary for land managers to meet their long-term goal. Illuminating these types of interactions will help managers make an educated decision about the pros and cons of their tamarisk control options.

Bottom-up cascades have also been associated with disturbances to the ecosystem. Nakamura et al. (2005) revealed a bottom-up cascade where heavily damaged willow trees (primary producer) from a flood had an increased abundance of leaf beetle (herbivores), ladybirds, and web-building spiders (predators). In this case the herbivores (and therefore predators) were higher in abundance on the regrowth of the heavily damaged willows compared to the lightly damaged willows. If herbivore biocontrols acts like a disturbance and induces heavy foliar damage to tamarisk, like the flood did to willows, then perhaps herbivores and therefore predators will increase on the regrowth of the tamarisk causing a positive impact to the trophic dynamics of terrestrial insects.

Several theoretical discussions in trophic ecology literature provide some basis for what trophic interactions to expect when herbivorous biocontrol is added to
a monotypic tamarisk stand. Montoya et al. (2006) suggested that the more abundant a species (relative to other members in their trophic unit), the more connected it is within their trophic web and therefore the more robust it is to extinction from disturbance. It has been suggested that spatial and temporal heterogeneity, in natural ecosystems contributes to the trophic spectra by protecting resources from consumer regulation (Polis and Strong 1996, Polis 1999, Boror 2005). Kagata and Ohgushi (2006) suggests that higher order trophic units (omnivores and predators) generally respond in the same direction as the changes in their resources. Ellis et al. (2000) found that predator richness and abundance was higher in monotypic tamarisk stands than in native cottonwood stands. The desired result of adding herbivorous biocontrol to tamarisk is to over-exploit the primary producer. If these suggestions and findings from other literature are applied to monotypic tamarisk stands then the addition of biocontrol to consume tamarisk stands, which have low spatial heterogeneity and high predator richness and abundance, may cause (1) the primary producer to be to be over-exploited leading to a reduction of the predators and omnivores (by using Kagata and Ohgushi 2006 suggestion) or (2) because tamarisk has higher predator diversity and abundance the addition of biocontrol (a disturbance) will only help trophic web by adding more connections between the predators and the herbivorous biocontrol (by using Ellis et al, 2000 findings and Montoya 2006 suggestions). If the desired result from using herbivorous biocontrol is to regulate the ‘resource’, in this case tamarisk, then according to the above suggestions, the direct and indirect impact on higher order trophic units could be negative or positive. In other words, tamarisk simplified the trophic structure with its homogenous nature,
which reduced the trophic structure robustness to disturbance but it also lead to an increase in predators which may protect the system from disturbance.

In order to fully understand how the herbivorous biocontrol may affect the trophic dynamics, it is important to consider the direct effects each trophic unit (predators, omnivores, herbivores, and detritivores) has in the trophic structure. Omnivory, which is very common among detritivores, predators, and intra-trophic competitors (Polis and Strong 1996) adds to trophic complexity and connectivity because it effects multiple players in the trophic spectrum which can have unexpected impacts (Pace et al. 1999, Pimm 1978). Omnivory has been suggested to prevent cascades (Pace et al. 1999) and influence stability (Pimm 1977). Omnivores can be opportunistic, obligatory, or facultative depending on the species, and do not necessarily lead to suppression of prey (Coll and Guershon 2002). Holt (1984) equated the effects of omnivory to the trophic structure similar to that of competition. Herbivorous biocontrol could act as food and/or competition to omnivores, increasing the connectivity and therefore the complexity of the ecosystem. If omnivores play a significant role in the tamarisk ecosystem, then they may be able to reduce the offset the impacts that might be occurring from biocontrol discussed in the previous paragraph.

Detritivores, which had rarely been considered in early theory, play a critical role in processing the detritus in the form of plant matter, considering that the ratio of detritivore to herbivore consumption is 1.7:1.0 of plant matter in a natural ecosystem (Hairston and Hairston 1993). Because herbivorous biocontrol can consume near 100% of the plant foliage within a short time span, they could be indirectly destroying
the food and habitat for detritivores. Several studies have suggested habitat quality (Bultman and Uetz 1984, Gratton and Denno 2003, Ostfeld and Keesing 2000), and in some cases litter complexity has a stronger influence on predators than the abundance of prey. In addition, Finke and Denno (2004) found that increased predator diversity reduced cascades by relaxing the impact on herbivores (higher diversity, more competition). Ellis et al. (2000) found that predators were more diverse in monotypic tamarisk stands than in natural riparian ecosystems. If this is because tamarisk provides better litter habitat as suggested, then biocontrol may negatively impact predators despite the additional food source because it presumably reduces the amount of detritus in the system via consumption. Several theories suggest that the trophic spectra of terrestrial insects will react in various ways to biocontrol based on either: other experiments, models, or trophic theory. However, with the exception of a few (Louda et al. 1997, Pearson et al. 2006), there are no comprehensive published natural ecosystem studies that examine the impact herbivorous biocontrol has on the trophic spectra of terrestrial insects despite the clear benefits from such studies.

Critics of biocontrol are concerned that these organisms may compete with native species and disrupt the trophic dynamics or consume plants other than the target, leaving the invaded ecosystem even further from their natural state than intended (Simberloff and Stiling 1996, Pearson and Callaway 2003, Raghu and Dhileepan 2005). These critics advocate intensive monitoring programs and experiments on the trophic spectrum to determine the full impact of the biocontrol (Hoodle 2003, Raghu and Dhileepan 2005). Studies have shown that little risk exists that D. elongata will consume or survive on plants other than its target, Tamarix spp.
(Milbrath and DeLoach 2005, Lewis et al. 2003, Dudley and Kazmer 2005) but no studies exist that elucidate the relationship between arthropod abundance and diversity and biocontrol. The research presented in this thesis will connect theory about how trophic dynamics could be affected by biocontrol to the actual impact biocontrol has on terrestrial insects in tamarisk stands.
METHODS

Study Sites

To explore the effects of biocontrol on the trophic composition of terrestrial insects in tamarisk I selected two sites (labeled 1 and 2) in Grand County, Utah along the Colorado River, where monotypic tamarisk stands and biocontrol were both present. The first site was located across from Jaycee campground on Highway 279, approximately 4 miles from the intersection with Highway 191. The second site is located approximately 4 miles southwest of where Highway 128 historically crossed the Colorado River at Dewey Bridge (Figure 1). A narrow ribbon of well established, dense tamarisk runs between the Colorado River and the highway at both sites. The majority of the vegetative biomass at both sites is tamarisk. Each site met two additional criteria: 1) the tamarisk stands are parallel to the Colorado River and extend at least 100 continuous meters, with ninety percent defoliation; and 2) an additional continuous 100 meters are at least ninety percent covered with green tamarisk foliage and have D. elongata larva present. I assumed that 1) if the tamarisk was mostly defoliated then the biocontrol had over-wintered at that location and had been present for at least one previous season; and 2) if the biocontrol were present but there was minimal sign of foliage damage, than biocontrol had not been present in previous season(s). I set up the sites on 15-June-2007, which was the beginning of the active season for D. elongata.
For each site, I established two 100 m transects: one where insects appear to have been interacting with biocontrol for at least one previous season due to the obvious presence of biocontrol and defoliated trees 15-June-2007 (henceforth referred to as “P”), and one where terrestrial insects were assumed to have not been interacting with biocontrol in the previous season due to low levels of defoliation and biocontrol on 15-June-2007 (henceforth referred to as “N”). It is important to note, however, that on 15-June-2007, when site selection occurred, there were no sites available in the region where we were studying that were free of *D. elongata*. Thus, no control (a site at which no biocontrol were present) site was established.
**Figure 1** Field sites on the Colorado River in Utah, USA. Site 1 is along Highway 279 and Site 2 is along Highway 128. Satellite imagery of the state taken from Google Earth (© 2009 –Digital Globe Image, Image of State of Utah, USDA Farm Service Agency, ©2009 Tele Atlas) and the close up image of the sites are taken from Google Maps (©2009 – Google Imagery ©2009 TerraMetrics, Map data ©2009 Tele Atlas).

**Field Sampling**

I determined the richness and abundance of active terrestrial insects by establishing 160 pitfall traps in pairs along the four 100-meter transects. Transects paralleled both the river and the edge of the tamarisk stand. I installed paired pitfall traps halfway between the canopy edge and the base of tamarisk trees at five-meter intervals along each of the four transects (see Figure 2), yielding 20 paired pitfall traps per transect. I placed the pitfall traps below the tamarisk canopy, with each trap within a pair approximately 1 meter apart. On the rare occasion that a tamarisk tree
and canopy was not present at the five-meter interval, the interval was skipped and pitfall traps were installed at the next five-meter interval where tamarisk was present. Transect length was adjusted accordingly so that 20 pairs of pitfall traps were installed beneath the tamarisk canopy.

![Diagram of tamarisk stand and Colorado River with transects and pitfall traps](image)

**Figure 2** Example of two transects with pairs of pitfall traps beneath the tamarisk canopy. Each transect was 100 meters long with stations located every 5 meters.

Each pitfall trap consisted of two 16-ounce plastic cups, one placed inside of the other. The cups were submerged in the ground so that the lip of the cup was even with the soil level. The innermost cup was filled with 4-6 ounces of propylene glycol to preserve the insects for collection during periodic field visits. Ceramic tiles supported on each corner by a 4-centimeter-tall nail sheltered each cup to prevent rain- and litter-fall from compromising samples (Figure 3). This style of pitfall trap is consistent with the design of Barber (1931) and is commonly used to trap invertebrates.

Sites were established on 15-June-2007 and visited 4 additional times to collect the insects from the pitfall traps: 26-June-2007, 9-July-2007, 2-August-2007, and 16-August-2007. At each of these visits, insects were removed from the propylene glycol in each pitfall trap and placed in a labeled vial with 70% ethanol.
solution. To remove the insects, a fine wire mesh strainer was used to separate the insects from the propylene glycol, which were then funneled from the strainer to the vial. Insects from the pair of pitfall traps at each station were pooled into the same vial. At each visit (except for the last visit on 16-August-2007 when pitfall traps were removed) we refilled the propylene glycol in each of the pitfall traps and reset the ceramic tile. All 80 pairs of pitfall traps were in operation for a total of 62 days.

![Figure 3](image)

**Figure 3** Cross section of one pair of pitfall traps. For clarity, only one cup is shown; two cups, one nested within the other, were used for each pitfall trap (see text for description). Images taken from www.tolweb.org and www.img.tfd.com.

Due to the high abundance of insects collected from the pitfall traps, data sufficient for analysis was available from the first ten pairs of pitfall traps on each transect, for each visit. All organisms in the class Insecta were sorted and counted to
morphospecies (Oliver and Beattie 1996) with a microscope, followed by expert or specialist identification to the lowest taxonomic level possible. In nearly all cases, insects were identifiable to at least genus. Spiders (Order: Araneae) were not identifiable beyond order due to their fragility and the processing technique used. Because spiders have been found to be higher richness and abundance in tamarisk stands compared to native stands (Ellis et al. 2000), they may be playing a critical role as a predator and therefore were counted for abundance and treated as a singular group within the trophic unit, predators. Mites (Order: Araneae, Suborder: Acari) and isopods (Order Isopoda, Family: Armadillididae) were also observed regularly in the pitfall traps. Unlike spiders, which have been suspected as having a significant trophic role as a primary predator for *D. elongata*, there is no previous literature that alludes to a relationship(s) between *D. elongata*, mites, and/or isopods. Because they are not in the class Insecta, and therefore outside of the scope of this study, they were treated like all other organisms not in the class Insecta and were not counted or identified beyond the above mentioned taxonomic level.

Each identified terrestrial insect and spider was assigned to a trophic unit. The trophic units consisted of predators, detritivores, herbivores, omnivores, and liquid feeders (organisms that feed on honeydew). For this study, liquid feeders (in this case two specific species of ants) were categorized into their own trophic unit because they may exert a trophic effect on par with predators, but do not directly feed on other organisms. With these data I determined the richness and abundance of insects from each of the pairs of pitfall traps at each transect for each of the visits. My pitfall traps collected high numbers of *D. elongata* in the larval and adult stages.
\textit{D. elongata} were counted and separated into three categories: larva, adult, and total. These data were used to calculate the abundance of \textit{D. elongata} at each pair of pitfall traps and for each transect at each time-point.

Trophic dynamics were measured in terms of trophic unit abundance and richness and, abundance of common families. A family was considered common if it had more than one-hundred individuals present throughout the season over all transects. Although evaluating the abundance and richness of trophic units will detect trophic shifts in response to biocontrol, trophic interactions happen on a taxonomically-finer scale (community or species level) that would not be detected at the trophic level (Pace et al. (1999) and Polis et al. (2000) offer a review and discussion on this topic). In order to detect such responses, I also evaluated the reactions of the common families to biocontrol. Families that were considered common were: Blattellidae, Carabidae, Cryptophagidae, Elateridae, Formicidae, Gryllidae, Histeridae, Lygeaede, Ptinidae, Rhaphidophoridae, Tenebrionidae, and Araneae. Spiders were treated as one group in the family abundance data and as predators in the trophic abundance data.

\textit{Data analysis}

To address the question, ‘Is biocontrol (\textit{D. elongata}) affecting the trophic dynamics of other terrestrial insects?’ I used a correlative approach with \textit{a priori} assumptions about the biocontrol presence in the previous season. A statistical model using Proc MIXED in SAS® 9.2 (2002) was employed to explain each trophic unit abundance and richness and common family abundance as a function of biocontrol abundance. The random effects were ‘site’ and ‘time’ and the fixed effects were
biocontrol status in the previous season (present or not present), biocontrol abundance, and the interaction between previous seasons status and biocontrol abundance. I used repeated measures with ‘transect’ (representing duplicate transects for previous seasons’ biocontrol status [present or not present]) and ‘timepoint’ (representing four pitfall collection dates). I used several covariance structures (variance components, compound symmetry, heterogenous compound symmetry and autoregressive(1)) to model the lack of independence between pitfall traps within a transect and selected the form that gave the smallest Akaike information criterion for the final model. I used the SUBJECT option to set transect as the unit of replication across all four timepoints. To meet the normality assumption required by this type of analysis, all data were adjusted up by one unit and log-transformed.

Several researchers have suggested that members of the Formicidae family consume *D. elongata* (Dudley 2005, C.J. DeLoach February 2009). A large proportion of the insects collected for this study are from this family, so I used a similar statistical model to explain the *D. elongata* abundance as a function of the most common genus in this dataset, *Formica*. In this model, the random variable was ‘site’ while the fixed variables were previous seasons status, biocontrol abundance, and the interaction previous seasons status by biocontrol abundance. A repeated measures analysis identical to that used in the above models was employed.

Using Proc MIXED (SAS® 9.2, 2002) with the repeated measures option creates covariance matrices to calculate the estimated β values. In order to maximize the fit of the matrices to the data, a structure type must be specified in the repeated statement of the SAS code. To determine which covariance structure is most
appropriate, I first ran each model described above with multiple types of covariance structures that could fit the model, and then chose the model with the smallest Akaike information criterion (AIC on the SAS output). This value represents the ‘goodness of fit’ of the covariance matrices by measuring the amount of ‘information lost’ with each structure type. Because the covariance matrix can be incorrectly constructed if the denominator’s degrees of freedom are not controlled during this process, I employed the Satterwaithe approximation method to ensure proper calculation of the denominator’s degrees of freedom. These modeling adjustments follow the recommendations of Littell et al. (2006). Once the appropriate covariance matrices were determined, I modeled each of the trophic units and families to determine significance when \( \alpha = 0.05 \). Appendix 1 contains the raw data and summary tables, Appendix 2 contains the SAS code, and Appendix 3 contains the output for the aforementioned models.
RESULTS

The data collected indicate that biocontrol abundance and the biocontrol status in the previous season (“N” or “P”) lead to different responses from each trophic unit and their associated families. Approximately 66,263 organisms were identified by trophic units and family. Of those, 19,894 were *D. elongata* and 23,768 were in the Formicidae family. Twenty-nine families were identified in the class Insecta. When biocontrol had not been present in the previous season twenty-six families were identified while twenty-three families were identified when biocontrol had been present in the previous season. Of those families, Carabidae, Tenebrionidae, Formicidae, Cryptophagidae and Gryllidae and spiders (Order: Araneae) were the most abundant regardless of biocontrol status. Biocontrol was most abundant at the first collection date and rapidly declined thereafter (Figure 4). Higher biocontrol abundance was found on transects that did not have biocontrol in the previous season compared to the paired transects that did have biocontrol in the previous season. Biocontrol abundance was higher overall at site 2 compared to site 1. Table 1 displays the statistical results for each trophic unit and family. Appendix 1 displays a summary of trophic units’ abundance and biocontrol at each of the transects per timepoint and the abundance of each family when the biocontrol had been present/absent in the previous season.
Figure 4 Mean biocontrol abundance per pair of pitfall traps for all “N” (biocontrol not present in the previous season) or “P” (biocontrol present in the previous season) at each timepoint. The error bar represents one standard error. The biocontrol abundance data was adjusted up by one and log transformed.
Table 1 Mixed-model analysis results to test for significance of the fixed effects [biocontrol abundance, previous season biocontrol status and the interaction] on trophic unit abundance and richness and family abundance when $\alpha=0.05$. Significant p-values are bolded. When $\beta$ is positive for the fixed effect previous season biocontrol status, the trophic unit abundance or richness is higher when biocontrol abundance is not present in the previous season. When $\beta$ is positive for the fixed effect biocontrol abundance, the trophic unit abundance or richness increases with biocontrol abundance. When $\beta$ is positive for the interaction term, biocontrol abundance by previous seasons biocontrol status, the effect of biocontrol abundance is greater when biocontrol had not been present compared to when it had been present.

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<th>$P$</th>
<th>$\beta$</th>
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<td>0.43</td>
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</tr>
<tr>
<td></td>
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<td>3.4</td>
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<td>7.4</td>
<td>0.01</td>
<td>0.38</td>
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<td></td>
<td>Biocontrol abundance</td>
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<td>0.48</td>
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<td>Biocontrol abundance x Previous season biocontrol status</td>
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<td>3.7</td>
<td>0.06</td>
<td>-0.11</td>
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<td>Lygaeidae</td>
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<td>0.08</td>
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<tr>
<td><strong>Omnivores</strong></td>
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<td></td>
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<td>2.0</td>
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<td>0.11</td>
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<td><strong>Liquid Feeders</strong></td>
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<td>Previous season biocontrol status</td>
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<td>1.9</td>
<td>0.18</td>
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<tr>
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<td>Biocontrol abundance x Previous season biocontrol status</td>
<td>1,88.3</td>
<td>0.0</td>
<td>0.90</td>
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</tr>
</tbody>
</table>
**Predators**

Predator richness showed a significant relationship to biocontrol abundance and the biocontrol status in the previous season. When biocontrol had been present in the previous season, the predator richness increases with biocontrol abundance, while when biocontrol had not been present in the previous season, there appears to be no relationship between predator richness and biocontrol abundance (Figures 5). Histeridae abundance increased with biocontrol abundance and was higher when biocontrol had been present in the previous season (Figure 6). Regardless of whether biocontrol had been present in the previous season, Ptinidae abundance increased with biocontrol abundance; however, this response was stronger when biocontrol had been present in the previous season (Figure 7). In this dataset, predator, Carabidae, and Araneae abundance did not respond to the effects of biocontrol abundance or the previous season’s status of biocontrol.
Figure 5 Predator richness in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Predator richness showed a significant relationship with all fixed effects: previous season biocontrol status, biocontrol abundance and the interaction term. The biocontrol abundance data was adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(predator richness + 1) = (1.7)+(0.5) * [log(biocontrol abundance + 1)]; not present, log(predator richness + 1) = (1.7+-0.5)+(0.5+-0.4) * [log(biocontrol abundance + 1)].
Figure 6 Histeridae abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Histeridae abundance showed a significant relationship with the fixed effects: previous season biocontrol status and biocontrol abundance. The biocontrol abundance and Histeridae abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, \( \log(\text{Histeridae abundance} + 1) = (0.1)+(0.1) \times \log(\text{biocontrol abundance} + 1) \); not present, \( \log(\text{Histeridae abundance} + 1) = (0.1+-0.1)+(0.1+-0.04) \times \log(\text{biocontrol abundance} + 1) \).
Figure 7 Ptinidae abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Ptinidae abundance showed a significant relationship with the interaction term (previous season biocontrol abundance status * biocontrol abundance). The biocontrol abundance and Ptinidae abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(Ptinidae abundance + 1) = (0.1)+(0.1) * [log(biocontrol abundance + 1)]; not present, log(Ptinidae abundance + 1) = (0.1+-0.4)+(0.1+0.2) * [log(biocontrol abundance + 1)].

Detritivores

Detritivore abundance showed a significant relationship to biocontrol status in the previous year. Detritivore abundance was higher when biocontrol had been present in the previous season (Figure 8) for most biocontrol densities from the pitfall traps. Blattellidae abundance decreased as biocontrol abundance increased when biocontrol had been present in the previous season (Figure 9). When biocontrol abundance was low and biocontrol had not been present in the previous season, Tenebrionidae abundance was higher than when biocontrol had been present in the
previous season and biocontrol abundance was high (Figure 10). In this dataset, detritivore richness, and Cryptophagidae, Rhaphidophoridae, and Gryllidae abundance did not respond to the effects of biocontrol abundance or the previous season’s status of biocontrol.

**Figure 8** Detritivore abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Detritivore abundance showed a significant relationship with the fixed effect: previous season biocontrol status. The biocontrol abundance and detritivore abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(detritivore abundance + 1) = (1.7)+(0.06) * [log(biocontrol abundance + 1)]; not present, log(detritivore abundance + 1) = (1.7+0.4)+(0.06+-0.1) * [log(biocontrol abundance + 1)].
Figure 9 Blattellidae abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Blattellidae abundance showed a significant relationship with the fixed effects: previous season biocontrol status, biocontrol abundance and the interaction term (previous season biocontrol status * biocontrol abundance). The biocontrol abundance and Histeridae abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(Blattellidae abundance + 1) = (0.0004)+(0.002)*[log(biocontrol abundance + 1)]; not present, log(Blattellidae abundance + 1) = (0.0004+0.8)+(0.002+-0.15)*[log(biocontrol abundance + 1)].
Figure 10 Tenebrionidae abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Tenebrionidae abundance showed a significant relationship with the fixed effect: previous season biocontrol status. The biocontrol abundance and Tenebrionidae abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, \( \log(\text{Tenebrionidae abundance} + 1) = (0.8) + (0.2) \times \log(\text{biocontrol abundance} + 1) \); not present, \( \log(\text{Tenebrionidae abundance} + 1) = (0.8 + 0.4) + (0.2 - 0.2) \times \log(\text{biocontrol abundance} + 1) \).

**Herbivores**

Herbivore richness also showed a significant relationship with biocontrol abundance and the biocontrol status in the previous season. Herbivore richness increased with biocontrol abundance (Figure 11). When biocontrol had not been present in the previous season, the herbivore richness was higher than when biocontrol had been present in the previous season. Elateridae abundance was higher when biocontrol had not been present in the previous season at most of the biocontrol densities found in the pitfall traps compared to when biocontrol had been present in
the previous season (Figure 12). Lygeaidae abundance increased with biocontrol abundance (Figure 13). In this dataset, herbivore abundance did not respond to the effects of biocontrol abundance or the previous season’s status of biocontrol.

**Figure 11** Herbivore richness in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Herbivore richness showed a significant relationship with the fixed effects: previous season biocontrol status and biocontrol abundance. The biocontrol abundance data was adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(herbivore richness + 1) = (1.3)+(0.4) * [log(biocontrol abundance + 1)]; not present, log(herbivore richness + 1) = (1.3+0.9)+(0.4+0.1) * [log(biocontrol abundance + 1)].
Figure 12 Elateridae abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Elateridae abundance showed a significant relationship with the fixed effect: previous season biocontrol status. The biocontrol abundance and Elateridae abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(Elateridae abundance + 1) = (0.04)+(0.04) * [log(biocontrol abundance + 1)]; not present, log(Elateridae abundance + 1) = (0.04+0.3)+(0.04+-0.1) * [log(biocontrol abundance + 1)].
Figure 13 Lygeaidae abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Lygeaidae abundance showed a significant relationship with the fixed effect: biocontrol abundance. The biocontrol abundance and Lygeaidae abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(Lygeaidae abundance + 1) = (0.07)+(0.05) * [log(biocontrol abundance + 1)]; not present, log(Lygeaidae abundance + 1) = (0.07+0.3)+(0.05+0.1) * [log(biocontrol abundance + 1)].

Omnivores

Omnivore and Formicidae abundance and omnivore richness showed a significant relationship to biocontrol abundance. All response variables increased in abundance with biocontrol abundance (Figures 14, 15 and 16). In this dataset, omnivore abundance and richness and Formicidae abundance did not respond to the effects of the previous season’s status of biocontrol.
Figure 14  Omnivore abundance in tamarisk stands under the presence ("P") or absence ("N") of biocontrol during the previous season. Omnivore abundance showed a significant relationship with the fixed effect: biocontrol abundance. The biocontrol abundance and omnivore abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(omnivore abundance + 1) = (1.7)+(0.06) * [log(biocontrol abundance + 1)]; not present, log(omnivore abundance + 1) = (1.7+0.4)+(0.06+-0.1) * [log(biocontrol abundance + 1)].
Figure 15 Formicidae abundance in tamarisk stands under the presence ("P") or absence ("N") of biocontrol during the previous season. Formicidae abundance showed a significant relationship with the fixed effects: biocontrol abundance. The biocontrol abundance and Formicidae abundance data were adjusted up by one and log transformed. Equations for the "P" or "N" from the mixed-model: present, \[
\log(\text{Formicidae abundance } + 1) = (1.8)+(0.09) \times \log(\text{biocontrol abundance } + 1);\]
not present, \[
\log(\text{Formicidae abundance } + 1) = (1.8+-0.2)+(0.09+0.1) \times \log(\text{biocontrol abundance } + 1).\]
Figure 16 Omnivore richness in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Omnivore richness showed a significant relationship with the fixed effect: biocontrol abundance. The biocontrol abundance data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, Omnivore richness = (1.235)+(0.131) *[log(biocontrol abundance + 1)]; not present, Omnivore richness = (1.24+0.09)+(0.13+-0.07) *[log(biocontrol abundance + 1)].

*Formica spp. abundance*

Biocontrol abundance showed a significant relationship with *Formica* abundance (Table 2, Figure 17). Regardless of the status of biocontrol in the previous season, biocontrol increased with *Formica* spp abundance.

**Table 2** Mixed-model analysis results to test for significance of the effect s previous season biocontrol status, *Formica* abundance and the interaction when α=0.05.

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<th>Effect</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>β</th>
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</thead>
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<td><em>Formica</em> abundance</td>
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<td>-0.58</td>
</tr>
<tr>
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<td>1.785</td>
<td>9.2</td>
<td>0.00</td>
<td>0.41</td>
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</table>
Figure 17  *Formica* spp. abundance in tamarisk stands under the presence (“P”) or absence (“N”) of biocontrol during the previous season. Biocontrol abundance showed a significant relationship with the fixed effects: *Formica* abundance, previous seasons biocontrol status and the interaction. The biocontrol abundance and *Formica* data were adjusted up by one and log transformed. Equations for the “P” or “N” from the mixed-model: present, log(bicontrol abundance + 1) = (0.2) + (0.2)[log(*Formica* abundance + 1)]; not present, log(*Formica* abundance + 1) = (0.2 + -0.6) + (0.2 + 0.4)[log(bicontrol abundance + 1)].
DISCUSSION

This study sought to determine if there was evidence that tamarisk biocontrol impacted with the trophic structure of terrestrial insects. There were two items of interest from these results: 1) the reaction of the trophic unit or family to biocontrol abundance and how they related to biocontrol presence/absence in the previous season and 2) the long-term implications biocontrol has on trophic structure of terrestrial insects. I will provide a discussion of my results in this order.

Of the metrics in this study (richness and abundance of trophic units and abundance of common families), predator, omnivore and herbivore richness, and omnivore, Ptinidae, Histeridae, Blattellidae, Lygaeidae, and Formicidae abundance showed a response to changes in biocontrol abundance. I had predicted that abundance of omnivores and predators and the richness of predators would increase with biocontrol abundance because biocontrol would serve as an additional food source. Likewise, I expected that the measured predatory and omnivorous families would follow this trend (Formicidae, Histeridae, Ptinidae, and Carabidae). I predicted that the richness of omnivores would decrease with biocontrol abundance because of competition with biocontrol for tamarisk. My former predictions were supported for omnivore, Ptinidae, Histeridae, and Formicidae abundance but not for omnivore richness; they all increased with biocontrol abundance, suggesting that biocontrol is supporting a larger abundance of some predators and omnivore and
higher diversity of omnivores. For predator richness, the response to biocontrol abundance was conditional on the status of biocontrol in the previous season. When the biocontrol had been present in the previous season, predator richness did increase with biocontrol, suggesting that the duration of biocontrol presence influenced the diversity of predators. I offer a possible explanation for this response in the following pages.

In the predatory family Histeridae, the most common species (in my dataset) is a specialized predator of the genus *Formica* (Family: Formicidae). *Formica* spp. was the most common ant in the Formicidae family (in this dataset) which also increased with biocontrol abundance. An analysis of biocontrol abundance as a function of the omnivorous genus *Formica* showed a strong response regardless of the biocontrol status. This suggests that, as tamarisk researchers have hypothesized (Dudley 2005, C. J. DeLoach February 2009), biocontrol has a strong relationship with ants. This relationship may be predation on biocontrol and/or competition for tamarisk. Therefore, the relationship between biocontrol, Histeridae, and Formicidae (and most likely omnivore abundance because *Formica* compose the majority of this trophic unit) is probably such that Formicidae (mostly the omnivorous genus *Formica* spp.) increases in abundance because of biocontrol consumption, which leads to an increased abundance of Histeridae which consume some Formicidae.

I had predicted that herbivore and detritivore richness and abundance would decrease as biocontrol abundance increased because the food sources for these trophic units would be altered. However, herbivore richness and Lygaeidae abundance (herbivorous family) both increased when biocontrol abundance increased. One
explanation for these responses is that even though the food sources for herbivores and detritivores are changing when biocontrol is added, the biocontrol may be alleviating predation pressure from these groups, allowing them to increase in abundance. Another possibility is that the defoliated tamarisk stems which becomes litter and detritus offer a better habitat and/or food source for herbivores and detritivores than the foliated stems. Although the response of Blattellidae was conditional on the biocontrol status in the previous season, this family was only present in high numbers at one of the four transects in the study (total abundance at the other three transects equals one) therefore I propose that unmeasured variables may be influencing the abundance of this group.

Predator richness was higher when biocontrol had been present in the previous season. Considering that biocontrol abundance was lower when biocontrol had been present in the previous season, this is somewhat counterintuitive, if it is true that multiple predator populations are consuming biocontrol, as I suggested previously. However, this could be explained if there is a time lag between peak biocontrol abundance and peak richness and abundance of predatory groups, where high biocontrol abundance would be observed before (within season or among seasons) the peak in predatory richness and abundance (families and or trophic units). The time lag may exist because (1) some predators are nomadic and time is required to reach locations where biocontrol are abundant, and (2) time is required for the increased food source to lead to higher predatory reproductive rates. Although we do not know what the biocontrol abundance was in the previous season, we can assume that biocontrol abundance was higher (relative to the measured year) during the first year
in which tamarisk was defoliated (this assumption is explained in detail in the following pages), which would explain why predator richness was higher when biocontrol had been present in the previous season. Another possible explanation for higher predator richness when biocontrol had been present in the previous season is that the litter/detritus post-biocontrol defoliation is preferable predator habitat. It has been suggested by Bultman and Uetz (1984) that predators respond to habitat alteration, and Gratton and Denno (2003) found that some predators respond to habitat alterations, regardless of specific food supply changes. Regardless of why predators are more diverse when biocontrol had been present in the previous season, the higher predator richness may explain why the detritivore and Tenebrionidae abundance is lower relative to when biocontrol had not been present in the previous season.

The following is a plausible set of interactions between terrestrial insect groups in terms of the biocontrol status in the previous season and the associated responses to biocontrol abundance. When the biocontrol had not been present in the previous season the tamarisk foliage is healthy and attracts high abundance of *D. elongata* (‘high’ is relative compared to when biocontrol had been present in the previous season). This high abundance of biocontrol attracted a high diversity of predators and abundance of Ptinidae, Histeridae (indirectly), omnivores, and Formicidae. However, because of a time lag between an increase in richness and abundance of some predators and high biocontrol abundance, an increase in predatory richness is not reflected within one season. Here, the predator richness and
abundance of Ptinidae and Histeridae are initially low (compared to when biocontrol had been present in the previous season). When the biocontrol disperse, predators switch prey to detritivores or herbivores. Because the predatory groups have not yet responded to the high levels of biocontrol, the predation pressure is not as high on detritivore abundance, Tenebrionidae, herbivore richness and Elateridae relative to when biocontrol had been present in the previous season.

Alternatively, when the biocontrol had been present in the previous season I assume that tamarisk foliage is less available and attractive to biocontrol. Dudley (2005) and Hudgeons et al. (2007) found a reduction in tamarisk foliage in subsequent seasons of biocontrol. In addition, Cosse et al. (2005) suggested that *D. elongata* are attracted to the pheromone emitted from male *D. elongata*, similar to a chemical produced by tamarisk. Therefore, it seems plausible that if the tamarisk is stressed from previous defoliation, it may not emit this chemical to the same extent or produce the same amount of foliage, which could lead to tamarisk that is less attractive to biocontrol and lower biocontrol abundance. I assume that the same tamarisk stands that had biocontrol present in the previous season, had also been healthier in the previous season, which would have led to higher biocontrol and therefore high richness and abundance of some predators (predator richness and Histeridae and Ptinidae abundance). However, if a time lag exists between when biocontrol abundance is high and when predators increase in richness or abundance than I would expect biocontrol abundance to be low and predator richness and abundance to be high. After the biocontrol disperse, some of these predatory groups
switch prey to Tenebrionidae and Elateridae therefore keeping the abundance of these families lower when biocontrol had been present in the previous season compared to when it had not.

The above explanations imply that the measured effect biocontrol is having on the trophic structure (in terms of trophic units and families) of terrestrial insects in more than one season is to increase the predator richness and decrease detritivore abundance and herbivore richness. However, *Formica* spp. (which compose the majority of the omnivore abundance and richness trophic unit) may be having a strong impact on the biocontrol abundance which, in turn will impact the way biocontrol abundance affect predator and herbivore richness and Histeridae and Lygaeidae abundance. As biocontrol abundance decreases after the initial tamarisk defoliation (as tamarisk dies, or from an increase in *Formica* spp. abundance), the effect that biocontrol has on the trophic units and families of terrestrial insects would also presumably decrease as well. If this reasoning is correct, then biocontrol is self-regulating its effect on the trophic structure of terrestrial insects by not revisiting tamarisk in the same abundance each year and therefore having less impact on the trophic structure of terrestrial insects as the tamarisk diminish. The other possibility is that if high abundance of *Formica* spp. is present then biocontrol will (1) not establish or (2) not have high abundance and therefore have lower impact on trophic responses from terrestrial insects. In other words, the presence of *Formica* spp., especially in high numbers, dampens the effect of biocontrol on local insect populations.
Data and inference suggest that a nonexistent response to the previous season’s status of biocontrol (in terms of detritivore and omnivore richness, and omnivore and predator abundance) and to biocontrol abundance (in terms of omnivore and detritivore richness, and herbivore and predator abundance) occurred for trophic units that are composed of several families which each reacted differently to biocontrol. This type of response creates too much ‘noise’ for a clear response to be evident when looking at these families together as a single trophic unit. Trophic ecologists (Pace et al. 1999, Polis 1999) have cautioned that cascades may happen only rarely at the community level but often at the species level. This result, and the cited work above, suggests that in order to understand the specifics of trophic relationships one must study species-level trophic interactions, which is especially difficult for the case of insects because of their poorly understood dietary habits or habitat requirements. Because each group within a trophic unit (family, genus, or species) is not reacting in the same way to the disturbance (here I refer to biocontrol), the collective response of all member groups acts like a buffer that reduces the chance of a trophic-unit level cascade. In other words, in this multi-family case, the abundance of each group within the trophic unit does not become over-inflated or severely reduced by a disturbance such as biocontrol. Data from this study provide a clear example of this hidden dynamic: Ptinidae (a predator) responded to biocontrol, while predator abundance as a whole (trophic unit) did not.

The manner of biocontrol dispersal, and the speed at which they do so, may also explain why more terrestrial insect trophic unit and family interactions have not been elucidated by this study. The biocontrol may not be present long enough,
regardless of abundance, to establish an effect on other insects, immediate or delayed. Instead, the biocontrol may be impacting terrestrial insects indirectly by changing their habitat through consumption of tamarisk foliage which may lead to a change in quality or quantity of detritus which serves as food (direct impact) and habitat (indirect impact) for multiple trophic units. Although these indirect impacts may have been initiated during the sampling season for this work, their effects may have only been evident after sampling had ceased, and thus not been identified in this study.

Although this study suggests that biocontrol affects some trophic units of terrestrial insects in tamarisk stands, it was limited spatially, temporally, and trophonically (to terrestrial insects by family). To test the robustness of these findings, studies should be conducted over larger spatial and temporal scales in order to confirm the long-term impact of _D. elongata_ on the inferred trophic structure of terrestrial insects. In addition, further research needs to be conducted to test the hypothesis that the duration that biocontrol is present leads to different responses from the terrestrial insect trophic units. As the relationship between the genus _Formica_ and biocontrol abundance demonstrated, the trophic dynamics of terrestrial insects are complex and without simple dependent-independent relationships among trophic units and therefore not easily modeled. Several taxa were observed in the pitfall traps that were not part of the class Insecta and therefore outside of the scope of this analysis. These groups may be playing a role in how terrestrial insects react to biocontrol, but would require a broader and more inclusive study to reveal the magnitude and direction of such relationships.
This study elucidated a response of predators (predator richness and abundance of Histeridae), omnivores (omnivore and Formicidae abundance and omnivore richness), and herbivores (herbivore richness and Lygaeidae abundance) to biocontrol abundance. I have made suggestions to why I think those responses have occurred. However, the relationship of herbivorous biocontrol on the trophic dynamics of terrestrial insects in monotypic tamarisk is complex and highlights the importance of studies that examine the full effect that biocontrol has on our riparian ecosystems. This research is one of the first steps in an attempt to understand the effects of herbivorous biocontrol on the trophic spectra of natural ecosystems. Knowledge from these types of studies adds pieces to the trophic dynamic puzzle and provides land managers with a clearer picture of the side effects of biocontrol.
LITERATURE CITED


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APPENDIX 1

Raw Data and Summary Tables
Abundance for predators, detritivores, herbivores, omnivores, liquid feeders and biocontrol are broken down by site, transect and transect by timepoint. Timepoint is measured in total days the pitfall traps had been set. Total biocontrol abundance included 18,748 larva and 1,146 adults.

<table>
<thead>
<tr>
<th>Trophic Unit Abundance</th>
<th>Predator</th>
<th>Detritivore</th>
<th>Herbivore</th>
<th>Omnivore</th>
<th>Liquid Feeder</th>
<th>Biocontrol Totals (excluding biocontrol)</th>
</tr>
</thead>
<tbody>
<tr>
<td>By Site</td>
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<td></td>
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<table>
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<th>Site-Transect By Transect</th>
<th>Totals (excluding biocontrol)</th>
<th>By Transect</th>
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</thead>
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<td>650</td>
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| 2-Present 10                                     | 32                             |
| 2-Present 24                                     | 23                             |
| 2-Present 48                                     | 31                             |
| 2-Present 62                                     | 14                             |

| 2-Not Present 10                                 | 28                             |
| 2-Not Present 24                                 | 25                             |
| 2-Not Present 48                                 | 31                             |
| 2-Not Present 62                                 | 16                             |

60
Abundance for each family represented in the dataset. ‘Not present’ represents the total abundance of each family at all transects where biocontrol had not been present in the previous season. ‘Present’ represents the total abundance of each family at all transects where biocontrol had been present in the previous season.

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**Order**

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Insect identification list for transects within sites for each collection date. Values represent the abundance of individuals trapped in all pairs of pitfall traps on each transect at each collection date. “N” refers to transects in tamarisk stands when biocontrol had not been present in the previous season and “P” refers to transects when biocontrol had been present in the previous season.

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<th>26-Jun-07 Site 1</th>
<th>26-Jun-07 Site 2</th>
<th>9-Jul-07 Site 1</th>
<th>9-Jul-07 Site 2</th>
<th>2-Aug-07 Site 1</th>
<th>2-Aug-07 Site 2</th>
<th>16-Aug-07 Site 1</th>
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65
APPENDIX 2

SAS output
DetritivoreA

The Mixed Procedure

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Carabidae

The Mixed Procedure

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Convergence criteria met.

| Covariance Parameter Estimates | 70 |
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### Solution for Fixed Effects

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|-----------------|------------|----------|----------------|----|---------|------|---|
| Intercept       |            | 1.3450   | 0.2734         | 2.72 | 4.92    | 0.0201 |
| PrevYrStat      | N          | 0.06470  | 0.1423         | 27.5 | 0.45    | 0.6528 |
| PrevYrStat      | P          | 0        | .              | .    | .       | .    |
| BC_Total        |            | -0.07630 | 0.1022         | 81.3 | -0.75   | 0.4576 |
| BC_Total*PrevYrStat | N    | -0.07087 | 0.1398         | 97   | -0.51   | 0.6133 |
| BC_Total*PrevYrStat | P    | 0        | .              | .    | .       | .    |

### Type 3 Tests of Fixed Effects

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### DetritivoreR

The Mixed Procedure

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Convergence criteria met.

## Covariance Parameter Estimates

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## Solution for Fixed Effects

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Elateridae

The Mixed Procedure

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Convergence criteria met.

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Solution for Fixed Effects

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Type 3 Tests of Fixed Effects

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Rhaphidiphoridae

The Mixed Procedure

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### Covariance Parameter Estimates

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### Fit Statistics

-2 Res Log Likelihood: 97.7
AIC (smaller is better): 117.7
AIC (smaller is better): 119.2
BIC (smaller is better): 104.7

### Solution for Fixed Effects

| Effect               | PrevYrStat | Estimate | Standard Error | DF | t Value | Pr > | |t| |
|----------------------|------------|----------|----------------|----|---------|------|---|---|
| Intercept            |            | 0.1332   | 0.07173        | 3.75| 1.86    | 0.1417|
| PrevYrStat N         |            | 0.07479  | 0.06450        | 3.87| 1.16    | 0.3128|
| PrevYrStat P         |            | 0        | .              | .   | .       | .    |
| BC_Total             |            | -0.01864 | 0.05352        | 39.8| -0.35   | 0.7295|
| BC_Total*PrevYrStat N|            | 0.05654  | 0.06368        | 8.02| 0.89    | 0.4005|
| BC_Total*PrevYrStat P|            | 0        | .              | .   | .       | .    |

### Type 3 Tests of Fixed Effects

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Convergence criteria met.

### Covariance Parameter Estimates

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Solution for Fixed Effects

---

80
### Effect PrevYrStat Estimate Standard Error DF t Value Pr > |t|

| Effect          | Estimate | Standard Error | DF  | t Value | Pr > |t|
|-----------------|----------|----------------|-----|---------|------|
| Intercept       | 1.6887   | 0.4277         | 3.34| 3.95    | 0.0238|
| PrevYrStat      | -0.4906  | 0.1887         | 27.9| -2.60   | 0.0148|
| PrevYrStat      | 0        | .              | .    | .       | .    |
| BC_Total        | 0.4712   | 0.1658         | 41.3| 2.84    | 0.0069|
| BC_Total*PrevYrStat | -0.4345 | 0.1699         | 29.1| -2.56   | 0.0160|
| BC_Total*PrevYrStat | 0       | .              | .    | .       | .    |

### Type 3 Tests of Fixed Effects

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**Ptilinidae**

The Mixed Procedure

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**Class Level Information**

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Convergence criteria met.
### Covariance Parameter Estimates

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### Fit Statistics

- **-2 Res Log Likelihood**: 4.3
- **AIC (smaller is better)**: 24.3
- **AICC (smaller is better)**: 25.8
- **BIC (smaller is better)**: 11.2

### Solution for Fixed Effects

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### Type 3 Tests of Fixed Effects

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OmnivoreA

The Mixed Procedure

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### Solution for Fixed Effects

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LiquidFeederA

The Mixed Procedure

Model Information

Data Set: SASUSER.LOGGEDDATASET

Dependent Variable: LiquidFeederA

Covariance Structures: Variance Components, Autoregressive

Subject Effect: Transect

Group Effect: Timepoint

Estimation Method: REML

Residual Variance Method: None

Fixed Effects SE Method: Model-Based

Degrees of Freedom Method: Satterthwaite

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| Timepoint | 4 |
|          |   |
|          | 10 24 48 62 |

| PrevYrStat | 2 |
|           |   |
|           | N P |

### Dimensions

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Convergence criteria met.

### Covariance Parameter Estimates
Cov Parm | Subject | Group | Estimate
---|---|---|---
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Timepoint | | | 0
Variance | Transect | Timepoint 10 | 0.1174
AR(1) | Transect | Timepoint 10 | 0.2744
Variance | Transect | Timepoint 24 | 0.07098
AR(1) | Transect | Timepoint 24 | 0.3436
Variance | Transect | Timepoint 48 | 0.007787
AR(1) | Transect | Timepoint 48 | -0.02744
Variance | Transect | Timepoint 62 | 0.01048
AR(1) | Transect | Timepoint 62 | -0.1128

Fit Statistics
-2 Res Log Likelihood: -101.6
AIC (smaller is better): -83.6
AICC (smaller is better): -82.4
BIC (smaller is better): -95.4

Solution for Fixed Effects

| Effect | PrevYrStat | Estimate | Standard Error | DF | t Value | Pr > |t|
|---|---|---|---|---|---|---|
| Intercept | | -0.00449 | 0.02260 | 12.1 | -0.20 | 0.8457 |
| PrevYrStat | N | 0.04178 | 0.03056 | 45.4 | 1.37 | 0.1784 |
| PrevYrStat | P | 0 | . | . | . | . |
| BC_Total | | 0.01412 | 0.03232 | 91.4 | 0.44 | 0.6632 |
| BC_Total*PrevYrStat | N | 0.002783 | 0.04201 | 91.6 | 0.07 | 0.9473 |
| BC_Total*PrevYrStat | P | 0 | . | . | . | . |

Type 3 Tests of Fixed Effects

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HerbivoreA

The Mixed Procedure

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### Covariance Structures
- Variance Components, Compound Symmetry

### Subject Effect
- Transect

### Group Effect
- Timepoint

### Estimation Method
- REML

### Residual Variance Method
- None

### Fixed Effects SE Method
- Model-Based

### Degrees of Freedom Method
- Satterthwaite

### Class Level Information

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- Columns in X: 6
- Columns in Z: 6
- Subjects: 1
- Max Obs Per Subject: 160

### Number of Observations
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- Number of Observations Used: 160
- Number of Observations Not Used: 0
### Iteration History

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Convergence criteria met.

### Covariance Parameter Estimates

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### Fit Statistics

- **-2 Res Log Likelihood**: 179.2
- **AIC (smaller is better)**: 195.2
- **AICC (smaller is better)**: 196.2
- **BIC (smaller is better)**: 184.7

### Solution for Fixed Effects

| Effect          | PrevYrStat | Estimate | Standard Error | DF | t Value | Pr > |t| |
|-----------------|------------|----------|----------------|----|---------|------|---|
| Intercept       |            | 0.7451   | 0.1091         | 19.3| 6.83    | <.0001 |
| PrevYrStat      | N          | 0.1385   | 0.1732         | 21 | 0.80    | 0.4328 |
| PrevYrStat      | P          | 0        | .              | .  | .       | .    |
| BC_Total        |            | 0.05598  | 0.07533        | 75.8| 0.74    | 0.4597 |
| BC_Total*PrevYrStat | N | 0.1034   | 0.1177         | 77.1| 0.88    | 0.3824 |
| BC_Total*PrevYrStat | P | 0        | .              | .  | .       | .    |

### Type 3 Tests of Fixed Effects

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The Mixed Procedure

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WARNING: Stopped because of too many likelihood evaluations.

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Cryptophagidae

The Mixed Procedure

**Model Information**

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<td>Group Effect</td>
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<td>REML</td>
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<tr>
<td>Residual Variance Method</td>
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**Class Level Information**

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**Dimensions**

| Covariance Parameters | 10 |
| Columns in X          | 6  |
| Columns in Z          | 6  |
| Subjects              | 1  |
Max Obs Per Subject | 160

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Convergence criteria met.

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<tr>
<td>AICC (smaller is better)</td>
</tr>
<tr>
<td>BIC (smaller is better)</td>
</tr>
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Solution for Fixed Effects

| Effect | PrevYrStat | Estimate | Standard Error | DF | t Value | Pr > |t| |
|--------|------------|----------|----------------|----|---------|------|---|
### Type 3 Tests of Fixed Effects

<table>
<thead>
<tr>
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<th>F Value</th>
<th>Pr &gt; F</th>
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Blattellidae

The Mixed Procedure

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<td>Group Effect</td>
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**Dimensions**

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**Number of Observations**

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Convergence criteria
### Covariance Parameter Estimates

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### Fit Statistics

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### Solution for Fixed Effects

<table>
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### Type 3 Tests of Fixed Effects

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<th>Den DF</th>
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<th>Pr &gt; F</th>
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Formicidae

The Mixed Procedure

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<td>Transect</td>
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<tr>
<td>Group Effect</td>
<td>Timepoint</td>
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<tr>
<td>Estimation Method</td>
<td>REML</td>
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<td>Residual Variance Method</td>
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<td>Degrees of Freedom Method</td>
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**Dimensions**

- Covariance Parameters: 10
- Columns in X: 6
- Columns in Z: 6
- Subjects: 1
- Max Obs Per Subject: 160

**Number of Observations**

- Number of Observations Read: 160
- Number of Observations Used: 160
Number of Observations Not Used 0

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### Solution for Fixed Effects

<p>| Effect       | PrevYrStat | Estimate | Standard Error | DF | t Value | Pr &gt; |t| |
|--------------|------------|----------|----------------|----|---------|------|---| |
| Intercept    |            | 1.8122   | 0.2671         | 1.32 | 6.78    | 0.0548 |
| PrevYrStat   | N          | -0.1774  | 0.1383         | 46.9 | -1.28  | 0.2061 |</p>
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<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
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Gryllidae

The Mixed Procedure

Model Information

- **Data Set**: SASUSER.LOGGEDDATASET
- **Dependent Variable**: Gryllidae
- **Covariance Structures**: Variance Components, Autoregressive
- **Subject Effect**: Transect
- **Group Effect**: Timepoint
- **Estimation Method**: REML
- **Residual Variance Method**: None
- **Fixed Effects SE Method**: Model-Based
- **Degrees of Freedom Method**: Satterthwaite

Class Level Information

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Convergence criteria met.
Covariance Parameter Estimates

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Solution for Fixed Effects

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Type 3 Tests of Fixed Effects

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Histeridae

The Mixed Procedure

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<th>Criterion</th>
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Convergence criteria met.

### Covariance Parameter Estimates

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<th>Group</th>
<th>Estimate</th>
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### Fit Statistics

-2 Res Log Likelihood: -22.1
AIC (smaller is better): -10.1
AICC (smaller is better): -9.5
BIC (smaller is better): -17.9

### Solution for Fixed Effects

| Effect          | PrevYrStat | Estimate | Standard Error | DF  | t Value | Pr > |t| |
|-----------------|------------|----------|----------------|-----|--------|-----|---|
| Intercept       |            | 0.1483   | 0.05063        | 3.08| 2.93   | 0.0592|
| PrevYrStat N    |            | -0.1283  | 0.04293        | 71.4| -2.99  | 0.0038|
| PrevYrStat P    |            | 0        | .              | .   | .      | .   |
| BC_Total        |            | 0.1181   | 0.03978        | 73.7| 2.97   | 0.0040|
| BC_Total*PrevYrStat N | | -0.03717    | 0.04578    | 83.5| -0.81  | 0.4191|
| BC_Total*PrevYrStat P | | 0        | .          | .   | .      | .   |

### Type 3 Tests of Fixed Effects

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<tr>
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<th>Den DF</th>
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<th>Pr &gt; F</th>
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The Mixed Procedure

<table>
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Convergence criteria met.

Covariance Parameter Estimates

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Solution for Fixed Effects
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### Type 3 Tests of Fixed Effects

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Tenebrionidae

The Mixed Procedure

---

**Model Information**

- **Data Set**: SASUSER.LOGGEDDATASET
- **Dependent Variable**: Tenebrionidae
- **Covariance Structures**: Variance Components, Autoregressive
- **Subject Effect**: Transect
- **Group Effect**: Timepoint
- **Estimation Method**: REML
- **Residual Variance Method**: None
- **Fixed Effects SE Method**: Model-Based
- **Degrees of Freedom Method**: Satterthwaite

**Class Level Information**

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<tr>
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<tr>
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Convergence criteria met.

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Araneae

The Mixed Procedure

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Convergence criteria met.

### Covariance Parameter Estimates

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### Fit Statistics

-2 Res Log Likelihood: 13.9

AIC (smaller is better): 33.9

AICC (smaller is better): 35.4

BIC (smaller is better): 20.8

### Solution for Fixed Effects

| Effect                | PrevYrStat | Estimate | Standard Error | DF  | t Value | Pr > |t| |
|-----------------------|------------|----------|----------------|-----|---------|------|---|
| Intercept             |            | 1.1571   | 0.08867        | 5.7 | 13.05   | <.0001 |   |
| PrevYrStat N          | -0.1068    | 0.05463  | 47.6           | -1.95| 0.0566  |       |   |
| PrevYrStat P          | 0          | .        | .              | .   | .       | .    |   |
| BC_Total N            | -0.04598   | 0.04824  | 91.5           | -0.95| 0.3430  |       |   |
| BC_Total P            | 0          | .        | .              | .   | .       | .    |   |
| BC_Total*PrevYrStat N | 0.07087    | 0.05904  | 48.4           | 1.20| 0.2358  |       |   |

### Type 3 Tests of Fixed Effects

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<th>Num DF</th>
<th>Den DF</th>
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111
HerbivoreR

The Mixed Procedure

**Model Information**

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**Class Level Information**

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- Columns in X: 6
- Columns in Z: 6
- Subjects: 1
- Max Obs Per Subject: 160

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OmnivoreR

The Mixed Procedure

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Convergence criteria met.

### Covariance Parameter Estimates

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### Fit Statistics

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AIC (smaller is better) 254.8

AICC (smaller is better) 256.0

BIC (smaller is better) 243.0

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LiquidFeederR

The Mixed Procedure

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Convergence criteria met.

### Covariance Parameter Estimates

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<tr>
<td>AICC (smaller is better)</td>
<td>58.2</td>
</tr>
<tr>
<td>BIC (smaller is better)</td>
<td>51.2</td>
</tr>
</tbody>
</table>

### Solution for Fixed Effects

| Effect            | PrevYrStat | Estimate | Standard Error | DF  | t Value | Pr > |t| |
|-------------------|------------|----------|----------------|-----|---------|------|---|
| Intercept         |            | 0.003748 | 0.04923        | 5.64| 0.08    | 0.9419|
| PrevYrStat        | N          | 0.08663  | 0.06019        | 107 | 1.44    | 0.1530|
| PrevYrStat        | P          | 0        | .              | .   | .       | .    |
| BC_Total*PrevYrStat| N         | 0.007270 | 0.05778        | 88.3 | 0.13 | 0.9002|
| BC_Total*PrevYrStat| P          | 0        | .              | .   | .       | .    |

### Type 3 Tests of Fixed Effects

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
</tr>
</thead>
<tbody>
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<td>107</td>
<td>2.07</td>
<td>0.1530</td>
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<tr>
<td>BC_Total</td>
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<td>90.1</td>
<td>1.15</td>
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<td>BC_Total*PrevYrStat</td>
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<td>88.3</td>
<td>0.02</td>
<td>0.9002</td>
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Formica and total biocontrol

The Mixed Procedure

<table>
<thead>
<tr>
<th>Model Information</th>
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<tbody>
<tr>
<td>Data Set</td>
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<tr>
<td>Dependent Variable</td>
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<tr>
<td>Covariance Structure</td>
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<tr>
<td>Subject Effect</td>
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<tr>
<td>Group Effect</td>
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<tr>
<td>Estimation Method</td>
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<tr>
<td>Residual Variance Method</td>
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<td>Fixed Effects SE Method</td>
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<td>Degrees of Freedom Method</td>
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<tr>
<td>Class</td>
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<tr>
<td>SITE</td>
</tr>
<tr>
<td>Transect</td>
</tr>
<tr>
<td>PITFALLTRAP</td>
</tr>
<tr>
<td>Timepoint</td>
</tr>
<tr>
<td>PREVYRSTAT</td>
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<table>
<thead>
<tr>
<th>Dimensions</th>
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<tbody>
<tr>
<td>Covariance Parameters</td>
</tr>
<tr>
<td>Columns in X</td>
</tr>
<tr>
<td>Columns in Z</td>
</tr>
<tr>
<td>Subjects</td>
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<tr>
<td>Max Obs Per Subject</td>
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</table>

<table>
<thead>
<tr>
<th>Number of Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Observations Read</td>
</tr>
<tr>
<td>Number of Observations Used</td>
</tr>
<tr>
<td>Number of Observations Not Used</td>
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</table>

<table>
<thead>
<tr>
<th>Iteration History</th>
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<tbody>
<tr>
<td>Iteration</td>
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</tbody>
</table>

119
Convergence criteria met.

### Covariance Parameter Estimates

<table>
<thead>
<tr>
<th>Cov Parm</th>
<th>Subject</th>
<th>Group</th>
<th>Estimate</th>
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</thead>
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<tr>
<td>SITE</td>
<td></td>
<td></td>
<td>0.02532</td>
</tr>
<tr>
<td>Residual</td>
<td>Transect</td>
<td>Timepoint 02AUG2007</td>
<td>0.1239</td>
</tr>
<tr>
<td>Residual</td>
<td>Transect</td>
<td>Timepoint 09JUL2007</td>
<td>0.4117</td>
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<tr>
<td>Residual</td>
<td>Transect</td>
<td>Timepoint 16AUG2007</td>
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<tr>
<td>Residual</td>
<td>Transect</td>
<td>Timepoint 26JUN2007</td>
<td>2.2145</td>
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</table>

### Fit Statistics

-2 Res Log Likelihood: 303.5
AIC (smaller is better): 313.5
AICC (smaller is better): 313.9
BIC (smaller is better): 306.9

### Solution for Fixed Effects

<table>
<thead>
<tr>
<th>Effect</th>
<th>PREVYRSTAT</th>
<th>Estimate</th>
<th>Standard Error</th>
<th>DF</th>
<th>t Value</th>
<th>Pr &gt;</th>
<th>t</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
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<td>0.1932</td>
<td>0.1891</td>
<td>5.64</td>
<td>1.02</td>
<td>0.3488</td>
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<tr>
<td>PREVYRSTAT N</td>
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<td>-0.5763</td>
<td>0.2364</td>
<td>86.3</td>
<td>-2.44</td>
<td>0.0168</td>
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<tr>
<td>PREVYRSTAT P</td>
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<td>0</td>
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<td>.</td>
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<td>.</td>
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<tr>
<td>FormicaT</td>
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<td>0.2302</td>
<td>0.08817</td>
<td>64.9</td>
<td>2.61</td>
<td>0.0112</td>
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<tr>
<td>FormicaT*PREVYRSTAT N</td>
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<td>0.4144</td>
<td>0.1363</td>
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<td>3.04</td>
<td>0.0032</td>
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<tr>
<td>FormicaT*PREVYRSTAT P</td>
<td></td>
<td>0</td>
<td></td>
<td>.</td>
<td>.</td>
<td>.</td>
<td></td>
</tr>
</tbody>
</table>

### Type 3 Tests of Fixed Effects

<table>
<thead>
<tr>
<th>Effect</th>
<th>Num DF</th>
<th>Den DF</th>
<th>F Value</th>
<th>Pr &gt; F</th>
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</thead>
<tbody>
<tr>
<td>PREVYRSTAT</td>
<td>1</td>
<td>86.3</td>
<td>5.94</td>
<td>0.0168</td>
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<tr>
<td>FormicaT</td>
<td>1</td>
<td>84.9</td>
<td>36.67</td>
<td>&lt;.0001</td>
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<tr>
<td>FormicaT*PREVYRSTAT</td>
<td>1</td>
<td>78.5</td>
<td>9.24</td>
<td>0.0032</td>
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</tbody>
</table>
APPENDIX 3

SAS Code for best fit models
*SAS code for a repeated measured analysis of the interaction between previous seasons biocontrol status and biocontrol abundance

*PrevYrStat*BC_total for signif dv USING SITE AND TIMEPOINT AS RANDOM

ODS Graphics on;
Ods html file="c:\Final_Model_Output.xls";

c proc sort data= sasuser.loggeddataset;
By Site  Transect Timepoint PitfallTrap;

c Proc Mixed data = sasuser.loggeddataset;
Title "DetritivoreA";
Class site transect pitfalltrap timepoint prevyrstat;
model DetritivoreA = PrevYrStat BC_Total PrevYrStat*BC_Total/ s CL ddfm = satterth outpred=sasuser.detritivoreA;
random site timepoint;
repeated/ group = Timepoint subject = Transect type=AR(1);
run;
quit;

Proc Mixed data = sasuser.loggeddataset ;
Title "Carabidae";
Class site transect pitfalltrap timepoint prevyrstat;
model Carabidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Carabidae;
random site timepoint ;
repeated  / group = Timepoint subject = Transect type=AR(1) ;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset ;
Title "DetritivoreR";
Class site transect pitfalltrap timepoint prevyrstat;
model DetritivoreR = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.detritivoreR;
random site timepoint ;
repeated  / group = Timepoint subject = Transect type=AR(1) ;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset ;
Title "Elateridae";
Class site transect pitfalltrap timepoint prevyrstat;
model Elateridae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Elateridae;
random site timepoint ;
repeated  / group = Timepoint subject = Transect type=AR(1) ;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset ;
Title "Rhaphidiphoridae";
Class site transect pitfalltrap timepoint prevyrstat;
model Rhaphidophoridae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Rhaphidophoridae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=CS;
run;
quit;

proc mixed data = sasuser.loggeddataset;
title "PredatorR";
class site Transect PitfallTrap Timepoint PrevYrStat;
model PredatorRm1 = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.PredatorR;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
run;
quit;

proc mixed data = sasuser.loggeddataset;
title "Ptinidae";
class site Transect PitfallTrap Timepoint PrevYrStat;
model Ptimidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Ptinidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
run;
quit;

proc mixed data = sasuser.loggeddataset;
title "OmnivoreA";
class site Transect PitfallTrap Timepoint PrevYrStat;
model OmnivoreA = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.OmnivoreA;
random site timepoint;
repeated / group = Timepoint subject = Transect type=CS;
run;
quit;

proc mixed data = sasuser.loggeddataset;
title "LiquidFeederA";
class site Transect PitfallTrap Timepoint PrevYrStat;
model LiquidFeederA = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.LiquidFeederA;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
run;
quit;

proc mixed data = sasuser.loggeddataset;
title "HerbivoreA";
class site Transect PitfallTrap Timepoint PrevYrStat;
model HerbivoreA = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.HerbivoreA;
random site timepoint;
repeated / group = Timepoint subject = Transect type=CS;
run;
quit;
Proc Mixed data = sasuser.loggeddataset;
Title "PredatorA";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model PredatorA = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.PredatorA;
random site timepoint;
repeated / group = Timepoint subject = Transect type=CS;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Cryptophagidae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Cryptophagidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Cryptophagidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Blattellidae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Blattellidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Blattellidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Formicidae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Formicidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Formicidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Gryllidae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Gryllidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Gryllidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Histeridae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Histeridae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Histeridae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=VC;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Lygaeidae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Lygaeidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Lygaeidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=CS;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Tenebrionidae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Tenebrionidae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Tenebrionidae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "Araneae";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model Araneae = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.Araneae;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "HerbivoreR";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model HerbivoreR = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.HerbivoreR;
random site timepoint;
repeated / group = Timepoint subject = Transect type=AR(1);
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "OmnivoreR";
Class site Transect PitfallTrap Timepoint PrevYrStat;
model OmnivoreR = PrevYrStat BC_Total PrevYrStat*BC_Total/ ddfm = satterth s CL outpred=sasuser.HerbivoreR;
random site timepoint;
repeated / group = Timepoint subject = Transect type=CS;
Run;
Quit;

Proc Mixed data = sasuser.loggeddataset;
Title "LiquidFeederR";
**SAS Code to test Formica’s relationship to Biocontrol abundance**

ODS Graphics on;
Ods html file="c:\PrevYrStat by Formica abundance and Biocontrol abundance Output.xls";

proc sort;
By Site Transect Timepoint PitfallTrap;

Proc Mixed data = sasuser.formica;
Title "Formica and total biocontrol";
Class site transect pitfalltrap timepoint prevyrstat;
model BiocontrolT = PrevYrStat FormicaT PrevYrStat*FormicaT/ s ddfm = sattherth;
random site;
repeated/ group = Timepoint subject = Transect type=VC;
Run;
Quit;

ODS Graphics off;