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The Conservation and Ecology of Carnivorous Plants

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The Conservation and Ecology of Carnivorous Plants

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree of
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Dedication

I am indebted to numerous people for their help over the past five years. Firstly, I want to thank Jason for accepting me into the lab, treating me as a colleague, greatly helping my development as a scientist, and providing me and my study organisms (mostly my study organisms) with all the fruit flies and pinhead crickets that they desired. I also want to thank my committee members Fred Essig, Gordon Fox, and Peter Stiling for challenging me and casting a critical eye over my research, and Dan Moon for chairing my defense and providing suggestions for my dissertation.

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Abstract

As discussed in Chapter 1, although our understanding of the ecology and evolution of carnivorous plants has greatly improved in recent years, many fundamental questions remain unanswered. Unfortunately, at the present time, many carnivorous plants are increasingly threatened by anthropogenic activities. Indeed, over half of the carnivorous plant species assessed by the International Union for the Conservation of Nature (IUCN) are listed as 'threatened', but the threats to carnivorous plants have not previously been quantified. In Chapter 2, I quantified the conservation threats to carnivorous plant taxa worldwide by searching peer-reviewed literature, and found data on the threats to 48 species of carnivorous plants from nine genera. The most common threat was habitat loss from agriculture, followed by the collection of wild plants, pollution, and natural systems modifications. As I found in Chapter 2, while agrochemical pollution is thought to be an important conservation threat to carnivorous plants, the effects of insecticides in particular on these taxa have not previously been quantified. Therefore in Chapter 3 I tested the effects of commercial and technical grades of three widely used insecticides (carbaryl, lambda-cyhalothrin, and malathion) on survival and the expression of traits associated with carnivory of pink sundews (*Drosera capillaris*) and Venus flytraps (*Dionaea muscipula*) using a combination of lab- and field-based experiments. Commercial grades were generally more harmful than technical grades under lab and

field conditions, but all three insecticides were capable of causing negative effects on the plants within recommended application rates. Pink sundews appeared to be more susceptible to insecticides than Venus flytraps, perhaps because of larger numbers of digestive glands on the leaf surfaces. Given the effects observed, I suggest that the use of insecticides should be carefully managed in areas containing vulnerable carnivorous plant species. For Chapters 4 and 5, I explored the ecological role of carnivorous plants, specifically if they could compete with animals for shared prey resources. In Chapter 4 I characterized the ground-surface spider and arthropod assemblages of two mesic flatwood habitats in Florida, to resolve what the most likely animal competitor was for pink sundews. I identified 31 spider species from 27 genera in 12 families, with wolf spiders (Lycosidae) being the dominant spider family at both sites. Based on their abundance and the behavioral traits they exhibited, I determined that the funnel-web-building wolf spider *Sosippus floridanus* was the most likely potential competitor with pink sundews. Collembola and Formicidae were the most abundant arthropod taxa present, but ground-surface spiders were not strongly associated with any typical prey groups, suggesting that environmental factors might also be important in structuring this community. Subsequently, in Chapter 5 I examined the potential for competition between carnivorous plants and animals by studying dietary and microhabitat overlap between pink sundews and wolf spiders in the field, and by conducting a lab experiment examining the effects of wolf spiders on sundew fitness. In the field, I found that sundews and spiders had high dietary overlap with each other and with the available arthropod prey. Associations between sundews and spiders depended on spatial-scale: sundews and spiders were both found more frequently in quadrats with more abundant

prey, but within quadrats spiders constructed larger webs and located them further away

from sundews as the total sundew trapping area increased. Spiders also constructed

larger webs when fewer prey were available. In the lab, my experiment revealed that

spiders can significantly reduce sundew fitness. All of these results suggest that members

of the plant and animal kingdoms can and do compete. These findings provided

inspiration for Chapter 6, where I explored if phylogenetic distance was a good predictor

of the strength of competition between taxa, using a meta-analytical approach. I

collected data from studies published from 1998-2008 in eight ecology journals using the

keyword 'interspecific competition', gathering a total of 191 effect sizes. I found no

significant relationship between phylogenetic distance and the strength of competition,

contrary to the long-standing assumption that it should be greatest in strength between

closely related species. However, these findings could presently be limited by

publication bias, and I suggest several directions for future research.

Chapter 1: General Introduction

In the late 1800s, Charles Darwin described the Venus flytrap as 'one of the most

wonderful plants in the world', a sentiment regarding this and other carnivorous plant

species that is shared by many of the general public to this day. Surprisingly, however,

scientific interest in carnivorous plants has taken much more time to gain momentum.

Pioneering work by Charles Darwin (1875) and his son Francis Darwin (1878), was the

first to demonstrate the nutritional benefits of capturing animals for carnivorous plants.

Later, Francis Lloyd (1942) completed the first comprehensive text on these plants,

which was followed by occasional papers on different aspects of their biology and

ecology (Chandler & Anderson 1976; Eisner & Shepherd 1965; Fish 1976; van

Achterberg 1973). However, it wasn't until the 1980s and early 1990s that interest in the

ecology of these plants intensified (Givnish 1989; Givnish et al. 1984; Juniper et al. 1989;

Zamora 1990). Although recent work has helped to elucidate much of the ecology of

these plants (Ellison & Gotelli 2001), many questions remain unanswered, particularly

concerning the evolutionary significance of botanical carnivory. Unfortunately, at the

present time, many carnivorous plants are increasingly threatened by anthropogenic

activities.

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As a group, carnivorous plants appear to be more threatened than many other taxa (IUCN 2011), probably because a number of species of these plants are highly endemic and known from only one or two locations. Determining what the threats are to these plants is imperative for developing appropriate management strategies. Consequently, Chapter 2 of this dissertation provides a detailed review of what the most commonly documented threats are to carnivorous plants worldwide. This review of threats allowed me to narrow my focus onto one of the most commonly suggested, but least quantitatively studied, threats, agrochemical pollution. Agrochemicals have been documented as threats to 16 species of carnivorous plants, and in Chapter 3 I explore the effects that three insecticides have on two species of carnivorous plant – pink sundews (*Drosera capillaris*) and Venus flytraps (*Dionaea muscipula*).

In an attempt to explore the ecological role of carnivorous plants, Chapters 4 and 5 examine the interactions between arthropod and carnivorous plant communities. Carnivorous plants are known to exhibit many different interactions with animals, for example as predators, prey, and mutualists. Indeed, the mechanisms of how carnivorous plants attract prey have been thoroughly studied (Bennett & Ellison 2009; Di Giusto et al. 2010; Di Giusto et al. 2008; Jurgens et al. 2009; Schaefer & Ruxton 2008; Zamora 1995), and we also know about herbivory (Eisner & Shepherd 1965; Moon et al. 2008) and mutualisms, with many arthropod species known to inhabit the phytotelms of pitcher plants (Buckley et al. 2010; Rymal & Folkerts 1982). Surprisingly however, the interaction between carnivorous plants and animals as competitors has only been anecdotally suggested (Cresswell 1991), even though small arthropods typically eaten by

carnivorous plants are a food source for many arthropod and vertebrate predators. Before exploring specific interactions between carnivorous plants and animals in a given area, there is a need to establish what taxa are most likely to be interacting with carnivorous plants. Accordingly, in Chapter 4 I examine the arthropod community of mesic flatwoods in Hillsborough County, Florida, and then in Chapter 5, I investigate competitive interactions between common wolf spiders (*Rabidosa rabida* and *Sosippus floridanus*) and pink sundews (*D. capillaris*).

Finally, I return to Darwin as inspiration for my last research chapter. In Darwin's *The Origin of Species* (1859), he suggested that more closely related species should compete more strongly with each other because of similarities in their behavior and morphology. This assumption has persisted in the ecological literature since *The Origin of Species* but has remained virtually untested. In Chapter 5, I show that that distantly related carnivorous plants and wolf spiders compete for arthropod prey. While this result belies Darwin's original hypothesis, it certainly does not overturn the hypothesis because the test was specific to two species and thus lacked generality. To more thoroughly address Darwin's hypothesis, I use a meta-analytical approach in Chapter 6 to test whether phylogenetic divergence time between species is a negative predictor of the strength of their competition. Examining such a relationship is important for both fundamental ecology, in terms of the foundations of competition theory, but also applied ecology, where it could help with predictions of the impacts of invasive species.

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Chapter 2: A Review of the Conservation Threats to Carnivorous Plants

Note to reader

Portions of this chapter have been previously published (Jennings & Rohr 2011) and are utilized with permission of the publisher.

2.1. Introduction

Identifying the conservation threats for taxa can have important management implications. For example, they can guide policy makers to prioritize certain areas of conservation when limited funding is available (Hughey et al. 2003), and also can be used to implement precautionary conservation measures for species which threats have not been directly assessed. While the conservation threats for different groups of mammals (Hayward 2009), birds (Feeley & Terborgh 2008), reptiles (Filippi & Luiselli 2000), and amphibians (Stuart et al. 2004) have been quantified both regionally and globally, less attention has been accorded to other groups, such as flowering plants. Furthermore, of the approximately 268 000 known species of angiosperms, only about three percent have been evaluated by the International Union for the Conservation of Nature (IUCN) (2010). However, of the relatively small number of angiosperm species that have been evaluated, 70 percent are listed as threatened (i.e. vulnerable, endangered, or critically endangered)

(IUCN 2010). One such group of angiosperms for which many species are thought to be imperiled are the carnivorous plants (Schnell 2002).

There presently are around 600 described species of carnivorous plants from 17 genera (Ellison & Gotelli 2009), with new species frequently being described (Cheek & Jebb 2009; Clarke et al. 2003; Clarke & Kruger 2006; Mann 2007). Of the 102 carnivorous plant species (from seven genera) that have been evaluated by the IUCN, seven are listed as critically endangered, 11 are listed as endangered, and 39 are listed as vulnerable (IUCN 2010). Consequently, of these IUCN-evaluated species, 56 percent are considered to be threatened. Although lower than the value for angiosperms as a whole (70 percent), 56 percent is still higher than the value for all taxa (33 percent), or for any evaluated vertebrate group (IUCN 2010). While there have been several species-specific studies regarding carnivorous plant conservation threats, and their threats as a group are often alluded to (Schnell 2002), threats to carnivorous plants have not previously been quantified in any systematic way. In this review, we provide a quantitative description of the conservation threats to carnivorous plant taxa worldwide.

2.1.1. Evolution and ecology of carnivorous plants
Carnivorous plants have arisen from at least six distinct lineages, all having evolved modified leaves specialized for capturing animals (predominantly arthropods) and digesting this prey to acquire nutrients (Albert et al. 1992; Bayer et al. 1996; Cameron et al. 2002; Ellison & Gotelli 2009; Juniper et al. 1989; Rivadavia et al. 2003). Utilizing animals as prey is thought to be an adaptation that carnivorous plants have for living in

moist, nutrient-poor soils (Juniper et al. 1989). Carnivorous plants generally are poor competitors for light and nutrients with non-carnivorous plant species, and therefore the terrestrial species often require fire to reduce the intensity of competition (Brewer 2001; Brewer 2003; Folkerts 1982; Juniper et al. 1989; Kesler et al. 2008). While in temperate regions most carnivorous plants are found in bog and fen habitats, in tropical and subtropical regions some species also inhabit forested areas with drier soils and greater shade (Juniper et al. 1989). Throughout all of these regions, many habitats for carnivorous plants are threatened by various factors such as agriculture, deforestation, drainage, eutrophication, and fire suppression (Brinson & Malvarez 2002; Folkerts 1982; Gardner et al. 2010; Moore 2002; Sodhi et al. 2010; van Diggelen et al. 2006).

Conserving carnivorous plants could also benefit many other taxa. Carnivorous plants often have surprising and sometimes complex interactions with animals aside from obtaining nutrients from them (Clarke et al. 2009; Jennings et al. 2010; Moon et al. 2010; Zamora & Gomez 1996), in some cases forming what are thought to be obligate mutualisms (Anderson & Midgley 2002). For example, pitcher plants are arguably foundation species (Ellison et al. 2005), providing habitat for entire communities of specialists that completely rely on pitcher plants for their existence (Buckley et al. 2010; Rymal & Folkerts 1982). Some species of pitcher plant can even act as refugia for certain amphibians (Das & Haas 2010; Russell 2008). Hence, the loss of carnivorous plants could result in secondary extirpations and extinctions.

Carnivorous plants also seem to provide humans with various ecosystem services. For instance, carnivorous plants consume large quantities of dipterans (Ellison & Gotelli 2009). Many dipterans, such as mosquitoes, midges, deerflies, and horseflies, are human pests that can transmit human diseases. In addition, the aquatic carnivorous plant genus, *Utricularia*, consumes mosquito eggs and larvae (Angerilli & Beirne 1974; Juniper et al. 1989), and even regularly depredates human schistosome miricidia and cercariae (Gibson & Warren 1970). Human schistosomes infect more than 207 million people worldwide, more than 700 million are at risk, and approximately 20 million suffer severe consequences annually (Steinmann et al. 2006). Hence, there is considerable evidence that carnivorous plants reduce human bites from insect pests and perhaps even diminish human disease risk. Consequently, the conservation of carnivorous plants could benefit humans.

2.2. Methods

2.2.1. Data collection

We used three methods to obtain data on threats to carnivorous plants. First, we searched the IUCN Red List database (www.iucnredlist.org) on 5 August 2010 for the presence of all carnivorous plant genera (*Aldrovanda*, *Brocchinia*, *Byblis*, *Catopsis*, *Cephalotus*, *Darlingtonia*, *Dionaea*, *Drosera*, *Drosophyllum*, *Genlisea*, *Heliamphora*, *Nepenthes*, *Pinguicula*, *Roridula*, *Sarracenia*, *Triphyophyllum*, and *Utricularia*). Second, on 10 August 2010 we conducted a search using Web of Knowledge (www.isiknowledge.com) to identify relevant peer-reviewed literature considering the threats to carnivorous plants, using 'carnivorous plants', 'conservation', 'threats', and each genus name as key words.

As we limited our search to peer-reviewed literature, we included both empirical and observational studies that provided an abstract in English. Third, we searched the National Red List database (www.nationalredlist.org) on 7 January 2011 for the presence of all carnivorous plant genera. Once the relevant literature was obtained, we classified any documented threats following the unified scheme proposed by Salafsky et al. (2008). In this scheme there are three hierarchical levels of threats which increase in specificity with each level. For example, there are 11 1st level categories, consisting of: (1) residential and commercial development, (2) agriculture and aquaculture, (3) energy production and mining, (4) transportation and service corridors, (5) biological resource use, (6) human intrusions and disturbance, (7) natural systems modifications, (8) invasive and other problematic species and genes, (9) pollution, (10) geological events, and (11) climate change and severe weather. After threats are assigned to this 1st level, there are further 2nd level categories (between three and six for each 1st level category) into which they can be classified (Salafsky et al. 2008).

2.2.2. Data analysis

We conducted a principal coordinate analysis (PCoA) based on Jaccard's distance to determine the relationship among threat categories, among carnivorous plant species, and between threat categories and species. The analysis was conducted on a matrix that described whether or not there was any evidence that a species was impacted by each of the 11 1st level threats. The ordination analysis was conducted using CANOCO 4.5 (ter Braak and Šmilauer 2002) and the biplot was created using CanoDraw 4.12 to display the ordination results (ter Braak and Šmilauer 2002). The scores were post-transformed so

that correlations of the species and threat categories with the ordination axes could be inferred by perpendicular projection.

To determine which taxa-threat associations were greater than expected by chance, we conducted an ''indicator species analysis'' in PC-ORD v. 5.01 (McCune & Mefford 1999), which follows the general guidelines of Dufrene and Legendre (1997). This analysis was conducted at the genus level given that we did not have replication at the species level and that species within a genus tended to have similar threats. We conducted the analyses on genera with five or more species in the database (*Drosera, Nepenthes, Pinguicula, Sarracenia,* and *Utricularia*) and used Monte Carlo permutation tests to evaluate the significance of the association for each genus, reassigning the sample units to the 11 threat categories 4999 times.

2.3. Results

We found data on the threats to 48 species of carnivorous plant (Table 2.1). The data available spanned nine genera of different growth forms (*Aldrovanda*, *Darlingtonia*, *Dionaea*, *Drosera*, *Drosophyllum*, *Nepenthes*, *Pinguicula*, *Sarracenia*, and *Utricularia*) and covered six continents (Africa, Asia, Australia, Europe, North America, and South America). The number of species with documented threats by continent was highly variable, with threats found for 19 species in North America, 15 species in Asia, seven species in Europe, six species in South America, two species in Africa, and one species in Australia (we found threats for two species on multiple continents). All 11 of the 1st level threat categories proposed by Salafsky et al. (2008) were documented as affecting

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carnivorous plants, as were 17 2nd level categories. However, 2nd level threats were not

equally distributed among all 1st level threats, with some 1st level threats, such as natural

system modifications, having three 2nd level threats (fire and fire suppression, dams and

water management/use, and other ecosystem modifications), while others, such as

geological events, only had one 2nd level threat (avalanches/landslides). Mean number of

2nd level threats per species was 2.9 (range = 1-8), with one species, the green pitcher

plant (*Sarracenia oreophila*), facing eight 2nd level threats. The most common 1st level

threats were agriculture and aquaculture, biological resource use, pollution, and natural

systems modifications (Fig. 2.1A), and consequently they are the only categories we

discuss in detail. Human intrusions and disturbance, and geological events were the two

least common 1st level threats with only one affected species each (Fig. 2.1A). For 2nd

level threats, gathering terrestrial plants from the wild was the most common, affecting

19 species, while recreational activities and avalanches/landslides were the least common

with only one affected species each (Fig. 2.1B).

2.3.1. Principal coordinate analysis

The PCoA revealed that species within a genus often faced similar threats (Fig. 2.2). For

instance, *Sarracenia* species were predominantly affected by natural system

modifications, invasive species, pollution, over-collection, and agriculture; *Utricularia*

species were predominantly affected by pollution; *Drosera* species were predominantly

affected by agricultural activities; and *Nepenthes* species were predominantly affected by

over-collection (Fig. 2.2). The indicator species analyses revealed positive associations

among species in the genus *Sarracenia* and agricultural activities (indicator value [IV] =

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31.6, $p = 0.045$), over-collection (IV = 32.0, $p = 0.039$), invasive species (IV = 46.8, $p = 0.0024$), and pollution (IV = 41.5, $p = 0.011$). We also detected positive associations between *Drosera* species and agricultural activities (IV = 46.0, $p = 0.012$; when excluding *Sarracenia*). Perhaps as a consequence of species within a genus having similar threats, some threats were also positively correlated, with residential and commercial development, natural systems modifications, invasive species, and pollution having positive associations (Fig. 2.2). However, other threats, such as agriculture and aquaculture and biological resource use, did not exhibit close relationships with any other threats.

2.3.2. Agriculture and aquaculture

The most common 1st level threat to carnivorous plants was from agriculture and aquaculture, which affected a total of 24 species (Fig. 2.1A). Agriculture and aquaculture generally involved direct habitat loss through the planting of various crops, but also covered impacts of grazing by animals, and construction of fish hatcheries (though we found no record of any aquacultural threats to carnivorous plant species). The threats were fairly evenly distributed among three 2nd level categories. Specifically, annual and perennial non-timber crops were a threat to 11 species, while wood and pulp plantations and livestock grazing were each threats to 10 species (Fig. 2.1B). Annual and perennial non-timber crop threats covered species from all genera in the review except *Darlingtonia*.

2.3.3. Biological resource use

Biological resource use was the second most common 1st level threat to carnivorous plants, with 21 species affected (Fig. 2.1A). This category covered the collection of wild plants, and also other activities such as logging and wood harvesting that result in direct habitat loss for carnivorous plants. Collection of plants from the wild was the most common 2nd level threat category (affecting 19 species) (Fig. 2.1B), and can exert strong negative effects on populations as collectors often remove larger individuals (Luken 2005). As many carnivorous plants are relatively slow to mature, the persistent loss of older individuals can severely impact the population structure. Collection of wild plants was a particularly common threat for pitcher plants (*Darlingtonia*, *Sarracenia*, and *Nepenthes*) and Venus flytraps (Folkerts 1977; Folkerts 1990; Luken 2005), where they are generally taken to be sold for profit or for private collections. Additionally, some species, such as *Drosera burmanii* and *D. indica*, are often collected for their perceived medical benefits (Jayaram & Prasad 2006).

2.3.4. Pollution

Pollution was the third most common 1st level threat to carnivorous plants, affecting 18 of the species examined (Fig. 2.1A). This category covered different forms of urban waste (solid and water-borne), fertilizer and pesticide run-off, and various industrial pollutants. Some forms of pollution (such as herbicides) can be lethal to carnivorous plants directly, while other forms (such as nutrient addition) have a more indirect effect by degrading the habitat and making conditions more conducive for other plants. Two 2nd level category were found to be a threat to carnivorous plants, that of agricultural and forestry effluents,

and air-borne pollutants (Fig. 2.1B). The category of agricultural and forestry effluents included nutrient loading from fertilizer run-off, herbicide run-off, and soil erosion, and affected 16 of the 18 species. Air-borne pollutants (in the form of nitrogen deposition), were a threat to two other species, *Drosera anglica* (Huntke 2007) and *Sarracenia purpurea* (Gotelli & Ellison 2002). Additionally, eutrophication (typically associated with fertilizer run-off from agriculture) has been implicated in population declines of species such as *Pinguicula vulgaris* (Eysink & De Bruijn 1997), *Utricularia fibrosa* (Morgan & Philipp 1986), and *U. purpurea* (Vaithiyanathan & Richardson 1999).

2.3.5. Natural systems modifications

The fourth most common threat to carnivorous plants was natural systems modifications, affecting 17 species (Fig. 2.1A). The 2nd level threats for this category included fire and fire suppression, dams and water management/use, and other modifications of the natural environment intended to improve human quality of life (Fig. 2.1B). These actions will typically cause carnivorous plant habitat to be degraded, but they can also result in loss of habitat. Indeed, fire suppression and drainage have been implicated as major causes of decline in suitable habitat for many carnivorous plant genera in the southeastern United States, such as *Sarracenia* (Folkerts 1982). For example, fire suppression can be harmful to carnivorous plants as it allows other non-carnivorous plants to encroach and out-compete them for light and nutrients. Water management changes are also capable of severely degrading the habitat for carnivorous plants, as even small drainage ditches can reduce the water level enough so that they are unable to survive. Other natural system modifications found to be threats to carnivorous plants included the addition of lime to

watersheds (Mackun et al. 1994), reduced grazing (Hugot 2009), and reduced mowing (Folkerts 1977).

2.4. Discussion

The most commonly documented threats to carnivorous plants were habitat loss from agriculture, collection of plants from the wild, and pollution. While habitat loss is known to be a major threat to biodiversity worldwide, over-collection in particular seems to be a much greater threat to carnivorous plants when compared with most other taxa (Gurevitch & Padilla 2004). The most common threats to carnivorous plants may also differ considerably even from other plants within the same country. For example, in the United States Wilcove et al. (1998) found that habitat loss and degradation, followed by invasive species, were the most common threats to plant species. In comparison, we found pollution, followed by habitat modification and over-collection to be the most common threats to carnivorous plants in the United States. It is also interesting to note that all of the 11 1st level threat categories proposed by Salafsky et al. (2008) affected carnivorous plants, indicating that a wide range of challenges lie ahead for their conservation. Furthermore, multiple threats were also very common for species which suggests that a holistic approach, targeted at the habitat-level of carnivorous plants, may be required for their successful conservation.

Perhaps unsurprisingly, residential and commercial development, natural systems modifications, invasive and other problematic species and genes, and pollution, were closely associated with one another and often combined to threaten species. Natural

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system modifications, invasive species, and pollution are all likely to be facilitated by urbanization, yet the documented pollution threats were almost exclusively from agricultural and forestry effluents. Thus, carnivorous plants may be affected by effluents at a considerable distance from the source of the pollution. Agriculture, and biological resource use (predominantly collection of plants from the wild), were not closely associated with any other threats. This suggests that the agricultural activities threatening carnivorous plants could be taking place away from urban areas, and additionally indicates that the collection of plants may be more common in undisturbed habitats. Nonetheless, it was surprising to find that agriculture was not more closely associated with natural systems modifications and pollution.

The results from the indicator species analysis suggest that *Sarracenia* spp. are the best indicators of threats from agriculture, over-collection, invasive species, and pollution, while *Drosera* spp. may also be particularly sensitive to agriculture. It seems unlikely that these two genera alone would be indicative of these threats, as they are morphologically very different. Additionally, while our results indicated that *Sarracenia* may be more sensitive to threats than other genera, considerably more research has been conducted on this genus and thus it is likely that their threats have been more thoroughly documented. Therefore, until more studies are conducted on a wider range of genera, it will be difficult to determine whether *Sarracenia* truly is a particularly sensitive genus, or if the results are simply a reflection of a bias in research effort.

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Given the available data on carnivorous plant threats, we suggest three areas of further study. First, we recommend more empirical studies quantifying the effects of pollution on carnivorous plants. Pollution is known to be an important threat to many taxa (Wilcove & Master 2005), yet very little empirical research has been conducted examining its effects on carnivorous plants, even though it was widely documented as a threat. For example, while there has been some research on the effects of an herbicide on aquatic carnivorous plants (Smith & Pullman 1997), no studies have examined their potential effects on terrestrial carnivorous plants. Furthermore, we are not aware of any studies that have examined the effects of insecticides on carnivorous plants. Empirical studies should elucidate the importance of these types of pollutants in carnivorous plant population declines. Second, we believe that it is worth further exploring the potential role of many carnivorous plants as indicator species for ecosystem health. Our rationale is that many species are fairly conspicuous and thus fairly easy to identify, they are often sensitive to changes in environmental conditions such as water levels, and some research has suggested that carnivorous plants can exhibit negative responses to increased levels of nutrients and pollutants (Ellison & Gotelli 2002; Guisande et al. 2000; Moody & Green 2010; Vaithiyanathan & Richardson 1999). Unfortunately, as collection from the wild is a major threat to these plants, their use as indicator species could draw attention to their locations, which could ultimately be counter-productive. Third, we recommend more research to quantify the extinction vulnerability of these taxa. While many carnivorous plant species have been assessed by the IUCN in recent years, the vast majority of species on the Red List are pitcher plants, and there are no representatives from the two most speciose carnivorous plant genera, *Utricularia* and *Drosera*.

However, quantifying extinction risk for carnivorous plants can be complicated by considerable differences in threat statuses at the country-level scale. For example, using the National Red List database (www.nationalredlist.org) we found the threat status of *Utricularia australis* from nine countries ranged from least concern to extinct, and broad ranges in threat statuses were also found for other species such as *Drosera anglica* and *Pinguicula alpina*.

Whilst we are confident that our data collection methods covered the majority of peer-reviewed literature on carnivorous plant conservation threats, we acknowledge several important caveats. Most importantly, there were undoubtedly biases both in the focal species and geographical regions of research, which means that any results extrapolated to all carnivorous plants should be interpreted with caution. For example, while we found 19 species with documented threats in North America, we found only two species with documented threats in Africa, and only one species with any documented threat in Australia. Considering the high diversity of carnivorous plant species found in parts of Africa and Australia, this is almost certainly an underrepresentation of the true threats encountered by species there. Furthermore, there were no documented threats to the genera *Brocchinia*, *Byblis*, *Catopsis*, *Cephalotus*, *Genlisea*, *Heliamphora*, *Roridula*, and *Triphyophyllum*, despite several species from these genera being listed as threatened by the IUCN (IUCN 2010). The biases in focal species and geographical regions of research combined with the relatively small sample size of documented threats, means that there are likely to be many threats that have thus far gone un-documented. However, we are

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hopeful that the present study will stimulate further research into the conservation of these plants.

2.5. Conclusions

Our results clearly demonstrate a need for more research into the threats facing carnivorous plants. Specific documented threats were found for just 48 species, even fewer than the 56 species listed as threatened by the IUCN (2010). Although many carnivorous plants are likely threatened simply because they are highly endemic (often inhabiting isolated bogs or forests), more quantitative data are needed on potential threats actually affecting the remaining 550 or so species. In particular, efforts should focus on those species from underrepresented genera and regions. We are hopeful that our recommendations may actively assist with carnivorous plant conservation, and the present study should draw attention to the dearth of information available for many of these species. Ensuring the conservation of carnivorous plants will not only help maintain the important ecosystem services they provide, but also likely prevent secondary extinctions of other specialist species that rely on them.

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Table 2.1: Carnivorous plant species for which documented threats were found.

Species	1st level threat category*											Reference(s)
	1	2	3	4	5	6	7	8	9	10	11	
Aldrovanda vesiculosa	x	x					x		x			(Adamec 1995; Adamec 2005; Kundu et al. 1996)
Darlingtonia californica				x								(Folkerts 1977)
Dionaea muscipula		x		x	x		x		x			(Folkerts 1977; Luken 2005)
Drosera anglica							x		x			(Huntke 2007)
Drosera brevifolia		x										(Saridakis et al. 2004)
Drosera burmanii	x	x		x			x	x		x		(Jayaram & Prasad 2006)
Drosera cendeensis		x		x								(Duno de Stefano & dos Santos Silva 2001)
Drosera communis		x										(Saridakis et al. 2004)
Drosera filiformis			x									(Freedman et al. 1992; Landry & Cwynar 2005)
Drosera grievei		x										(Lowrie & Marchant 1992)
Drosera indica	x	x		x			x	x		x		(Jayaram & Prasad 2006)
Drosera intermedia			x			x						(Mackun et al. 1994; Rassi et al. 2001)
Drosera montana		x										(Saridakis et al. 2004)
Drosera sp.		x			x							(Duno de Stefano & dos Santos Silva 2001)
Drosera villosa		x										(Saridakis et al. 2004)
Drosophyllum lusitanicum	x	x		x								(Correia & Freitas 2002; Garrido et al. 2003)
Nepenthes alata				x								(Simpson 1995)
Nepenthes ampullaria				x								(Simpson 1995)
Nepenthes bokor	x	x										(Cheek & Jebb 2009)
Nepenthes campanulata	x	x										(Simpson 1995)
Nepenthes clipeata				x								(Simpson 1995)
Nepenthes gracilis				x								(Simpson 1995)
Nepenthes gracillima	x			x								(Simpson 1995)
Nepenthes khasiana		x	x	x	x		x					(Mao & Kharbuli 2002)
Nepenthes northiana			x									(Simpson 1995)
Nepenthes rafflesiana				x								(Simpson 1995)
Nepenthes thai			x									(Cheek & Jebb 2009)
Pinguicula alpina			x		x							(Lilleleht 1998)
Pinguicula corsica						x	x	x				(Hugot 2009)
Pinguicula fontiqueriana		x			x							(Rhazi et al. 2007)
Pinguicula ionantha							x					(Folkerts 1977)
Pinguicula reichenbachiana	x			x	x		x					(de Belair & Diadema 2008)
Pinguicula vulgaris							x		x			(Eysink & De Bruijn 1997)

Species	1	2	3	4	5	6	7	8	9	10	11	Reference(s)
Sarracenia alabamensis subsp. *alabamensis*					x			x	x			(Folkerts 1977)
Sarracenia alabamensis subsp. *wherryi*		x		x								(Folkerts 1977)
Sarracenia alata	x	x		x			x	x	x			(Schnell et al. 2000a)
Sarracenia flava	x	x		x			x	x	x			(Schnell et al. 2000b)
Sarracenia jonesii	x	x		x			x	x	x			(Folkerts 1977)
Sarracenia leucophylla	x	x		x			x	x	x			(Folkerts 1990; Schnell et al. 2000c)
Sarracenia minor	x	x		x			x	x	x			(Schnell et al. 2000d)
Sarracenia oreophila	x	x		x			x	x	x			(Carter et al. 2006; Govus 1987; Schnell et al. 2000e)
Sarracenia psittacina	x	x		x			x	x	x			(Schnell et al. 2000f)
Sarracenia purpurea									x			(Gotelli & Ellison 2002)
Utricularia fibrosa									x			(Morgan & Philipp 1986)
Utricularia purpurea									x			(Vaithiyanathan & Richardson 1999)
Utricularia simulans	x			x		x						(Schnell 1980)
Utricularia sp.									x			(David 1996)
Utricularia striatula										x		(Chaturvedi 2005)

*1st level threat categories correspond to the classification proposed by Salafsky et al. (2008): (1) residential and commercial development, (2) agriculture and aquaculture, (3) energy production and mining, (4) transportation and service corridors, (5) biological resource use, (6) human intrusions and disturbance, (7) natural systems modifications, (8) invasive and other problematic species and genes, (9) pollution, (10) geological events, and (11) climate change and severe weather.
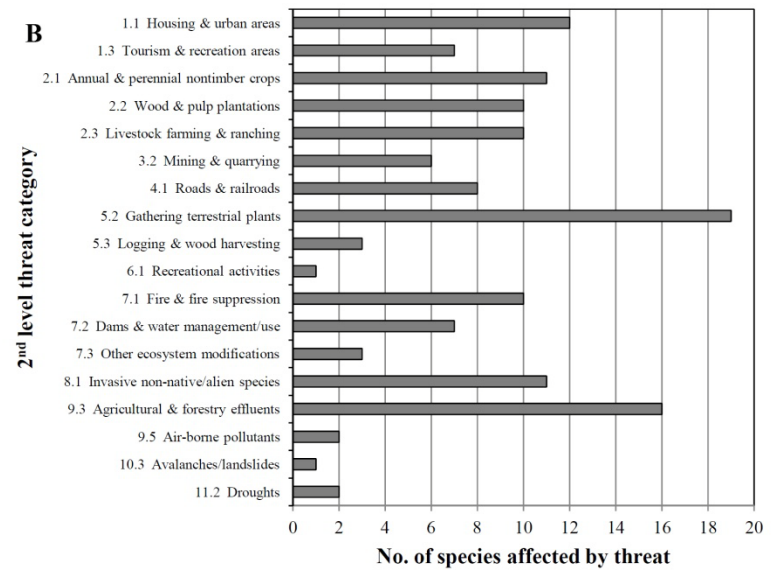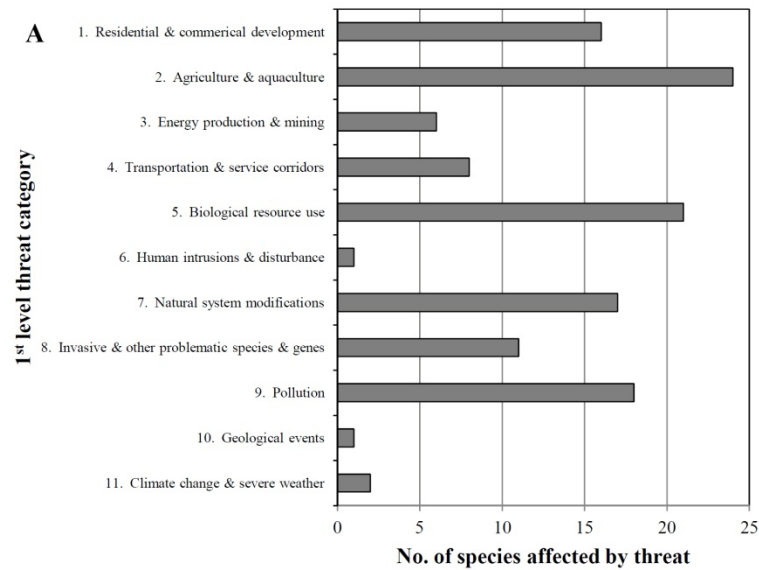
Fig. 2.1: Number of species affected by 1st level threat categories (A), and number of species affected by 2nd level threat categories (B). Numbers in parentheses correspond to the classification proposed by Salafsky et al. (2008).
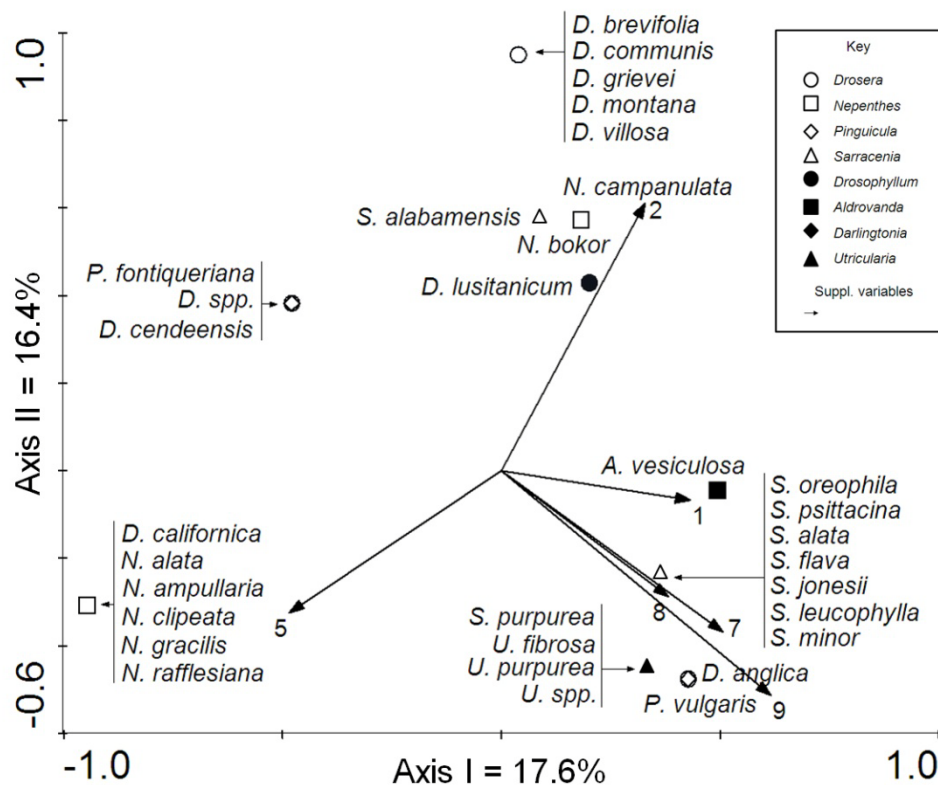
Fig. 2.2: Results of a principal coordinate analysis (based on Jaccard's distance) of the threats to carnivorous plant species. The 20 principal coordinates used in the analysis have been suppressed and the threat categories have been passively (post-hoc) projected into the ordination space. To reduce clutter in the biplot, we have only displayed species with fits of >20% and threat categories with correlation coefficients outside the range of -0.3 to 0.3. The distance of species and threat categories from the origin indicate their relative importance in the biplot. Perpendicularly projecting the threat categories to the axes provides an estimate of the correlation coefficient of that variable with that axis. The angle between threat categories is negatively proportional to the correlation of those threats. Distance among species approximates the dissimilarity of their threats. Each of the numbered 1st level threat categories shown (arrows in the biplot) correspond to the classification proposed by Salafsky et al. (2008): (1) residential and commercial development, (2) agriculture and aquaculture, (5) biological resource use, (7) natural systems modifications, (8) invasive and other problematic species and genes, and (9) pollution.

Chapter 3: Insecticides Reduce Survival and the Expression of Traits Associated

with Carnivory of Carnivorous Plants

3.1. Introduction

Pollution is thought to be one of the main causes of species declines in the United States

(Wilcove & Master 2005). Agrochemicals, in particular, are a widespread source of

pollution, whether through direct application of fertilizers, herbicides, and insecticides, or

through run-off and drift. While many studies have examined the indirect effects of

agrochemicals on non-target organisms (Desneux et al. 2007; Rohr et al. 2006), to the

best of our knowledge, only one previous study has quantitatively examined the effects of

any type of pesticide on carnivorous plants (Smith and Pullman (1997) examined the

effects of an aquatic herbicide on a *Utricularia* sp., among other freshwater plants). This

is surprising given that pollution is often cited as a threat to carnivorous plants (Folkerts

1977; Folkerts 1990; Jennings & Rohr 2011), ostensibly because these plants are

commonly found in wetland areas which frequently accumulate agrochemicals (Clark et

al. 1993; Davis & Froend 1999).

Among the main groups of agrochemicals, herbicides would likely be considered to pose

the greatest threat to non-target plants. However, some insecticides also are known to be

highly phytotoxic and capable of exerting direct negative effects on plants (Gange et al.

1992; Murthy & Raghu 1990; Peterson et al. 1994; Straw et al. 1996). Furthermore, insecticides could exert important indirect negative effects for carnivorous plants in particular, such as a reduction in the abundance of potential prey. Carbaryl, lambda-cyhalothrin, and malathion are three widely used insecticides in the United States (Kiely et al. 2004). Each is used to control adult or larval mosquitoes (Lawler et al. 2007; Milam et al. 2000; Suwanchaichinda & Brattsten 2001) and thus they are regularly applied either directly on or near wetlands that might contain carnivorous plants. Using a combination of lab- and field-based experiments, we quantified the effects of both commercial and technical grades of these insecticides on survival and the expression of traits associated with carnivory of two carnivorous plant species: pink sundews (*Drosera capillaris*) and Venus flytraps (*Dionaea muscipula*). Pink sundews capture insect prey with sticky mucilage secreted from modified leaf trichomes, and they are commonly found in wetland habitats throughout the southeastern United States (Schnell 2002). Conversely, Venus flytraps are limited to wet pine savannas in the Carolinas and are listed as vulnerable by the International Union for the Conservation of Nature (Schnell 2002; Schnell et al. 2000), with pollution often considered a threat (Jennings & Rohr 2011).

Along with most carnivorous plant species, pink sundews and Venus flytraps have small, fragile roots (Adlassnig et al. 2005) and their leaf surfaces are covered in digestive glands (Juniper et al. 1989), both of which could increase their susceptibility to insecticides in comparison to most other plants. Consequently, our hypotheses were as follows: 1) insecticides will directly reduce the survival of carnivorous plants, and 2) given that

carnivorous plants under stress often reduce their expression of traits associated with carnivory (i.e. investment in structures involved in prey capture), surviving pink sundews and Venus flytraps will produce fewer leaves with mucilage, and fewer traps respectively. Quantifying the effects of insecticides on the expression of traits associated with carnivory has important implications for carnivorous plants at the population-level, and at the broader community-level (Clements & Rohr 2009). For example, if insecticides are capable of changing the expression of these traits used by carnivorous plants for prey capture, they could be indirectly affecting the abundance of arthropods frequently utilized as prey.

3.2. Methods

Pink sundews were collected from the University of South Florida Ecological Research Area (ERA), and Venus flytraps were ordered from www.bugbitingplants.com (Venus flytraps are threatened, preventing us from studying them in or collecting them from the field). Plants in all lab experiments were maintained at 23°C under full spectrum lighting (14L/10D) and covered with Plexiglas to maintain humidity. Each experiment (lab- and field-based) ran for four weeks, and survival (plants were considered dead when all structures had turned black) and the expression of traits associated with carnivory (the number of leaves with mucilage and traps for pink sundews and Venus flytraps, respectively) were quantified on a weekly basis.

3.2.1. Experiment i: effects of commercial grade insecticides on pink sundews in the lab

Seventy-two pink sundews (mean diameter 2.28 cm ± 0.59 cm) were planted in

individual 9 cm diameter plastic cups filled to 5 cm with sand, as often they are locally

found in extremely sandy soils. Treatments consisted of a de-ionized (DI) water control

and commercial grades of the insecticides carbaryl (GardenTech® Sevin®), lambda-

cyhalothrin (Spectracide® Triazicide®), and malathion (Spectracide®), with 18

replicates of each of the four treatments. At the start of the experiment, 5 ml of the

appropriate insecticide was applied directly to the sundews using a spray bottle and

following the recommended application instructions on each product. This resulted in

nominal application rates for active ingredient (a.i.) of 9.91 kg/ha (0.126%) for carbaryl,

0.16 kg/ha (0.002%) for lambda-cyhalothrin, and 5.19 kg/ha (0.003%) for malathion (for

comparative purposes, percentages of a.i. per 5 ml are provided in parentheses

throughout). The rates of insecticide application used for this experiment represented an

overspray scenario for mosquito control, but were comparable to the rates used for

control of agricultural pests.

3.2.2. Experiment ii: dose-response of pink sundews to technical grade insecticides in the
lab

To each of five randomly chosen sundews, we applied 99.1 (1.26%), 9.91 (0.126%),

0.991 (0.0126%), or 0.0991 (0.00126%) kg of a.i./ha of carbaryl; 1.6 (0.02%), 0.16

(0.002%), 0.016 (0.0002%), 0.0016 (0.00002%) kg of a.i./ha of lambda-cyhalothrin; or

51.9 (0.03%), 5.19 (0.003%), 0.519 (0.0003%), 0.0519 (0.00003%) kg of a.i./ha of

malathion (based on serial dilutions of the highest concentration). The rates of

insecticide application used in this experiment represented a range of scenarios. The lowest rates were below those typically applied for mosquito control, while the highest rates exceeded those typically used for control of agricultural pests. All insecticides were technical grade (purities > 98%, Chemservice, PA). The highest rate of application of each chemical was one order of magnitude higher than the rates of application for the commercial forms (i.e. active ingredients) used in Experiment i. Additionally, we had five replicates of both DI water and acetone (10%, solvent used to get chemicals in solution) controls, resulting in 14 total treatments and 70 individual plants (mean diameter 2.13 cm ± 0.39 cm). Sundews were planted in individual 9 cm diameter plastic cups filled to 5 cm with sand, and at the start of the experiment, 5 ml of the appropriate insecticide was applied directly to the sundews using pipettes. Pipettes were used in this experiment for logistical purposes, and we are confident that similar amounts of insecticides reached both the plants and the substrate compared to the spray bottles in the other experiments.

3.2.3. Experiment iii: effects of commercial and technical grade insecticides on pink sundews in the field

To determine the ecological relevance of Experiments i and ii, we conducted a field experiment. We established 32 10-cm x 10-cm plots at the ERA, with each plot containing three sundews (mean diameter 5.07 cm ± 1.38 cm). To each of four randomly chosen plots, we applied one of eight treatments: DI water, acetone (10%), or commercial or technical forms of carbaryl, lambda-cyhalothrin, or malathion. At the start of the experiment 5 ml of the appropriate insecticide was applied directly to the sundews using

spray bottles, and there were two subsequent applications after 10 and 20 days (within the range of recommended application frequency). The field plots were slightly larger in area than the plastic cups used in the lab, and our field rates of application for insecticide a.i. per plot were: 6.3 kg/ha (0.126%) for carbaryl, 0.1 kg/ha (0.002%) for lambda-cyhalothrin, and 3.3 kg/ha (0.003%) for malathion. The rates of insecticide application used for this experiment represented an overspray scenario for mosquito control, but were comparable to the rates used for control of agricultural pests.

3.2.4. Experiment iv: effects of commercial and technical grade insecticides on Venus flytraps in the lab

Sixty-four 2-year old Venus flytraps (mean fresh-weight 1.03 g ± 0.41 g) were planted in individual 9 cm diameter plastic cups filled to 5 cm with a mixture of 2/3 peat moss and 1/3 perlite. We used plants of the same age and similar fresh-weight to minimize variation in trap size. To each of eight randomly chosen plants we then applied 5 ml of one of the following treatments using spray bottles: DI water, acetone (10%), or commercial or technical forms of carbaryl, lambda-cyhalothrin, or malathion, using the same concentrations as in Experiment i. There were two subsequent applications of each treatment after 10 and 20 days (within the range of recommended application frequency).

3.2.5. Statistical analyses

For each experiment we first tested for differences between water and solvent (acetone) controls. No significant differences between controls were detected for any experiment (all $p > 0.05$) and, consequently, the controls were pooled together. Survival analyses

were conducted using the Cox proportional hazards model (package 'survival', function 'coxph') in R 2.11.1 (R Development Core Team 2010), and for the survival dose-response in Experiment ii we compared each insecticide treatment to the controls separately. In all survival analyses, we then conducted multiple comparisons between treatments using log-likelihood ratio tests, controlling for the false discovery rate using the Benjamini-Hochberg correction (package 'multtest', function 'mt.rawp2adjp'). We used analysis of covariance (ANCOVA) in Statistica 9.1 to test for the effects of treatments on the difference in the number of traps or mucilage-producing leaves (i.e. the starting number of trap of mucilage-producing leaves minus the final number) with the starting number of traps or mucilage-producing leaves as the covariate. For the dose-response in Experiment ii we compared each insecticide treatment to the controls separately as continuous predictors, and then in separate tests as categorical predictors. All multiple comparisons on the difference in the number of traps or mucilage-producing leaves were made using Dunnett's test in Statistica 9.1.

3.3. Results

3.3.1. Experiment i: effects of commercial grade insecticides on pink sundews in the lab

We found significant effects of treatment on survival ($\chi^2_3 = 18.38$, $p < 0.001$) and the number of mucilage-producing leaves ($F_{3, 67} = 16.21$, $p < 0.001$). Relative to controls (0% mortality), carbaryl (28% mortality; $p = 0.018$) and malathion (66.7% mortality; $p < 0.001$), but not lambda-cyhalothrin (16.7% mortality; $p = 0.056$), significantly reduced survival (Fig. 3.1A). Carbaryl, malathion, and lambda-cyhalothrin significantly reduced the number of mucilage-producing leaves (all $p < 0.001$) (Table 3.1).

3.3.2. Experiment ii: dose-response of pink sundews to technical grade insecticides in the lab

There was a dose-response on survival of carbaryl-treated plants with all but the lowest concentration significantly reducing survival relative to controls, but there was no detected effect on survival for lambda-cyhalothrin- or malathion-treated plants (Fig. 3.1B). Additionally, there were significant dose-responses of carbaryl ($F_{1, 28} = 7.93$, $p = 0.009$) and lambda-cyhalothrin ($F_{1, 28} = 4.3$, $p = 0.048$) on the difference in mucilage-producing leaves, but there was no detected effect on the difference in mucilage-producing leaves for malathion-treated plants ($F_{1, 28} = 1.4$, $p = 0.246$) (Table 3.1).

3.3.3. Experiment iii: effects of commercial and technical grade insecticides on pink sundews in the field

There was a significant effect of treatment on sundew survival ($\chi^2_6 = 20.02$, $p = 0.003$), with the commercial grades of lambda-cyhalothrin (41.7% mortality; $p = 0.035$) and malathion (58.3% mortality; $p = 0.007$) significantly reducing survival relative to controls (4.2% mortality) (Fig. 3.1C). However, there was no significant effect of treatment on the number of mucilage-producing leaves of sundews in the field ($F_{6, 24} = 1.28$, $p = 0.302$) (Table 3.1).

3.3.4. Experiment iv: effects of commercial and technical grade insecticides on Venus flytraps in the lab

There were significant effects of treatment on survival ($\chi^2_6 = 23.64$, $p = 0.001$) and the number of traps per Venus flytrap ($F_{6, 56} = 19.05$, $p < 0.001$). Relative to controls (0% mortality), only commercial grade lambda-cyhalothrin (83.3% mortality; $p = 0.002$) reduced survival (Fig. 3.1D), but commercial grades of both carbaryl ($p = 0.003$) and lambda-cyhalothrin ($p < 0.001$) significantly reduced the number of traps per plant (Table 3.1).

3.4. Discussion

Our results demonstrate that both commercial and technical grade insecticides above, within, and below recommended application levels can be harmful to carnivorous plants, justifying agrochemicals as a common threat to these taxa. Insecticides appeared to act on the plants by causing a dieback of mucilage-producing leaves or traps, which in many cases resulted in the death of the plant (Fig. 3.2). Commercial grades of insecticides were generally more harmful than technical grades, causing significant reductions in sundew and Venus flytrap survival. The more severe effects of commercial grade insecticides could result from their inert ingredients possibly expediting delivery of the insecticide to within the leaf. However, technical grades of insecticide also reduced survival of plants under lab conditions, and frequently caused sub-lethal effects by significantly reducing the expression of traits associated with carnivory.

Pink sundews were generally more susceptible to insecticides than Venus flytraps, although it is important to note that the two species were not directly compared in the same experiment. Pink sundews possess larger numbers of digestive glands on their leaf surfaces than Venus flytraps (Juniper et al. 1989), which could facilitate faster uptake of the insecticides. Considering the sub-lethal effects of insecticides found in both plants, it is possible that there could be long-term consequences of exposure to them. For example, reduced expression of traits associated with carnivory will likely result in fewer prey items being captured, which can subsequently reduce growth and fitness in carnivorous plants (Krafft & Handel 1991). Reduced prey abundance could be an additional indirect effect of insecticides on carnivorous plants, exacerbating their effects on carnivorous traits such as mucilage production. Furthermore, recent evidence has shown that the accumulation of trace metals in invertebrate prey can cause a reduction in the biomass of carnivorous plants (Moody & Green 2010), and similar effects could be caused by insecticides. Given the apparent difference in susceptibility to insecticides between our study species, it would also be prudent to include representatives from a wider-range of carnivorous plant growth forms in future research, such as pitcher plants and fully aquatic species (e.g. many *Utricularia* spp.).

While our results demonstrate that insecticides can be harmful to carnivorous plants, we did not determine the mechanism by which they are damaging the plants. For example, our methods did not allow us to determine exactly which part of the plant is being affected (i.e. leaves or roots), as the insecticides were applied to both the leaves and the substrate. Future research could examine the effects of insecticides when applied

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exclusively to either the leaves or the substrate in which the plants are growing, thereby isolating their effects on each structure. Additionally, pesticides have been shown to cause damage to the mutualistic mycorrhizae of some plants (Ocampo & Hayman 1980), and while these fungi have not been well-studied in carnivorous plants, there is evidence that they are associated with some species (Fuchs & Haselwandter 2004; Quilliam & Jones 2010). If the application of insecticides to the substrate is found to be more harmful than their application to leaves, then their potential effects on the mycorrhizae associated with carnivorous plants should also be investigated. It could also be beneficial to explore the effects of insecticides on these plants at a molecular level, perhaps by examining the response of enzymes and other proteins to exposure.

Relatively few peer-reviewed studies have examined the phytotoxic effects of the three insecticides used in the present study, making it difficult to generalize our results to other plant taxa. However, there is some evidence that all three insecticides can have negative effects on plants. For example, carbaryl has been shown to reduce the growth of barley (*Hordeum vulgare*) (Murthy & Raghu 1990) and can be phytotoxic to aquatic plants (Peterson et al. 1994), lambda-cyhalothrin has been shown to reduce coleoptile growth in rice (*Oryza sativa*) (Moore & Kroger 2010), and malathion has been shown to be phytotoxic to Sitka spruce (*Picea sitchensis*) and cause a reduction in needle size (Straw et al. 1996). In comparison to these previous studies, the more frequently observed lethal effects we found with carnivorous plants could therefore be attributed to their digestive glands, and possibly their smaller size than some of the previously studied plants. Consequently, with a range of organophosphate and pyrethroid insecticides used

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worldwide, broad application of these chemicals could be threatening carnivorous plant species.

3.5. Conclusions

We found that three widely used insecticides can reduce survival and the expression of traits associated with carnivory in carnivorous plants. Given that many carnivorous plant species are found in habitats where insecticides are often directly applied, we recommend longer-term studies on these plants under field conditions to determine the consequences of insecticide exposure at the population-level. Future research should also determine the effects of insecticides on other growth forms of carnivorous plant, such as pitcher plants and aquatic species. Use of these insecticides should be carefully managed in areas containing vulnerable carnivorous plant populations.

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Table 3.1: Summary of the effects of three insecticides on carnivorous traits in pink sundews (PS) and Venus flytraps (VF).

Treatment	Mean difference in mucilage-producing leaves, or traps			
	Experiment i PS (lab)	Experiment ii PS (lab)	Experiment iii PS (field)	Experiment iv VF (lab)
Carbaryl				
99.1 kg/ha		-4.2*** (0.84)		
9.91 kg/ha (commercial)	-8.23*** (3.43)		-10.25 (3.42)	-3.38*** (3.46)
9.91 kg/ha (technical)		-5.4*** (1.52)	-9.08 (2.68)	2 (1.77)
0.991 kg/ha		-5.2*** (1.3)		
0.0991 kg/ha		-2.4 (2.3)		
Lambda-cyhalothrin				
1.6 kg/ha		-4** (1)		
0.16 kg/ha (commercial)	-8.28*** (3.74)		-7.92 (3.06)	-9.25*** (3.96)
0.16 kg/ha (technical)		-3.2** (1.92)	-9.25 (2.67)	0.13 (1.89)
0.016 kg/ha		-2.8* (2.39)		
0.0016 kg/ha		-3* (2.12)		
Malathion				
51.9 kg/ha		-2.4 (2.7)		
5.19 kg/ha (commercial)	-9.39*** (1.31)		-5.92 (3.92)	0.25 (2.25)
5.19 kg/ha (technical)		-3* (3.16)	-8.25 (4.54)	0.38 (3.38)
0.519 kg/ha		-3.6** (2.07)		
0.0519 kg/ha		-2 (2)		
Controls	-1.06 (6.44)	0 (2.49)	-6.5 (3.66)	0.88 (1.36)

Shown are means (SEM) (Dunnett's test: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$).
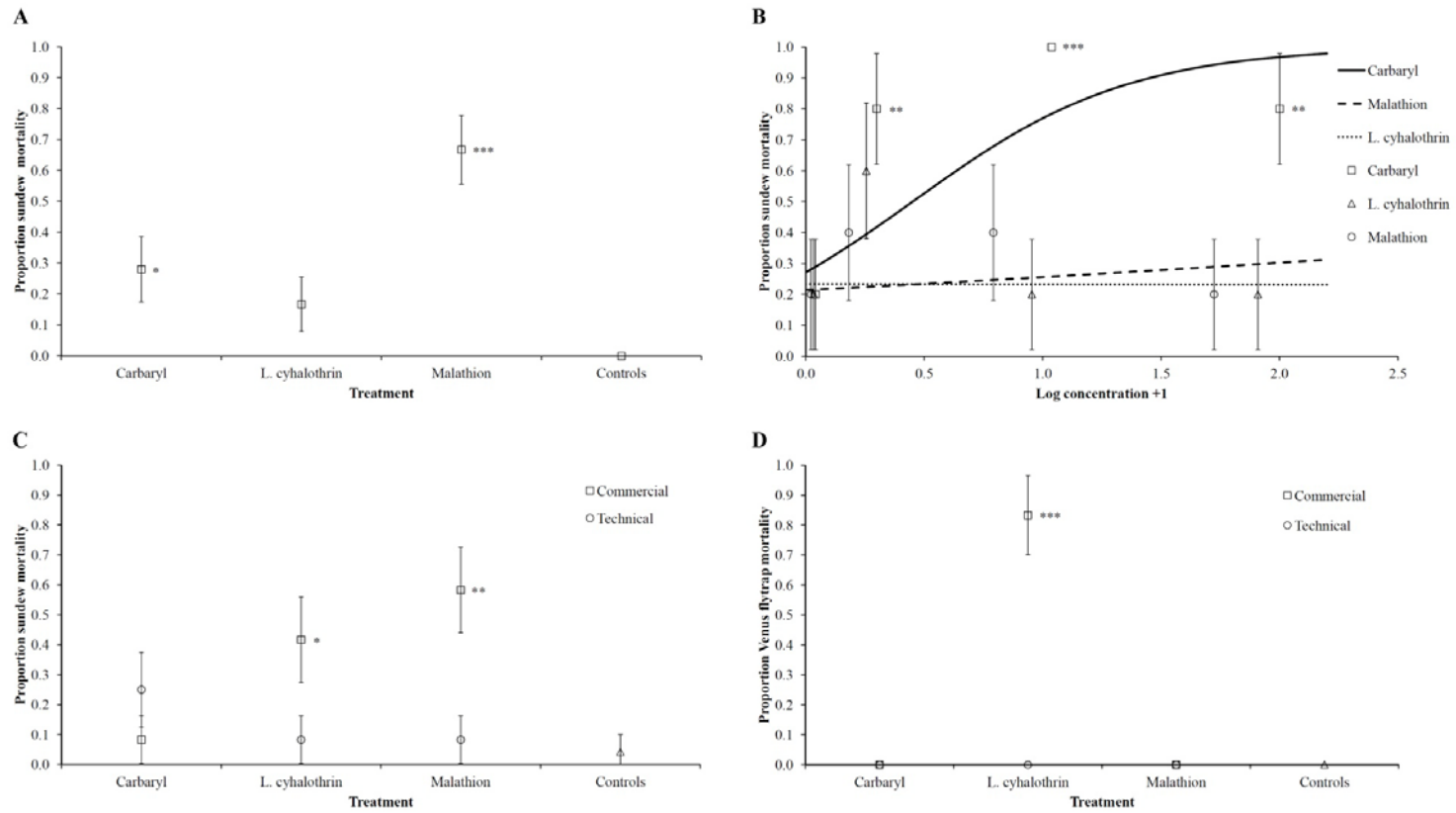
Fig. 3.1: Proportion mortality from Experiments i (A), ii (B), iii (C), and iv (D) (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$). Points represent means and error bars are derived from proportion mortality. Curves for B represent logistic regression.
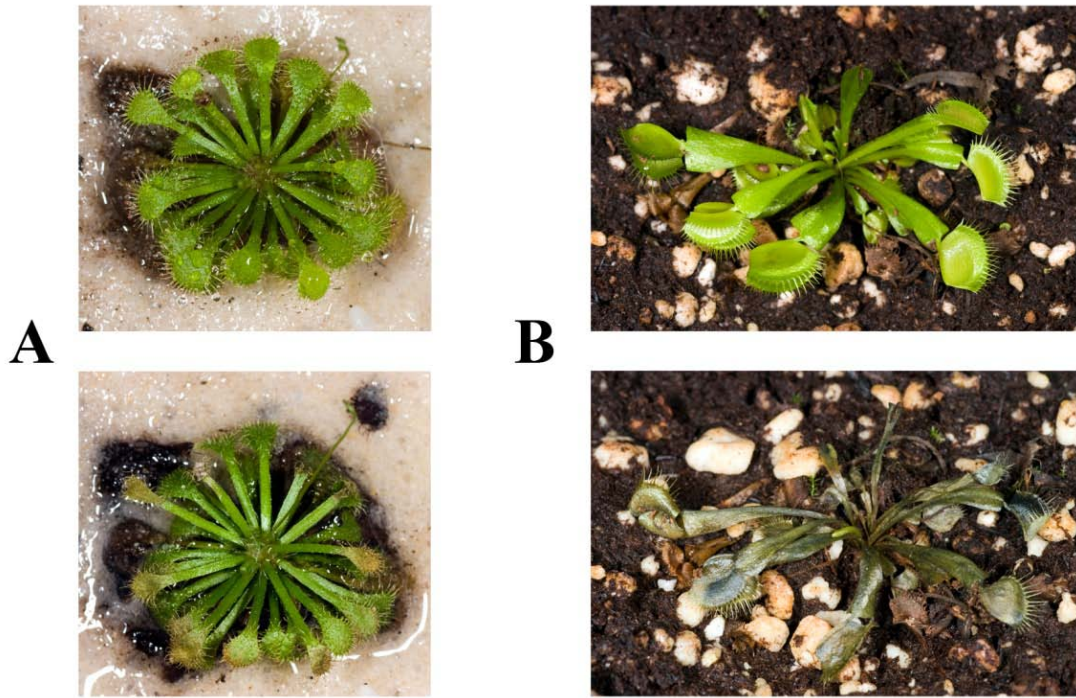
Fig. 3.2: Comparisons of a pink sundew (*Drosera capillaris*) (A) and a Venus flytrap (*Dionaea muscipula*) (B) before and after treatment with commercial grades of carbaryl and lambda-cyhalothrin, respectively.

Chapter 4: Associations between Ground-Surface Spiders and Other Arthropods in Mesic Flatwoods

4.1. Introduction

Mesic (or wet) flatwood habitats are typically dominated by slash pine (*Pinus elliottii*) or longleaf pine (*P. palustris*), and because of the poor drainage of their soils they experience seasonal inundation with water (Harms et al. 1998). Historically these habitats stretched across the Atlantic and Gulf coastal plains of the United States, but increasingly they are threatened by anthropogenic activities and, in recent decades, their range has been greatly reduced (Harms et al. 1998). In addition to their importance economically as a source of timber and fiber, mesic flatwoods are known to support diverse communities of macrofauna (Geneva & Roberts 2009). However, relatively few quantitative data exist on the arthropod assemblages that inhabit mesic flatwoods.

Given that a distinguishing feature of mesic flatwoods is their periodic flooding, the arthropod assemblages found in these habitats could be considerably different from those in nearby xeric or even hydric habitats. Indeed, classical intermediate disturbance theory (Connell 1978; Grime 1973) suggests that such periodic flooding in mesic flatwoods could even lead to higher arthropod diversity than in habitats with more consistent hydrological regimes, and thus they may host a relatively unique arthropod community.

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Collecting baseline data on the arthropod communities in these habitats is therefore important for several reasons. For example, because many arthropod taxa often are sensitive to changes in environmental conditions they can be utilized as indicators of pollution or other anthropogenic disturbances (Kremen et al. 1993; Schweiger et al. 2005), which could be useful for the management of mesic flatwoods. Furthermore, by determining the associations between different arthropod groups in a community at a coarse taxonomic level, it could also be possible to predict changes in the assemblages based on the loss of certain taxa or the type of disturbance.

Spiders in particular have frequently been utilized as indicator taxa because of their abundance and the relative ease with which they can be collected (Buchholz 2010; Shochat et al. 2004; Wise 1993). In addition to being utilized as indicator taxa, spiders can play an important role in many ecosystems because of the top-down effects they exert on their arthropod prey (Riechert & Bishop 1990; Wise 2004), which often includes pest species. Given that exhaustive species surveys of sites often are impractical for taxa such as spiders, using species richness estimators to extrapolate the true species richness for a site could be more useful (Colwell & Coddington 1994). Perhaps most importantly the species accumulation curves could be useful for informing decisions on sampling effort at other sites with similar habitat.

Accordingly, we surveyed arthropods at two relatively undisturbed mesic flatwood sites in Hillsborough County, Florida, with a further focus on ground-surface spiders. Our objectives were as follows: 1) to collect baseline data on the richness and abundance of

ground-surface spiders and other arthropods, 2) to examine the associations among arthropod taxa in the community, and 3) to use species richness estimators to extrapolate the true species richness for ground-surface spiders at these sites.

4.2. Methods

4.2.1. Study sites and sample collection

Our two study sites were Brooker Creek Headwaters Nature Preserve (BCH) (28° 08.32' N, 82° 33.32' W) and the University of South Florida Ecological Research Area (ERA) (28° 04.24' N, 82° 23.44' W). Common flora at both sites include bald cypress (*Taxodium distichum*) and slash pine, while saw palmetto (*Serenoa repens*) and hardwoods such as laurel oak (*Quercus laurifolia*) are occasionally found in patches. While BCH is open to the public and experiences relatively low-levels of anthropogenic disturbance from hiking, the ERA is closed to the public and therefore experiences virtually no anthropogenic disturbance. To collect arthropod samples from these sites, we deployed 10 pitfall-traps filled with 100 ml of soapy-water set 2 m apart along a 10 m transect (two transects per site). These transects were surveyed approximately once every two weeks between July 1st and September 10th 2008 at BCH, and between September 22nd and November 10th 2008 at the ERA, for a total of 16 transect surveys and 160 pitfall-trap samples. Pitfall-traps were left out for 48-hours before the contents were collected and returned to the lab for identification. Spiders were identified to genus or species, and voucher specimens have been placed in the Florida State Collection of Arthropods. Other arthropods were identified to the order level or below. While it would have been desirable to obtain a higher taxonomic resolution for all arthropods, a coarse,

order-level identification could be more useful for management purposes, as there are rarely the funds or expertise to identify many arthropods to genus or species (Rohr et al. 2007).

4.2.2. Statistical analyses

We compared the pooled spider richness and abundance of both sites by generating species accumulation curves and asymptotic richness estimates using the program EstimateS v. 8.0 (Colwell 2005). The species richness estimators we used were: Chao 2, ICE (incidence-coverage based estimator), and Michaelis-Menten means. Frequently there can be considerable variation in the results produced by different estimators, so by using multiple estimators we were able to more effectively evaluate the reliability of their performance (Rohr et al. 2009). The Chao 2 and ICE estimators use the number of uniques and duplicates (species that occur in only one or two samples respectively) to estimate the number of species that were missed in the sampling procedures, while the Michaelis-Menten means estimator is based on the same equation used in enzyme kinetics (Colwell & Coddington 1994). All curves were generated based on the mean of 1000 randomizations of the sample order.

To determine the relationships between the abundances of all arthropod taxa, we conducted a principal coordinate analysis (PCoA) based on Hellinger's distance. The ordination analysis was conducted using CANOCO 4.5 (ter Braak & Šmilauer 2002), and we created the biplot using CanoDraw 4.12 to display the results (ter Braak & Šmilauer

2002). We post-transformed the scores so that the relationships between different arthropod groups could be inferred based on perpendicular projection.

4.3. Results

4.3.1. Spider species richness and abundance

We collected a total of 71 spiders, composed of 31 species from 27 genera in 12 families (24 species at BCH, 15 at ERA) (Table 4.1). Lycosidae was the dominant family at both sites (70.4% of the total spiders at BCH, 56.8% at ERA), followed by Salticidae (6.8% at BCH, 11.1% at ERA) and Tetragnathidae (6.8% at BCH, 3.7% at ERA). Eight species were common to both sites and the most abundant species overall were *Hogna* spp., *Pirata suwaneus*, *Schizocosa humilis*, and *Sosippus floridanus*, all of which are lycosids. To determine guild composition, we followed the general classification of Young & Edwards (1990), who proposed five guilds of spiders based on hunting behaviors: wandering-active, wandering-ambush, web-matrix, web-orb, and web-sheet. The guild of wandering-active spiders was by far the most abundant, comprising 75% and 92.6% of spiders at BCH and the ERA respectively. We found representatives from only two other guilds present: web-sheet spiders (13.6% of spiders at BCH and 3.7% at ERA), and web-orb spiders (11.4% of spiders at BCH and 3.7% at ERA).

4.3.2. Arthropod richness and abundance

Including spiders, we collected a total of 3,001 arthropods (1,591 at BCH, 1,510 at ERA) from 11 taxonomic groups (Actindedida, Araneae, Coleoptera, Collembola, Diptera, Formicidae, Hemiptera, Homoptera, Hymenoptera (excluding Formicidae), Lepidoptera,

and Orthoptera) (Fig. 4.1). Collembola was the most abundant taxa at both sites (58.5%

of the total arthropods at BCH, 60.3% at ERA), followed by Formicidae (29.5% at BCH,

21.6% at ERA). With the exception of Diptera at ERA (9.3%), all other taxa comprised <

3% of the total number of arthropods each for both sites.

4.3.3. Spider species richness estimators

None of the species richness estimators we used reached a clear asymptote, however the

curve generated using Michaelis-Menten means appeared to be closest to approaching

this (Fig. 4.2). The Chao 2 estimator yielded the highest number of species (91), almost

double the number generated by Michaelis-Menten means (53). The ICE estimator

produced a species number that was slightly above the Michaelis-Menten means (67).

We also found that there was always a greater number of uniques than duplicates, with

uniques steadily increasing while the number of duplicates eventually started to decrease.

4.3.4. Principle coordinate analysis

PCoA revealed that arthropod assemblages differed at both sites, particularly driven by

variation in abundance of Diptera and to a lesser extent Orthoptera (Fig. 4.3). Ground-

surface spiders were strongly negatively associated with Diptera, and only weakly

associated with other common prey taxa such as Collembola and Homoptera. Formicidae

also appeared to be negatively associated with Collembola and Homoptera.

4.4. Discussion

At the family level, ground-surface spider diversity and relative abundance was fairly similar to sandhill and xeric or hydric flatwood habitats elsewhere in Florida (Corey et al. 1998; Corey & Taylor 1988; Muma 1973). For example, Muma (1973) found Lycosidae to be the most dominant ground-surface spider family at a hydric pine flatwoods site in central Florida, comprising 64% of the total number of spiders. At another site in central Florida, Corey & Taylor (1988) examined more mesic flatwoods and found that lycosids also dominated the habitat (47.2%), although not quite to the same extent as found by Muma (1973). Our results at the family level are even fairly similar to those of Corey et al. (1998), who examined ground-surface spider assemblages at several sandhill sites and found Lycosidae to be the most dominant family (75.2%). However, at the species level some differences between the communities we examined and those from previously published work by Muma (1973) and Corey & Taylor (1988) become apparent. For instance, we identified nine species of lycosids compared to 13 by Muma (1973), with only three species common to both studies (*Hogna lenta*, *Pirata suwaneus* and *Sosippus floridanus*). Furthermore, of the 15 most common species found in mesic flatwoods by Corey & Taylor (1988), only two were present at our sites (*Ctenus captiosus* and *S. floridanus*). These observed patterns could represent true differences between the communities, but perhaps more likely result from the less intensive sampling we conducted compared to the previous studies of Muma (1973) and Corey & Taylor (1988).

None of our species accumulation curves reached an asymptote, which further suggests that we did not sample all of the ground-surface spider species present at our study sites.

The overall performance of the estimators used was similar to the results of Toti et al. (2000), who examined the species richness of spider assemblages in Appalachian balds and found that the Michaelis-Menten means estimator performed best when judged by their indirect criteria (that the curve was close to reaching an asymptote with fewer samples than the observed species curve, and that the estimates were close to a visual extrapolation of the asymptote of the observed species curve). Based on the performance of the three estimators, it appears as though the true spider species richness is at least 50-70 species (where the ICE and Michaelis-Menten means curves were more closely grouped together). This number seems to be consistent with the more extensive previous surveys in flatwoods by Muma (1973) and Corey & Taylor (1988), who found 55 and 48 species respectively.

We found that ground-surface spiders were not strongly associated with typical prey groups, supporting the idea that environmental factors can have an important influence on spider distribution (Greenstone 1984). However, many other studies have found strong associations between spiders and their prey (Harwood et al. 2001), somewhat contrary to our results. Indeed, even within the same study sites, we have previously found one species of spider (*S. floridanus*) to track the abundance of their common prey (Jennings et al. 2010). Our results could be explained by the fact that the majority of the spiders we collected were lycosids, which generally are not web-builders. Therefore lycosids tend to be more transient (with *S. floridanus* being a notable exception to this) and might not follow their prey as closely.

The associations between other groups of arthropods were not particularly surprising. Collembola and Formicidae were clearly the two most abundant taxa, as has been found in ground-surface habitats elsewhere in Florida (Stiling et al. 2010), and both are known to be mobile foragers in the soil and leaf litter. They were negatively associated with each other, which could have been a result of microhabitat differences. For example, standing water was found at our sites on several occasions during our sampling period and certain groups of Collembola have a high affinity for these types of conditions, which conversely could have been prohibitive to many Formicidae. Diptera was responsible for most of the difference in the arthropod assemblages between our study sites, and the most parsimonious explanation for this is because of seasonal differences. Both study sites are close to lentic water-bodies and they have a similar habitat structure, but the sampling at the ERA was conducted after BCH and therefore may have coincided with increased abundance for certain species, perhaps for breeding events.

4.5. Conclusions

Our study provides baseline data on the ground-surface spider and other arthropod assemblages of mesic flatwoods. The guild structure of the study sites was similar to previous work in other flatwood habitats, being dominated by wandering-active spiders (primarily Lycosidae). The ground-surface spider species accumulation curves indicated that more intensive sampling of these habitats would be required to comprehensively sample and identify all of the species present, but from a management perspective, our results appear to be relatively consistent with previous surveys elsewhere.

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Table 4.1: Spiders collected at Brooker Creek Headwaters Preserve (BCH) and the University of South Florida Ecological Research Area (ERA).

Family/Species	BCH	ERA	Total
Agelenidae			
Baronopsis sp.	1		1
Araneidae			
Gea heptagon	2		2
Corinnidae			
Phrurotimpus alarius		1	1
Ctenidae			
Ctenus captiosus		1	1
Gnaphosidae			
Gnaphosa sericata	1		1
Zelotes sp.	1	1	2
Hahniidae			
Neoantistea magna	2	1	3
Linyphiidae			
Ceratinella sp.	1		1
Ceratinops crenatus	1		1
Meioneta sp.	1		1
Lycosidae			
Allocosa mulaiki	1	2	3
Hogna lenta		1	1
Hogna sp.	6	5	11
Pirata insularis		4	4
Pirata suwaneus	2	5	7
Rabidosa rabida	3		3
Schizocosa humilis	6		6
Schizocosa sp.	2	1	3
Sosippus floridanus	5	1	6
Oonopidae			
Heteroonops spinimanus	1		1
Pisauridae			
Dolomedes sp.	1		1
Pisaurina sp.	1		1
Salticidae			
Habronattus sp.		1	1
Naphrys bufoides		1	1
Neon sp.	1		1
Phidippus sp.	1		1

Family/Species	BCH	ERA	Total
Zygoballus rufipes		1	1
Tetragnathidae			
Glenognatha foxi	1		1
Leucage sp.	1		1
Pachygnatha autumnalis	1	1	2
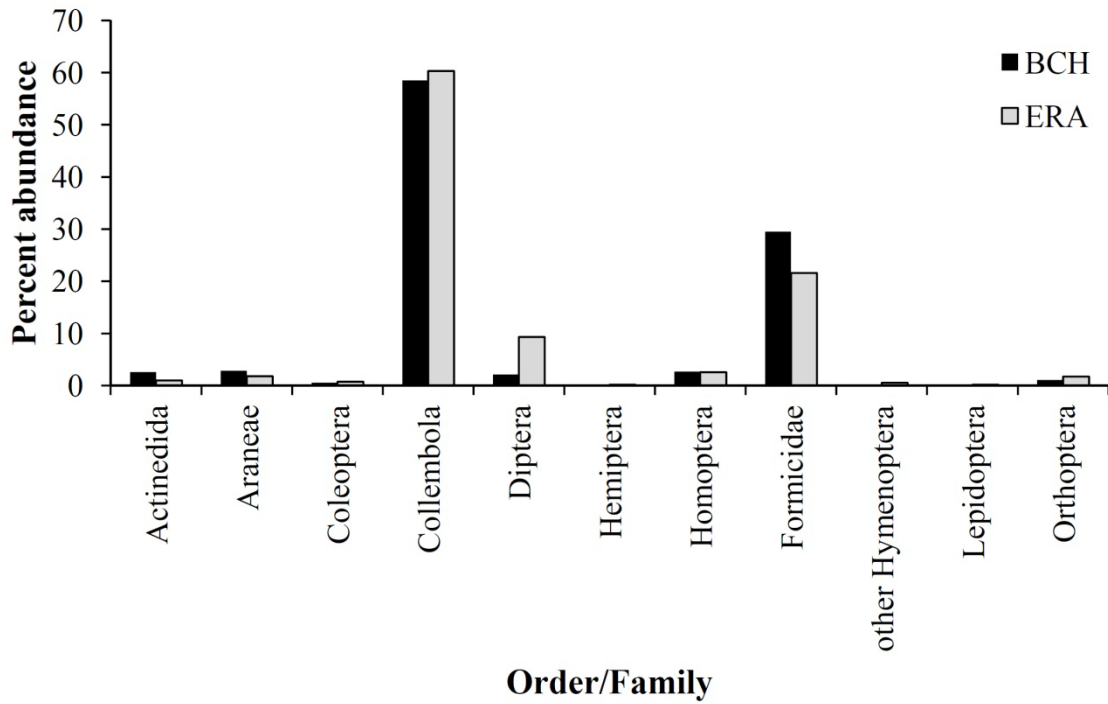
Fig. 4.1: Percent abundance of different arthropod families at Brooker Creek Headwaters Preserve (BCH) and the University of South Florida Ecological Research Area (ERA).
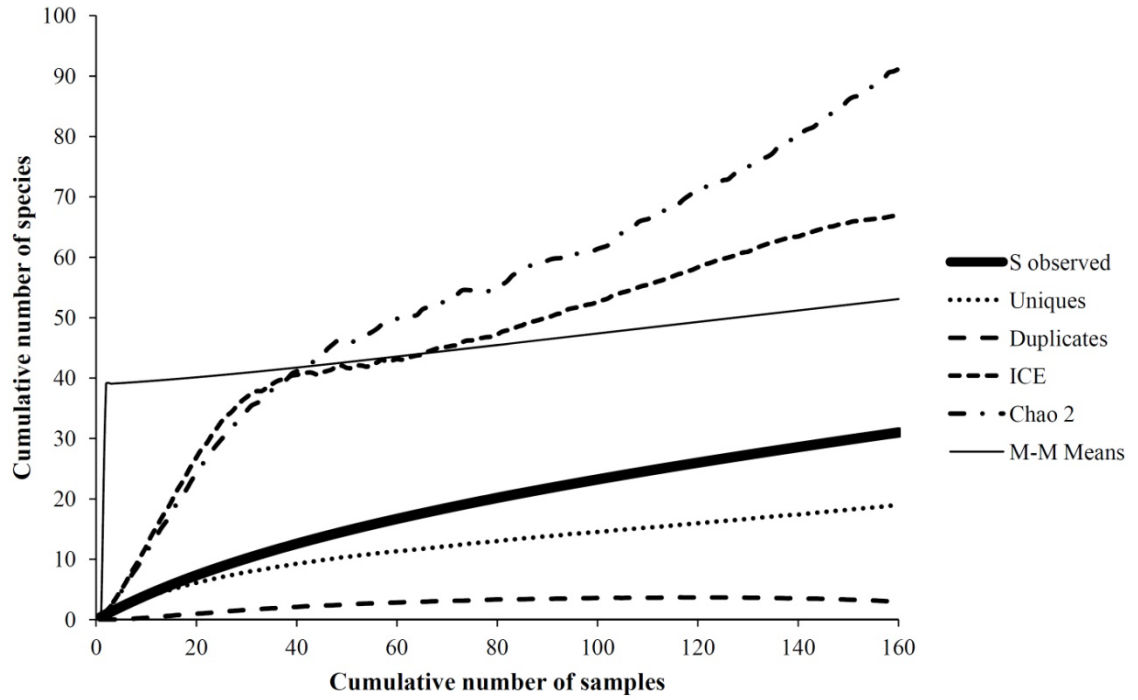
Fig. 4.2: Individual-based spider species rarefaction (S observed), estimated true richness (Chao 2, ICE, and Michaelis-Menten means), and unique and duplicates.
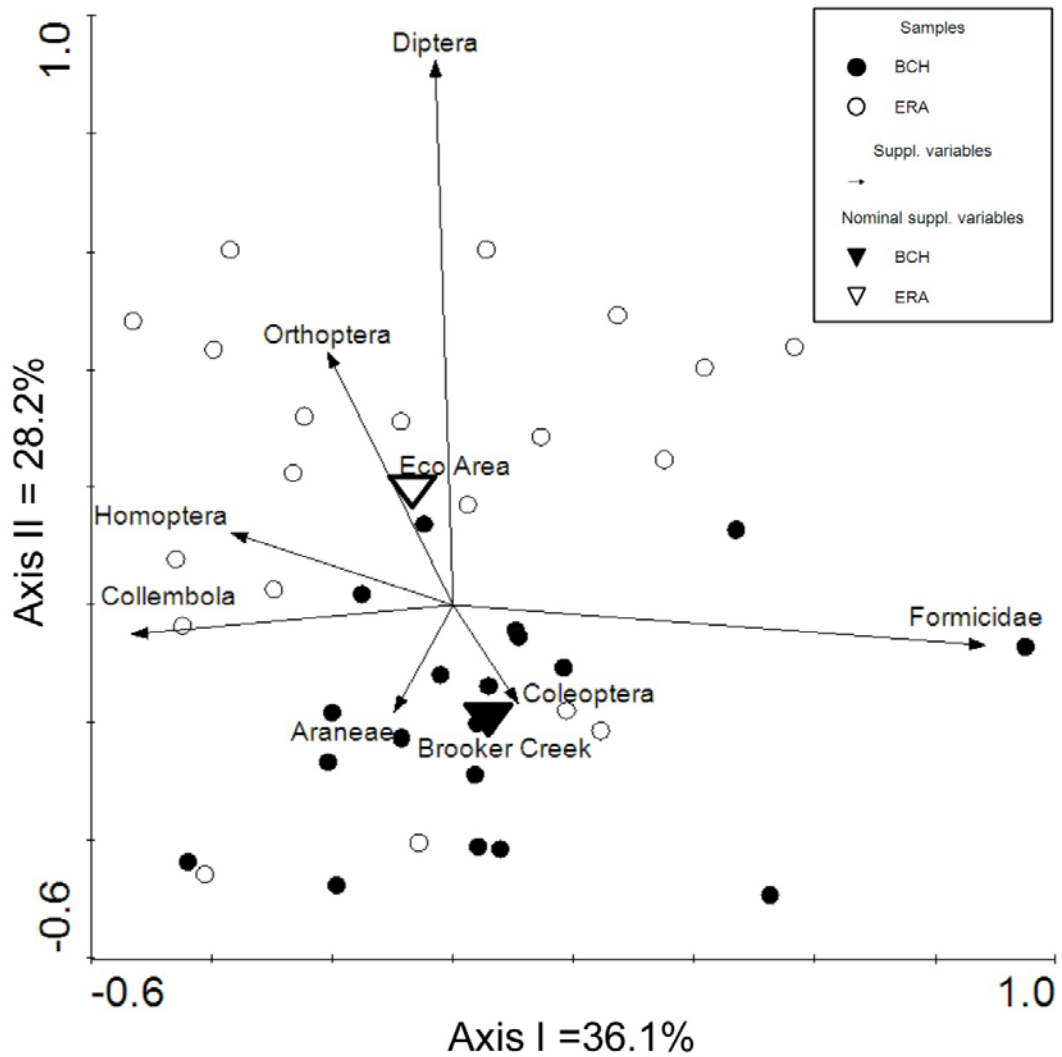
Fig. 4.3: Results of a principal coordinate analysis (based on Hellinger's distance) of the relationships between arthropods at Brooker Creek Headwaters Preserve (BCH) and the University of South Florida Ecological Research Area (ERA).

Chapter 5: Evidence for Competition between Carnivorous Plants and Spiders

Note to reader

Portions of this chapter have already been published (Jennings et al. 2010) and are utilized with permission of the publisher.

5.1. Introduction

Competition is a fundamental ecological process in determining the structure of communities. Historically, competition was assumed to be strongest between closely related taxa, an idea dating back to Darwin (1859) and persisting into the recent past (Connell 1983; Schoener 1983; Gurevitch *et al*. 1992). For example, out of 112 interspecific competition studies in terrestrial and freshwater ecosystems reviewed in Schoener (1983) and Gurevitch *et al*. (1992), the vast majority of those involving animals were conducted on closely related taxa, while only one study focused on species from different kingdoms (Fig. 5.1). Nonetheless, competition between disparate taxa is frequently found to be strong when examined (Brown & Davidson 1977; Schoener & Spiller 1987; Morin *et al*. 1988; Mokany & Shine 2003). These findings suggest that ecologists might be missing important competitive interactions among distantly related species, or those that have few morphological similarities.

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To the best of our knowledge no previous studies have quantified competitive interactions between the plant and animal kingdoms, although carnivorous plants and animals seem likely to compete for arthropod prey. Sundews (Droseraceae: *Drosera*) are carnivorous plants that catch prey using sticky mucilage secreted from glands on the tips of modified trichomes found on their leaves, and research suggests that they are generalist arthropod predators (van Achterberg 1973; Thum 1986; Porch 1989; Verbeek & Boasson 1993). Spiders are candidate animal competitors with carnivorous plants because they are abundant, have considerable spatial overlap with carnivorous plants, and are often generalist arthropod predators that can reduce arthropod populations (Riechert & Bishop 1990; Buddle 2002; Wise 2004).

We conducted a field census to quantify the microhabitat and dietary overlap of pink sundews (*D. capillaris*, Poiret 1804) and funnel-web building wolf spiders (Lycosidae: *Sosippus floridanus*, Simon 1898), and the plasticity of their phenotypic traits in the presence and absence of one another – all of which are potentially indicative of competition (Schoener 1983; Goldberg & Barton 1992; Agrawal 2001; Callaway *et al*. 2003). Additionally, we conducted a laboratory experiment to determine if wandering wolf spiders (Lycosidae: *Rabidosa rabida*, Walckenaer 1837) could negatively impact growth and fitness of sundews by depleting the availability of a common prey.

D. capillaris is a small perennial carnivorous plant commonly found in mesic habitats throughout the southeastern USA. This species forms basal leaf rosettes with an average diameter of 3.5 cm, reaching up to 7 cm (Schnell 2002). *S. floridanus* is found in webs

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on or close to the ground in scrub and mesic habitats throughout Florida and southern Georgia (Brady 1972; Muma 1973; Punzo & Haines 2006), while *R. rabida* inhabits grasslands and open woodlands in the central and eastern USA (Brady & McKinley 1994). Both species mature at approximately 2 cm in length (Brady 1972; Brady & McKinley 1994; Punzo & Haines 2006) and along with various other spiders are consistently found on and around sundews (D. Jennings, unpublished data).

We hypothesized that sundews and spiders compete for arthropod prey, generating the following six predictions: 1) because both sundews and spiders use relatively opportunistic and passive prey capture mechanisms, they will be generalist arthropod predators with considerable dietary overlap; 2) on a large spatial-scale, sundews and spiders will be positively associated with each other, because both will be more abundant where prey resources are abundant, but 3) on a small spatial-scale, spiders will avoid building webs near sundews to avoid utilizing the same prey resources. To compensate for competition for prey resources, 4) spider web area will be positively correlated with sundew trapping area, and 5) sundew trichome density will be positively correlated with spider density. Finally, 6) sundew fitness will be lower in the presence of spiders.

5.2. Methods

5.2.1. Censusing procedure

This research was conducted at Brooker Creek Headwaters Nature Preserve (BCH) in Odessa, Florida (28° 08.32' N, 82° 33.32' W), and the University of South Florida Ecological Research Area (ERA) in Tampa, Florida (28° 04.24' N, 82° 23.44' W). Two

20 m transects (30 m apart at BCH and 200 m apart at the ERA) were surveyed at each

study site, and 0.5 m x 0.5 m quadrats were censused every 2 m along the transects.

These transects were surveyed approximately once every two weeks between July 1st and

September 10th 2008 at BCH, and between September 22nd and November 10th 2008 at

the ERA, for a total of 16 transect surveys and 160 quadrat censuses. All censuses were

conducted between 0700 and 1100. Within each quadrat the following data were

recorded: number of sundews, leaves per sundew, *S. floridanus* webs, web area, and prey

per web. If applicable, we also recorded distance from webs to the nearest sundew. One

leaf was also removed from up to 10 randomly selected sundews per quadrat, for

subsequent analysis in the lab.

5.2.2. Dietary selectivity and overlap

To sample arthropod availability, we used 4 cm x 4 cm sticky-traps with no attractants

(Olson Products, Medina, OH, USA). These were set approximately 0.5 cm off the

ground, the height at which sundew leaves and *S. floridanus* webs are typically found in

these locations (D. Jennings, unpublished data). For each quadrat, one sticky-trap was

placed at least 15 cm away from sundews and webs, and when present, one sticky-trap

was placed adjacent to a randomly selected sundew and/or a web, and thus there were up

to three sticky-traps per quadrat. Traps were left out for 24 hours. Arthropods caught

were identified to the order level or below, and measured to the nearest 0.1 mm. We then

estimated arthropod biomass using the general formula derived by Rogers *et al*. (1976):

$$W = 0.0305 \; L^{2.62}$$

where W represents the mass in mg and L represents the length in mm.

Sundew leaves were examined under a dissecting microscope to record prey items. Prey items were identified to order level or below and measured to the nearest 0.1 mm. To reduce the likelihood of damaging or losing prey items through destructive web sampling, we recorded the number, size and order of prey caught in webs or chelicerae in the field using a 16 x hand-lens. The hand lens, however, did not provide adequate magnification to detect many smaller arthropods, such as Collembolans. To adjust for this, we examined 24 randomly selected sticky-traps from the quadrat censuses and identified and measured arthropods on them using both the 16 x hand-lens and the dissecting scope and adjusted the spider diet for these missed prey items. In no case did including these missed prey items change the results, so we present only those results that included these prey items.

5.2.3. Phenotypic plasticity in leaf and web traits

After being examined for prey, sundew leaves were photographed under a dissecting microscope to count the number of trichomes per leaf and to calculate individual leaf capture area. All webs were photographed with a 30 cm ruler, and leaf capture area and web area were calculated using SigmaScan Pro 4 (SPSS Inc., Chicago, IL, USA). For each quadrat, total trapping area was estimated by multiplying the mean capture area per leaf by the mean number of leaves per sundew by the total number of sundews.

5.2.4. Statistical analyses for field census

To determine if sundews and spiders track arthropod prey in the environment, we used the Generalized Linear Model to evaluate whether spider abundance (Poisson error and

log link) and sundew presence or absence (binomial error and logit link) could be predicted by arthropod biomass in quadrats (cubed-root transformed). If variation in arthropod biomass is high at large spatial-scales (among quadrats) but low at small spatial-scales (within quadrats), we would expect the two species to co-occur at large spatial-scales in order to track prey biomass but to avoid one another at small spatial-scales. To evaluate the level of variation in arthropod biomass within versus among quadrats, we compared the among quadrat variation in arthropod biomass to the biomass variation among the three types of sticky-traps (next to web or sundew, away from both) within quadrats using variance partitioning (Gotelli & Ellison 2004). To assess whether sundews or spiders were depressing local arthropod resources, we conducted a one-way ANOVA, blocking by quadrat, to compare arthropod biomass among traps directly next to sundews, directly next to webs, and away from both. Data were log-transformed when necessary to meet the assumption of the parametric analyses.

Co-occurrence and dietary overlap were both analyzed using χ^2 tests. Additionally, we analyzed co-occurrence, and dietary overlap and selectivity, using EcoSim (Gotelli & Entsminger 2001). To test for sundew and spider co-occurrence, we calculated a *C*-score (Stone & Roberts 1990) from observed data (presence/absence of each species within each quadrat) and compared it with *C*-scores obtained from 5000 randomly generated matrices (i.e. a Monte Carlo permutation test). Dietary overlap was estimated using Pianka's (1973) index (PI), which generates a value between 0 (complete segregation) and 1 (complete overlap). We used the 'RA3' algorithm, which retains the niche breadth of each species but randomizes the resource states that are actually used, and also

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incorporated our arthropod availability data into the resource-state matrix. The observed overlap was then compared to the indices from 1000 randomly generated matrices to test for the probability that it would have been generated by chance alone.

We were also interested in how sundew trapping area, arthropod biomass, and other webs influenced the distance that spiders constructed their webs from the nearest sundew. However, measuring the distance of webs to the nearest sundew within a quadrat has clear limitations regarding the inferences that can be made from the results. For example, as the density and/or size of sundews per quadrat increases, the observed distance of webs will ultimately decrease because more of the space within the quadrat will be occupied by sundews. Therefore, we calculated the expected distance of a spider web from the nearest sundew at a given sundew density using a simulated null model in the statistical software R 2.8.1, available at www.r-project.org (R Development Core Team 2008). For a given number of sundews, positions of sundews and a single spider web were randomly assigned within a simulated 50 cm by 50 cm plot. Radii of sundews and of the spider web were selected from normal distributions with means and standard deviations calculated from the observed dataset (sundews: mean = 0.94 cm, SD = 0.54 cm; spider webs: mean = 2.76 cm, SD = 1.15 cm). The distance from the edge of each spider web to edge of the nearest sundew (0 if they overlapped) was then calculated, and this was repeated 10,000 times for each number of sundews to obtain an average (expected) distance at that sundew density.

We used path analysis to evaluate the effects of sundew trapping area, arthropod biomass (mean of sticky-traps), and other webs on mean web area and the observed minus expected distance of webs from sundews. We chose to use path analysis because it allowed us to evaluate both the indirect and direct effects that each variable has on the focal response variable. All variables were log-transformed except for the observed minus expected web distance, and we used a least-trimmed squares regression approach and estimated regression coefficients using maximum likelihood estimation (Gotelli & Ellison 2004). The significance of each path was evaluated by comparing the chi-square value of the full model to that of the model excluding the given path. Given that sundews are stationary, we assumed that they could depress local arthropod biomass and be influenced by local arthropod biomass (bidirectional path) and affect spider traits. Conversely, given that spiders are mobile and thus more transient than sundews, we assumed that spider webs would not affect the traits of sundews or arthropod biomass at the scale of the quadrat. Path analyses were conducted using the SEPATH module of Statistica 8.0 (StatSoft Inc., Tulsa, OK, USA).

5.2.5. Laboratory experiment

In 2004, immature sundews in winter dormancy and *R. rabida* nymphs were collected from a bog in Liberty County, Florida (30° 02.32' N, 85° 00.11' W) and transported to the University of Kentucky. In the laboratory, 40 glass terraria (21 L) with glass tops were filled with soil from the Florida bog to a depth of 3 cm, and six young sundews (approximately 1 cm diameter with 2 to 8 leaves) were planted in each terrarium. Eight shelves (spatial blocks) each held five terraria, and four florescent bulbs were positioned

5 cm above each terrarium to provide a range of light wavelengths. We simulated winter dormancy with a photoperiod of 9D/15N and temperatures of 15 C from January 5th to February 1st 2004 and again from November 1st 2004 to February 1st 2005. During all other times, a photoperiod of 14D/10N and temperatures of 24 C was maintained (until November 1st 2005).

The 40 terraria were divided into five treatments (spider present + high food; spider present + low food; spider absent + high food; spider absent + low food; spider absent + no food) with eight replicates per treatment. Low- and high-food terraria received six and 24 pinhead crickets (2 mm in length) twice per week, respectively. By June 1st 2004, one large (12 mm body length) spider nymph, without stored sperm, was added to each of the 16 terraria with spiders. On October 1st, we stopped supplying crickets and removed spiders. For each sundew on five occasions from September 2004 to June 2005, we counted the number of: leaves, flower stalks, flowers per stalk, and seeds. We included seed production from the 2005 growing season as sundew reproduction can be influenced by the previous growing season (Thum 1989; Krafft & Handel 1993).

5.2.6. Statistical analyses for laboratory experiment

Because we lacked a complete factorial design (spider + no food treatment was not possible), statistical analyses involved a two step, hierarchical approach. We first tested for an effect of spider and a spider x food interaction by ignoring the no spider + no food treatment. This created a complete 2 x 2 factorial design. The second step was to test for the effect of food level (a continuous predictor) by using the three food treatments and

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controlling for the effect of spiders. Analyses for both steps involved the use of the General Linear Model. We first tested for multivariate effects using number of flowers, stalks and seeds as the responses, and if significant, we then evaluated the univariate effects. These were repeated measures analyses, where the repeated measures variables were the five dates when data were collected.

5.3. Results

5.3.1. Field Census

For all analyses, the effect of site did not interact with any factors and was non-significant when arthropod biomass was included as a covariate in the statistical model because the sites differed in arthropod biomass. Consequently, we excluded site from the statistical models in favour of arthropod biomass which seemed to account for more variation.

5.3.2. Dietary selectivity and overlap: Prediction 1

A total of 565 arthropods were quantified from 294 sticky-traps, and there were no significant differences in their biomass among traps adjacent to sundews, adjacent to *S. floridanus* webs, or located at least 15 cm from both ($F_{2,88} = 1.12$, $p = 0.331$). Dietary analyses of sundews and *S. floridanus* were calculated from 665 leaves and 45 webs. Eighty-one prey items were located on sundew leaves (mean = 1.4 mm, range = 0.1-3.6 mm, SD = 0.7 mm) and fifty-four prey were identified on *S. floridanus* webs. We were able to record prey size for only thirty-three *S. floridanus* prey items (mean = 3.13 mm,

range = 1.1-8.7 mm, SD = 1.9 mm) because the remaining prey had been partly

consumed or damaged.

The results generally supported our first prediction, that both sundews and spiders would

be generalist arthropod predators with considerable dietary overlap. Orders Diptera and

Collembola, and family Formicidae, were the most frequently captured taxa by both

sundews (33.3, 29.6, and 23.5%, respectively) and *S. floridanus* (22.1, 26.5, and 20.6%,

respectively; Fig. 5.2). When estimating dietary selectivity, we included only arthropods

captured on sticky-traps within the size range of prey that the sundews (0.1-3.6 mm) and

S. floridanus catch (<16 mm in size because spiders generally eat prey 50-80% smaller

than themselves; Nentwig 1987). The overlap of arthropods available in the environment

and arthropods captured by sundews (0.93 PI) and *S. floridanus* (0.92 PI) was greater

than expected by chance ($p = 0.005$, $p = 0.030$, respectively). As predicted, sundews and

S. floridanus diets exhibited significant overlap ($\chi^2_5 = 6.99$, $p = 0.22$; 0.76 PI, $p = 0.033$)

within the prey size range of 0.1-3.6 mm, which included 100% and 79% of the sundew

and spider prey, respectively.

5.3.2. Spatial associations on a large spatial-scale: Prediction 2

The results supported our second prediction, that on a large spatial-scale, sundews and

spiders would be positively associated with each other because both would be where prey

were abundant. At the level of the quadrat, co-occurrence of sundews and *S. floridanus*

was highly significant ($\chi^2_1 = 10.78$, $p < 0.001$). Specifically, in 28 of the 35 quadrats in

which *S. floridanus* was present, sundews were also present. The *C*-score obtained from

the observed data was significantly different from the mean C-score obtained from the simulated indices (standardized effect size = -2.95, $p < 0.001$), indicating that these species significantly co-occurred.

As predicted, sundews and *S. floridanus* significantly tracked arthropod biomass because plots with more arthropods were more likely to have sundews (Model deviance = 1.29, Coefficient = 1.400, SE = 0.490, $Wald_{1, 158}$ = 8.17, p = 0.004) and *S. floridanus* (Model deviance = 0.89, Coefficient = 0.850, SE = 0.411, $Wald_{1, 158}$ = 4.28, p = 0.039). This likely accounts for the positive covariance of these two species among quadrats. In fact, variation among quadrats accounted for 27% of the variation in arthropod biomass, whereas variation within a quadrat among the three sticky-traps accounted for only 2% of the variation in arthropod biomass. These results indicate considerable arthropod heterogeneity among quadrats, but a relatively homogenous distribution of arthropods within quadrats. This analysis could be conducted only on plots with sundews and spiders because they were the only plots with three sticky-traps. If we could have conducted the variance partitioning analyses on plots with and without sundews or *S. floridanus*, we would have seen even greater among quadrat variation in arthropod biomass.

5.3.3. Spatial associations on a small spatial-scale: Prediction 3

The results supported our third prediction, that on a small spatial-scale, spiders would avoid building webs near sundews to reduce utilizing the same prey resources. Within each quadrat, *S. floridanus* located their webs further away from sundews as the total

sundew trapping area increased, representing a deviation from the expected distance values obtained from the null model (Fig. 5.3A). Mean arthropod biomass per sticky-trap, and the presence of other webs within the quadrat, did not significantly affect the distance that *S. floridanus* located their webs from sundews (Fig. 5.3A).

5.3.4. Phenotypic plasticity in web traits: Prediction 4

Web area was positively correlated with total sundew trapping area (Fig. 5.3B), consistent with competition and in support of our fourth prediction. *S. floridanus* webs had a mean area of 28 cm^2 (range = 3.7-98.6 cm^2, SD = 23 cm^2), and web area was negatively correlated with mean arthropod biomass on sticky-traps (Fig. 5.3B). However, there was no significant association between web area and the presence of other webs (Fig. 5.3B).

5.3.5. Phenotypic plasticity in sundew traits: Prediction 5

We found no support for our fifth prediction, that sundew trichome density would be positively associated with spider density or traits (all $p > 0.05$), likely because spiders are transient and do not live near a given sundew long enough to induce phenotypic changes. In addition, arthropod biomass on sticky-traps was not associated significantly with mean number of leaves per sundew ($\beta = -0.017$, SE = 0.075, $F_{1,\,85} = 0.05$, $p = 0.823$), mean number of trichomes per individual leaf ($\beta = 0.081$, SE = 0.063, $F_{1,\,84} = 1.68$, $p = 0.199$), or mean trichome density per sundew leaf ($\beta = -0.025$, SE = 0.055, $F_{1,\,83} = 0.020$, $p = 0.653$). Mean number of trichomes per individual sundew leaf was 68.7 (range = 14-143,

SD = 24.7), and mean trichome density per sundew leaf was 139.2/cm^2 (range = 21.8-1300/cm^2, SD = 147.8/cm^2).

5.3.6. Laboratory experiment: Prediction 6

Our laboratory results supported our sixth prediction, that spider presence would reduce sundew fitness. *R. rabida* had an adverse multivariate effect on sundew fitness (Wilk's $F_{3, 27} = 4.14$, $p = 0.015$) that was independent of food level (spider x food: Wilk's $F_{3, 27} = 0.53$, $p = 0.668$; Fig. 5.4A). *R. rabida* reduced the production of flower stalks ($F_{1, 29} = 13.10$, $p = 0.001$), flowers ($F_{1, 29} = 7.87$, $p = 0.009$) and seeds ($F_{1, 29} = 4.18$, $p = 0.049$; Fig. 5.4A). Cricket additions had a significant, positive multivariate effect on sundew fitness (Wilk's $F_{3, 35} = 6.01$, $p = 0.002$; Fig. 5.4B), increasing flower stalks ($F_{1, 37} = 11.81$, $p = 0.001$), flowers ($F_{1, 37} = 18.94$, $p < 0.001$) and seeds ($F_{1, 37} = 8.51$, $p = 0.006$; Fig. 5.4B).

5.4. Discussion

The results from our field census indicate that both sundews and *S. floridanus* are generalist predators, consuming arthropods in proportion to their availability in the environment, consistent with previous qualitative findings (Porch 1989; Punzo & Haines 2006). More importantly for the question of whether these species compete, the diets of these two species had a high overlap, which might lead to competition for shared prey.

The high dietary overlap between sundews and *S. floridanus* might be explained by the passive trapping mechanisms used by each species and the similar heights at which the

sundew leaves and webs are set above the ground. Some pitcher plants release certain chemicals that are thought to attract prey (Moran 1996; Di Giusto *et al*. 2008), and it has been implied that the red pigmentation common to many carnivorous plants might increase rates of prey capture (Schaefer & Ruxton 2008). In the present study, sundews did not appear to attract any arthropod taxa in particular because the diet matched the arthropod prey in the environment, and generalist diets appear to be common among carnivorous plants (Ellison & Gotelli 2009). However, the results could change with a higher taxonomic resolution of prey.

The spatial associations between sundews and *S. floridanus* were largely dependent on scale. At a large spatial-scale (i.e. among quadrats) there was a positive correlation between the two species, yet at a smaller spatial-scale (i.e. within each quadrat) there was a negative correlation between them. Sundews are sessile predators that are likely to have more specific abiotic requirements (particularly light and water) than the relatively mobile *S. floridanus*, and thus the patterns at small spatial-scales are perhaps best explained by assuming spiders respond to sundews and not vice versa. At the scale of the entire transects, *S. floridanus* were predicted to preferentially select areas of high prey abundance, a behaviour that has been demonstrated in a number of other spider taxa (Sunderland *et al*. 1986; Harwood *et al*. 2001). However, at the smaller scale of each individual quadrat, *S. floridanus* were predicted to locate their webs further away from sundews to reduce competition for shared prey resources. In support of these predictions, the variance partitioning results suggested that positive spatial covariance between sundews and *S. floridanus* on a large spatial-scale (among quadrats) was driven by the

two species being found where there was high prey biomass, whereas the two species had negative spatial covariance within quadrats, probably due to niche partitioning in light of the relatively homogeneous distribution of prey at this smaller scale.

Our observation that *S. floridanus* increased web area in response to a putative competitor contrasts with a previous finding that spiders reduced the area of webs they constructed when there were higher densities of conspecific competitors, presumably because of interference competition (Harwood & Obrycki 2005). Interference competition is unlikely to occur between *S. floridanus* and sundews, and we found no evidence that small *S. floridanus* were consumed by the carnivorous plants. Therefore, in the absence of interference competition with sundews, *S. floridanus* near sundews might invest more resources into web construction to mitigate the effects of exploitative competition with sundews. Spiders have also been shown to increase web area in response to reduced prey abundance (Sherman 1994), suggesting that prey resources were limited in the field.

Some carnivorous plants, such as pitcher plants (Ellison & Gotelli 2002), bladderworts (Englund & Harms 2003) and different species of sundew (Thorén *et al*. 2003), have been found to reduce their investment in carnivory (e.g. produce fewer traps) in response to increased nutrient levels. Hence, it was surprising that trichome density per leaf area was not negatively associated with the arthropod biomass from sticky-traps. Further, there was no evidence that *S. floridanus* affected phenotypic traits of sundews at the scales studied, possibly because *S. floridanus* are transient in comparison to sundews and are therefore unlikely to remain close to a focal sundew on a small spatial-scale.

Additionally, effects on phenotypic traits might not have been detected if competition for prey was intense at a large spatial-scale (i.e. among quadrats). Under such conditions, all of the sundews we observed might have been responding to competitive interactions of similar strength, and therefore no difference between them would have been detected. Although the spatial-scale of our survey seemed too small to detect any detrimental effects of *S. floridanus* on sundews, our laboratory experiment supported the hypothesis that spiders adversely affect the fitness of sundews. Specifically, the presence of *R. rabida* in terraria resulted in a reduced number of flower stalks, flowers, and seeds produced by the sundews. Furthermore, as food levels increased, sundews produced more seeds, and grew more leaves. Sundews are known to invest nutrients obtained from prey into reproductive structures (Krafft & Handel 1993; Hanslin & Karlsson 1996) and *R. rabida* were observed consuming many of the crickets offered during feedings. Thus, it appears that *R. rabida* reduced arthropod prey causing the decrease in sundew fitness.

5.5. Conclusions

Our field census found a high dietary overlap between these two predatory species, and in the presence of greater total sundew trapping area, *S. floridanus* located their webs further away from sundews and increased the area of their webs. Additionally, our laboratory experiment demonstrated that *R. rabida* can negatively affect sundew fitness by depriving them of nutrients normally obtained from prey. All of this evidence is consistent with competition between the plant and animal kingdoms, but more work will be necessary to fully understand the implications of these findings. For example, we predict that competitive interactions between sundews and spiders will also reduce spider

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fitness, and that any competitive effects on sundew and spider traits and fitness will be stronger at lower arthropod prey densities. Future work should test these predictions using field experiments with manipulations of sundew, spider, and arthropod prey densities. Quantifying the shapes of sundew and spider functional responses as a function of resource availability, and determining the fitness consequences of different traits and competitive interactions, will then allow generation of parameters for predictive population- and community-level models.

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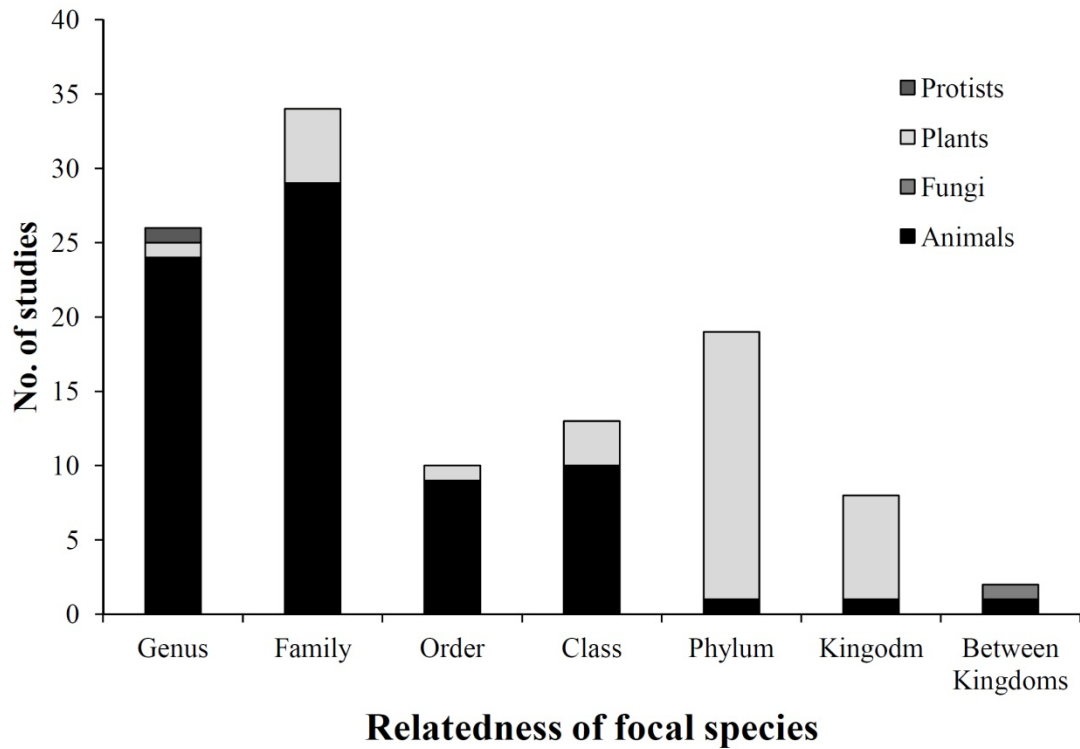
Figure 5.1: The relatedness of focal animal, fungal, plant, and protist species from terrestrial and freshwater interspecific competition studies considered by Schoener (1983) and Gurevitch *et al.* (1992). Each level of classification indicates that all focal species from the study in question were within that classification (e.g. if two species were from different orders but within the same class, the study would be recorded under 'Class'). We used the lowest level of classification possible for all interactions, and we did not double-count classifications for any studies.
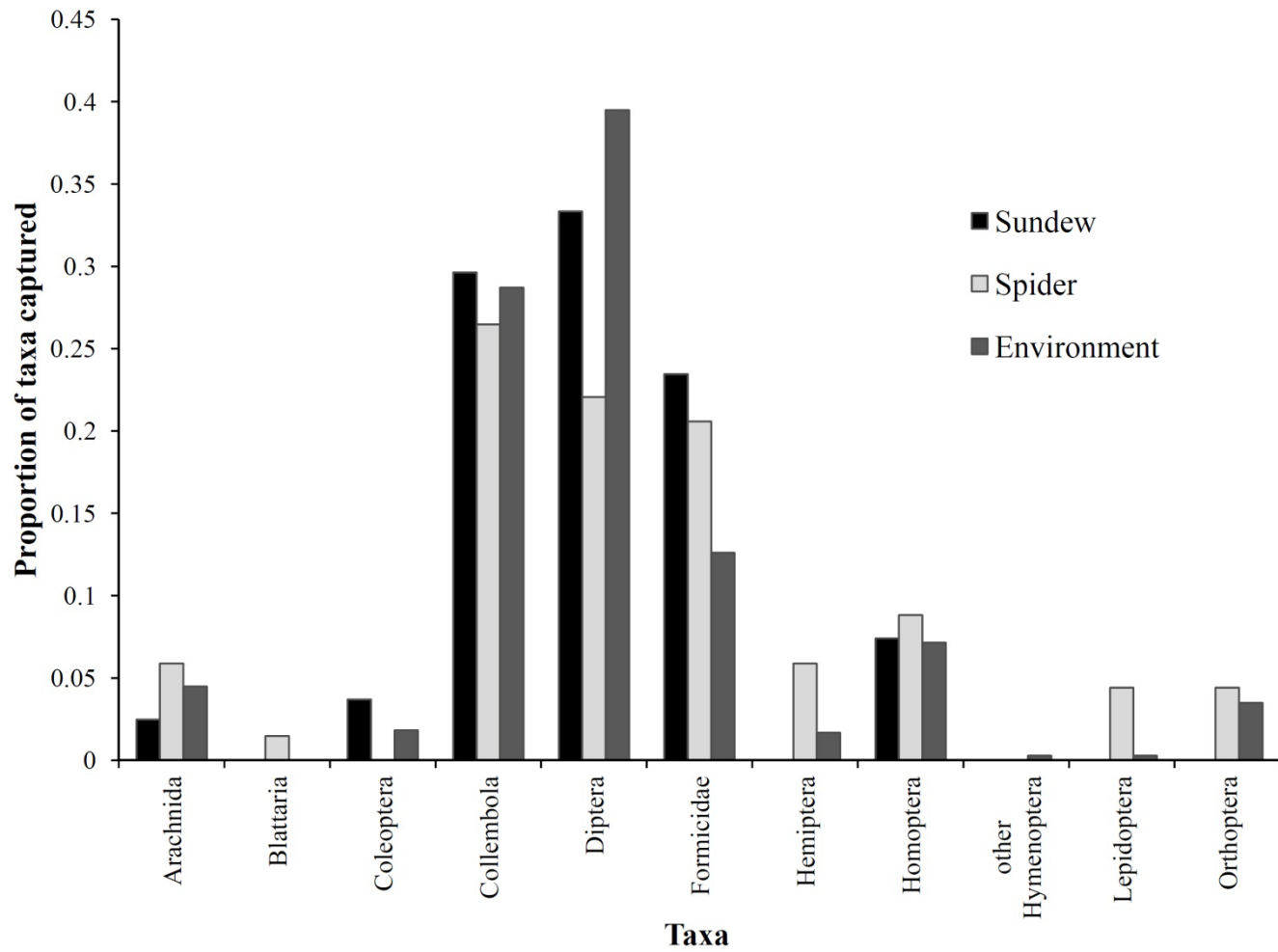
Figure 5.2: The relative proportions of arthropods caught by *D. capillaris*, *S. floridanus*, and from the environment (sticky-traps).
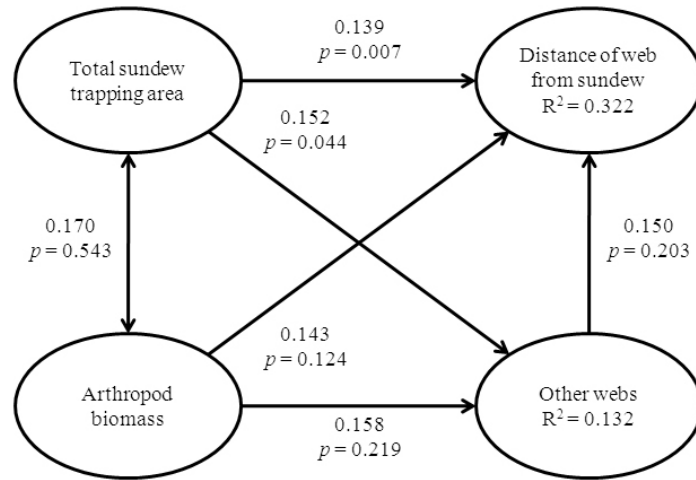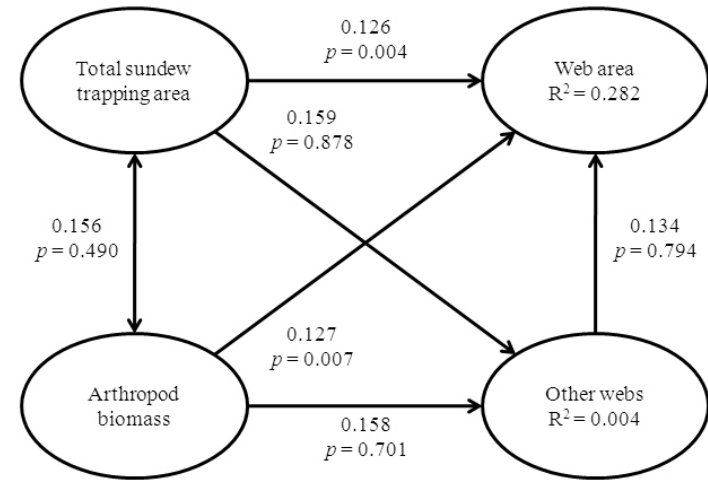
Figure 5.3: Path analysis models using A) distance of web to nearest sundew, and B) web area, as the response variable. None of the indirect effects were significant for the models and therefore they are not displayed. Shown are standardized coefficients, probability values for each path, and R^2 values for each submodel.
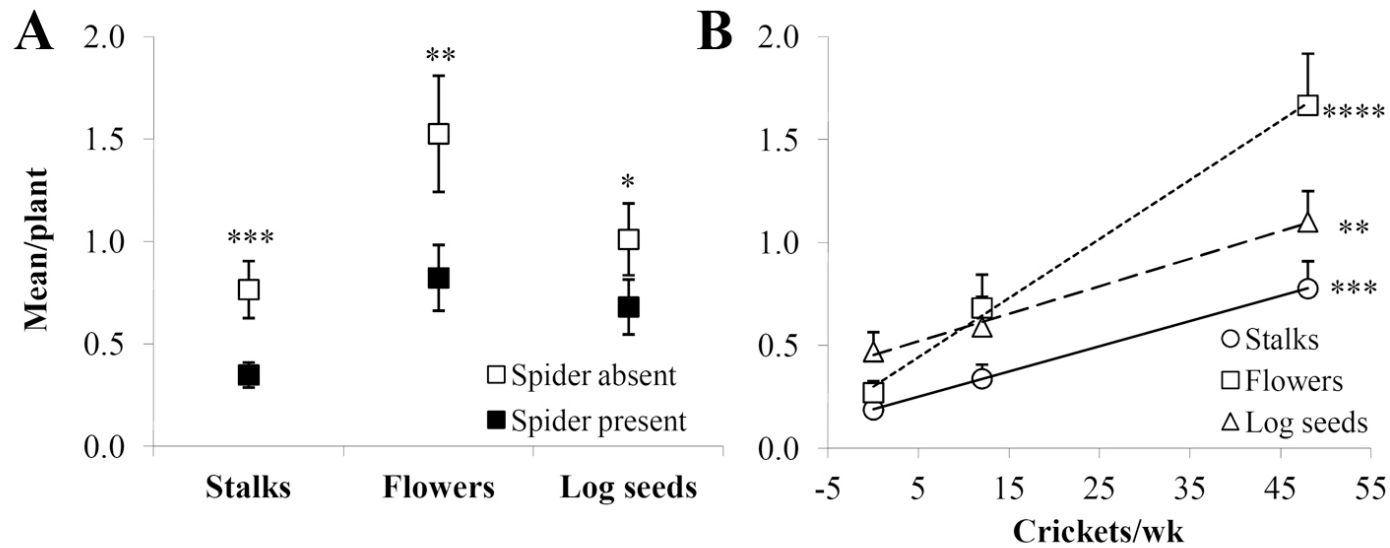
Figure 5.4: Effects of spider (presence or absence, A) and food level (0, 12, or 48 crickets/week, B) on the number of stalks, flowers, and seeds produced per sundew. There was no interaction between the spider and food treatments so only main effects are shown. In panel B, we provide best-fit lines, and asterisks represent the significance of the relationship between food level (continuous predictor) and the response variable. Shown are means and standard errors; n = 8. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.005$, **** $p < 0.001$.

Chapter 6: The Importance of Phylogeny in Dictating the Strength of Competition

6.1. Introduction

Competition has been one of the most extensively studied ecological processes, and yet

its relative importance in determining the structure of communities remains controversial.

Furthermore, one of the core tenets of competition theory, that competitive interactions

should be strongest between closely related species (ostensibly because of similarities in

behavior and morphology), has remained virtually untested since Darwin (1859) first

suggested it over 150 years ago. Although traits can certainly be conserved

phylogenetically, over large evolutionary timescales, we might expect convergent

evolution to mitigate any effects this conservatism might have on competitive

interactions. Indeed, convergent evolution between distantly related species has often

been shown to result in strong competition for resources (e.g. Brown & Davidson 1977;

Mokany & Shine 2003; Polis & McCormick 1986), and while most competition studies

have chosen to focus on closely related species (Jennings et al. 2010), sufficient data exist

to enable us to examine the strength of competition between species with a range of

divergence times. Understanding how phylogenetic relatedness affects the strength of

competition is important from a fundamental ecology perspective (Dayan & Simberloff

2005), and could also inform applied areas of ecology such as invasive species

management (Strauss et al. 2006).

With detailed phylogenies available for an increasing number of taxa, the importance of relatedness for interspecific interactions has become more prominent in ecology (Helmus et al. 2007; Losos 2008; Webb et al. 2002), including for competitive interactions. For example, Kaplan and Denno (2007) conducted a meta-analysis on the importance of competition in phytophagous insects, and found that the importance of phylogenetic relatedness in determining the strength of competition was dependent on the insect feeding guild. Specifically, for sap-feeding species, more closely related species did compete more strongly, but phylogenetic relatedness was not an important predictor for chewing insects. Similarly, Cahill et al. (2008) investigated the importance of phylogenetic relatedness for competition by examining published data on vascular plants and found no strong relationship between phylogenetic relatedness and strength of competition. More recently Burns and Strauss (2011) tested the effects of phylogenetic relatedness on interspecific interactions experimentally, using 32 native plant species in California. They found that the direction of the interaction depended partly on the soil composition, but that phylogeny could indeed be a good predictor of the strength of interactions, with plants performing better when grown with distantly related species. Violle et al. (2011) also experimentally tested the effects of phylogenetic relatedness on interspecific interactions, except using protists in microcosms, and found that closely related species did compete more strongly.

With the contrasting results from these studies of different taxonomic groups, it is clear that a broader-scale approach is needed if we are to make generalizations regarding the

utility of phylogenetic relatedness for predicting the strength and outcome of competitive interactions. Accordingly, we conducted a meta-analysis of published competition studies, placing no limits on the relatedness of the species in the study. Our specific objectives were: 1) to determine if phylogenetic distance can predict the strength of competitive interactions between two species from any taxonomic group, and 2) because the variability in the results of previous studies could be context dependent, we wanted to determine the importance of different biotic factors (i.e. habitat type, predation presence/absence, resource levels) and the experimental venue (i.e. field, mesocosm, or microcosm) in influencing the effect of phylogenetic relatedness on the strength of competition.

6.2. Methods

6.2.1. Data collection

We used Web of Knowledge to search for the keyword 'interspecific competition' in studies published from 1998-2008 in eight ecology journals (American Naturalist, Ecological Monographs, Ecology, Journal of Animal Ecology, Journal of Ecology, Journal of Experimental Marine Biology and Ecology, Oecologia, and Oikos). After studies were collected, they were examined to determine if they met a set of six criteria, many of which were similar to those used by Gurevitch et al. (1992). First, the study species needed to have phlyogenetic information deposited in the TimeTree database, an online resource which has a comprehensive list of estimated divergence times across all the major taxonomic groups (Hedges et al. 2006). If both species were located in the TimeTree database, we preferentially used the expert opinion before the averaged value.

Second, the density of at least one of the study species must have been manipulated experimentally. Third, appropriate controls must have been used (e.g. non-manipulated groups of individuals). Fourth, the means, variance, and sample size must have been reported or displayed, allowing us to calculate effect sizes (studies with sample sizes of one were excluded from the analyses). Fifth, there must have been clear pair-wise interactions in the study (e.g. species A and species B were grown together and separately as controls). Sixth, the response variable measured must have been one that was broadly applicable across different taxonomic groups (i.e. biomass, survival, growth, or density, as opposed to a variable such as time to metamorphosis). Once studies had been examined and determined to meet the criteria for inclusion, we collected data on means, variances, sample sizes, experimental venue, habitat, and whether or not the experiment manipulated the presence of predators and/or resource levels.

6.2.2. Statistical analyses

We used the software MetaWin 2.1 to calculate Hedges' *d*, which is the standardized magnitude of difference between a treatment and control mean (Rosenberg et al. 2000). Random-effects models were used because there was significant heterogeneity in the effect sizes that could not be explained by sampling error alone. Between-study variance (τ) for the random-effects models was estimated using the DerSimonian-Laird method calculated in the *metafor* package (Viechtbauer 2010) in R 2.12 (R Development Core Team 2011), with the appropriate model design (e.g. τ was estimated from an ANCOVA with a design: effects vs. $\log_{10}$(relatedness) + type of experiment + type of experiment * $\log_{10}$(relatedness)). This between-study variance (τ) was then added to all the variances

of Hedges' d (var_d + τ), and the inverse of (var_d + τ) was then included in regression models as a weighting term to reduce the influence of effect sizes with large variances (as required by meta-analysis), using the software jmp. The sums of squares of each factor in the regression models then became the Q-tests, which have a Chi-square distribution with the df's of the model factor. However, the standard errors of the regression parameters reported in jmp are incorrect, and we adjusted these parameters by dividing their SE with the square root of the mean-square residual of the regression model (Lipsey & Wilson 2001). Confidence intervals were then calculated with these SE to evaluate non-zero effects among regression slopes and pooled effects (d ++) among moderator groupings.

6.3. Results

Our initial search yielded a total of 818 studies (American Naturalist – 94, Ecology – 147, Ecological Monographs – 22, Journal of Animal Ecology – 100, Journal of Ecology – 68, Journal of Experimental Marine Biology and Ecology – 61, Oecologia – 143, Oikos – 183). After being screened against our criteria for inclusion, we gathered a total of 191 effect sizes from 39 of these studies (Appendix A). The divergence times of the species included in the studies ranged from 0.8 million years ago (MYA) (for two congeneric shrew species), to 4200 MYA (for a coral and a blue-green alga), with a median of 159 MYA.

There was no significant relationship between phylogenetic distance and effect size in our full model meta-regression ($Q_1 = 0.068$, $p = 0.794$), with an extremely small R^2 value

(Fig. 6.1). The confidence intervals for d++ did not overlap zero (d++ = -0.86, 95% CI = -1.22, -0.53), indicating that the mean effect size was not significant in a positive or negative direction.

When comparing the different venues where experiments were conducted, we found a significant interaction between experimental venue and phylogenetic distance (Table 6.1). This appeared to be driven by experiments conducted in microcosms, in which there was a small increase in the strength of competition as species became more distantly related (Table 6.2 and Fig. 6.2). In contrast, experiments conducted in the field or in mesocosms showed a slight trend in the opposite direction (Fig. 6.2).   The confidence intervals for d++ from field and mesocosm studies did not overlap zero, while for microcosm studies they did (Fig. 6.3).

We found no significant interaction between habitat type and phylogenetic distance (Table 6.1). No individual habitat types were significant (Table 6.2), but competition in marine and terrestrial habitats tended to be slightly stronger between more distantly related species, while the opposite was true for freshwater species (Fig. 6.4). The confidence intervals of d++ for both marine and terrestrial habitats overlapped zero, but for freshwater they did not (Fig. 6.5).

There was no significant interaction between predation presence/absence and phylogenetic distance (Table 6.1 and Table 6.2). Although with predators both present and absent, the general trend was for competition to be greater in strength between more

closely related species (Fig. 6.6). The confidence intervals of d++ for predators both present (d++ = -1.82, 95% CI = -2.65, -0.99) and absent (d++ = -1.11, 95% CI = -1.97, -0.25) did not overlap zero, indicating that they were significantly negative.

There was no significant interaction between resource level and phylogenetic distance (Table 6.1). However, there was a significant relationship between low resources and phylogenetic distance (Table 6.2), and competition tended to be greater in strength between more distantly related species under both types of resource conditions (Fig. 6.7). The confidence intervals for d++ both high (d++ = -0.34, 95% CI = -1.38, 0.68) and low (d++ = -0.30, 95% CI = -1.38, 0.78) resource levels overlapped zero, indicating that they were not significantly positive or negative.

A funnel plot of effect size versus the variance of the effect size indicated that there may be evidence of publication bias in our results (Fig. 6.8). Publication bias is the problem of studies with non-significant results tending not to be published, and ideally a funnel plot should contain more effect sizes with lower variance. However, because the effect sizes used in our models were weighted, the influence of those with larger variances should have been reduced.

6.4. Discussion

The results from our full model meta-regression suggest that phylogenetic relatedness is not a significant predictor of the strength of competition, contrary to the assumption that it should be greatest in strength between more closely related species. These results also

contrast with some of the recent findings of Burns and Strauss (2011) and Violle et al. (2011), but those studies only considered singular taxonomic groups (vascular plants and protists, respectively). However, as the results from those two studies suggest, it does appear as though phylogenetic relatedness can still be a good predictor of the strength of competition within certain groups of taxa.

Previous work by Skelly (2002) repeated the same experiment under field and mesocosm conditions, and found that the intensity of competition was greatest under the more manipulated conditions of the mesocosms. Thus, while it was not surprising that our analyses found detected an effect of the venue of an experiment on the strength of competition, it was surprising to find that in our analysis field studies had the largest $d{++}$ and microcosm studies the smallest. This suggests that the experimental venue could have at least some influence on the strength of competition, and possibly explains some of the variation in the findings of the previous studies by Cahill et al. (2008) (data from mesocosms and microcosms), Burns and Strauss (2011) (data from field and mesocosms), and Violle et al. (2011) (data from microcosms).

Habitat type showed no significant pattern with the strength of competition and phylogenetic relatedness. Many of the studies comparing distantly related species were conducted in the marine habitat (particularly intertidal habitats), which is likely explained by the number of studies conducted there that examine interactions between different sessile animals and algae. The freshwater habitats group was the only one to have a $d{++}$

that was significantly different from zero, and this could potentially be explained by effect sizes from freshwater studies comprising over half of the data we used.

While we were only able to use a subset of our data (with a much smaller number of effect sizes) for exploring the effects of predation compared to experimental venue or habitat type, our results were generally consistent with previous work by Gurevitch et al. (2000) who conducted a meta-analysis focusing on the interaction between competition and predation. As in the present study, Gurevitch et al. (2000) found that in the presence of predators, competition tended to be stronger. However, Chase et al. (2002) cautioned against the use of broadly applying those results, and recommended that more studies on this interaction be conducted over larger spatial-scales and under manipulated resource levels to improve our understanding of the importance of predation for competitive interactions.

There was no significant pattern with resource levels and the strength of competition and phylogenetic relatedness. Additionally, there was surprisingly very little difference in the mean effect sizes between high and low resource levels, which is likely attributable to us using a subset of our data once again for this predictor. The lack of a difference in the mean effect sizes of high and low resource levels was surprising because traditionally theory would predict that under low resource levels, competition should be more intense.

Although our results showed no indication of a significant pattern between phylogenetic relatedness and the strength of competition, we suggest several directions for future

research. Firstly, it would be desirable to include a larger sample of studies. While we managed to collect 191 effect sizes, our number of samples was small for examining certain predictors such as resource levels and predation presence/absence. By expanding our sample size we might be able to elucidate more about these relationships with greater confidence. Another potential benefit of expanding our sample size would be to include more studies that compare pair-wise interactions of three of more species within the same study. This would provide an internal control for each effect size, allowing us to simply rank the relatedness of species within individual studies and then compare the results between studies. It could also be beneficial for future work to consider the importance of functional traits, such as body size or metabolic rate. To address the potential publication bias in our study, it could also be useful to expand the range of journals included, perhaps by searching through more 'low' impact ecology journals. This would allow us to examine whether or not lower impact journals are more likely to publish studies with extreme effect sizes.

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Table 6.1: Summary of the results from ANCOVA for different predictors.

Source	Q	df	p
Experiment type	15.20	2	<0.001
Log_{10} relatedness	2.70	1	0.100
Experiment type * Log_{10} relatedness	12.87	2	0.002
Habitat	4.30	2	0.118
Log_{10} relatedness	1.53	1	0.216
Habitat * Log_{10} relatedness	3.15	2	0.207
Predation presence/absence	0.44	1	0.509
Log_{10} relatedness	4.68	1	0.031
Predation presence/absence * Log_{10} relatedness	0.20	1	0.652
Resource level	0.58	1	0.476
Log_{10} relatedness	5.57	1	0.018
Resource level * Log_{10} relatedness	0.62	1	0.420

Table 6.2: Individual based meta-regressions. k indicates the number of effect sizes calculated.

Source	k	Q	df	p
Experiment type				
Field	68	3.52	1	0.061
Mesocosm	63	0.18	1	0.675
Microcosm	60	9.20	1	0.002
Habitat				
Freshwater	101	0.87	1	0.351
Marine	35	2.12	1	0.145
Terrestrial	55	0.17	1	0.685
Predation presence/absence				
Present	21	4.04	1	0.045
Absent	17	1.27	1	0.260
Resource level				
Low	12	4.70	1	0.030
High	12	1.31	1	0.253
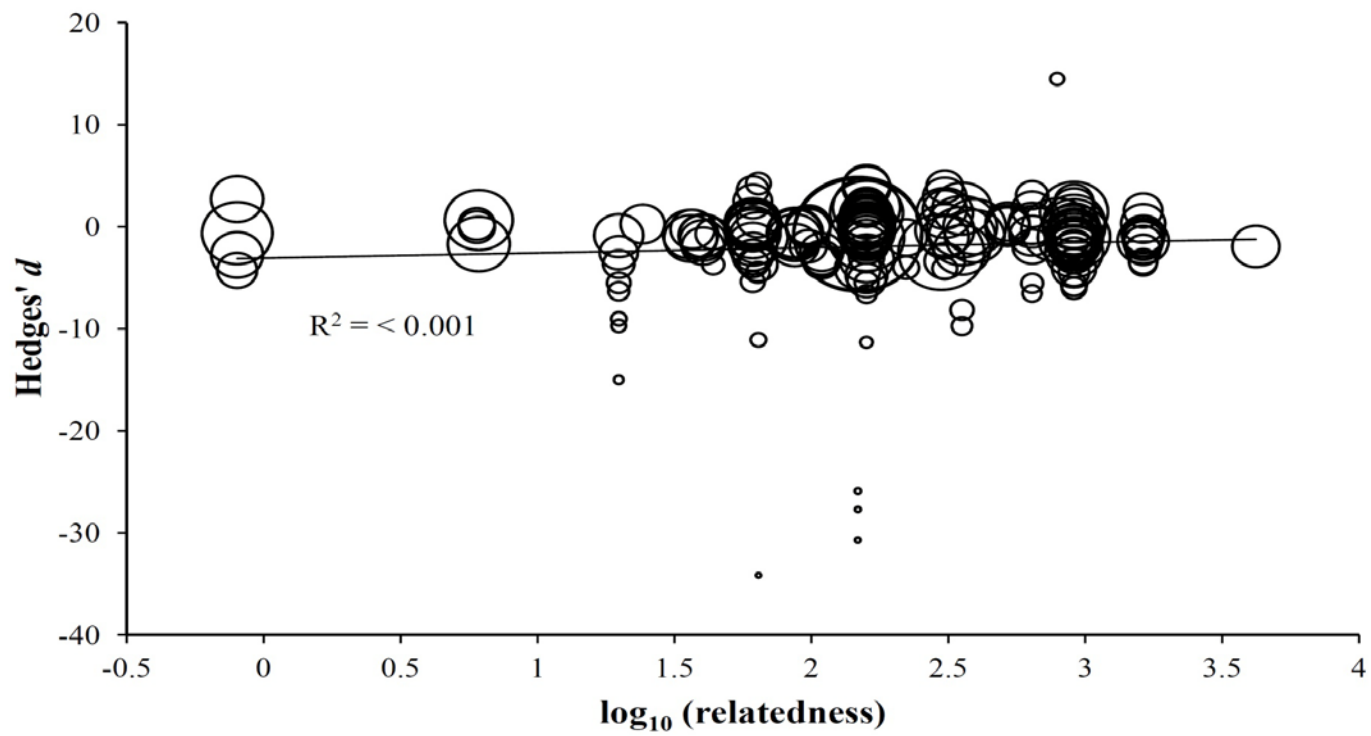
Fig. 6.1: Meta-regression of the full model of the interaction between phylogenetic relatedness and the strength of competitive interactions. The area of each circle (data point) indicates the overall weight of that data point in the model.
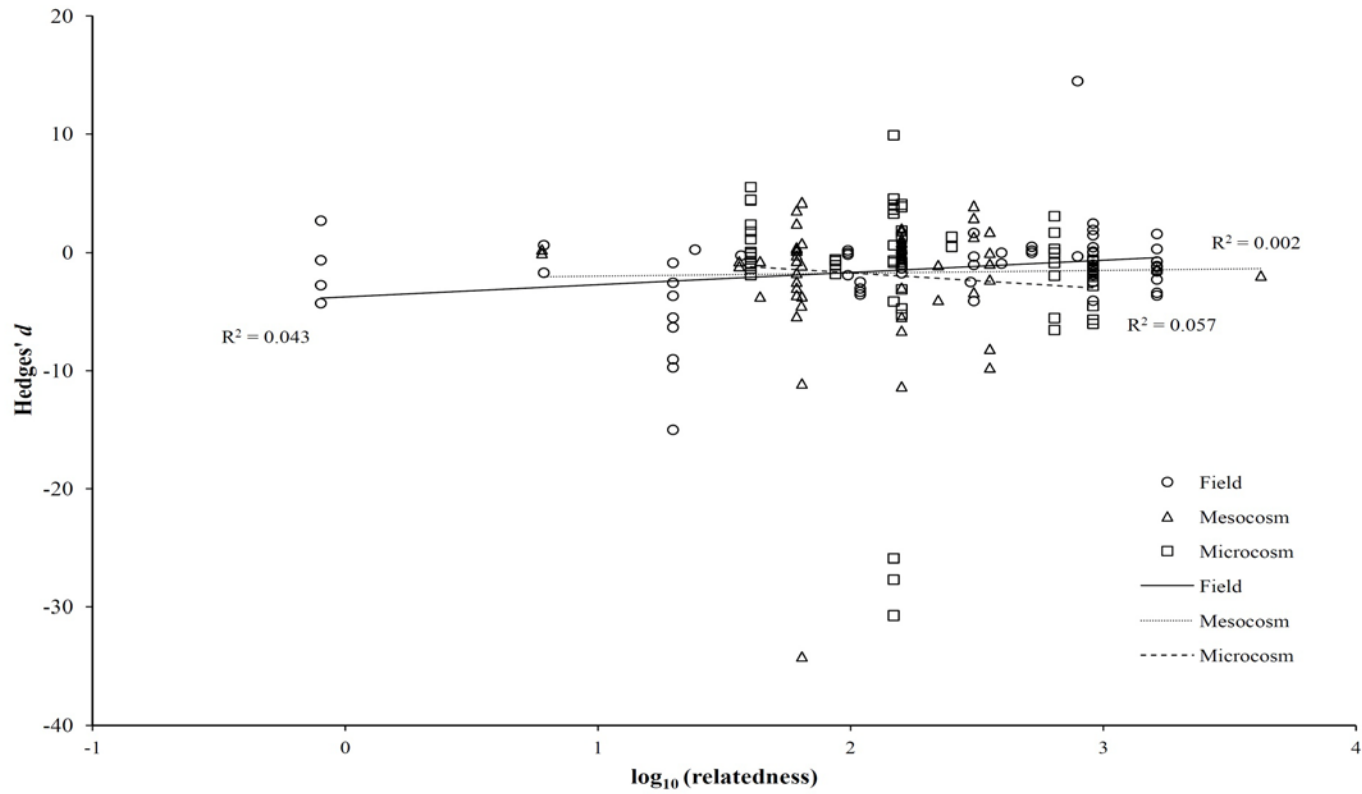
Fig. 6.2: Meta-regression of the interaction between experimental venue, phylogenetic relatedness and the strength of competitive interactions.
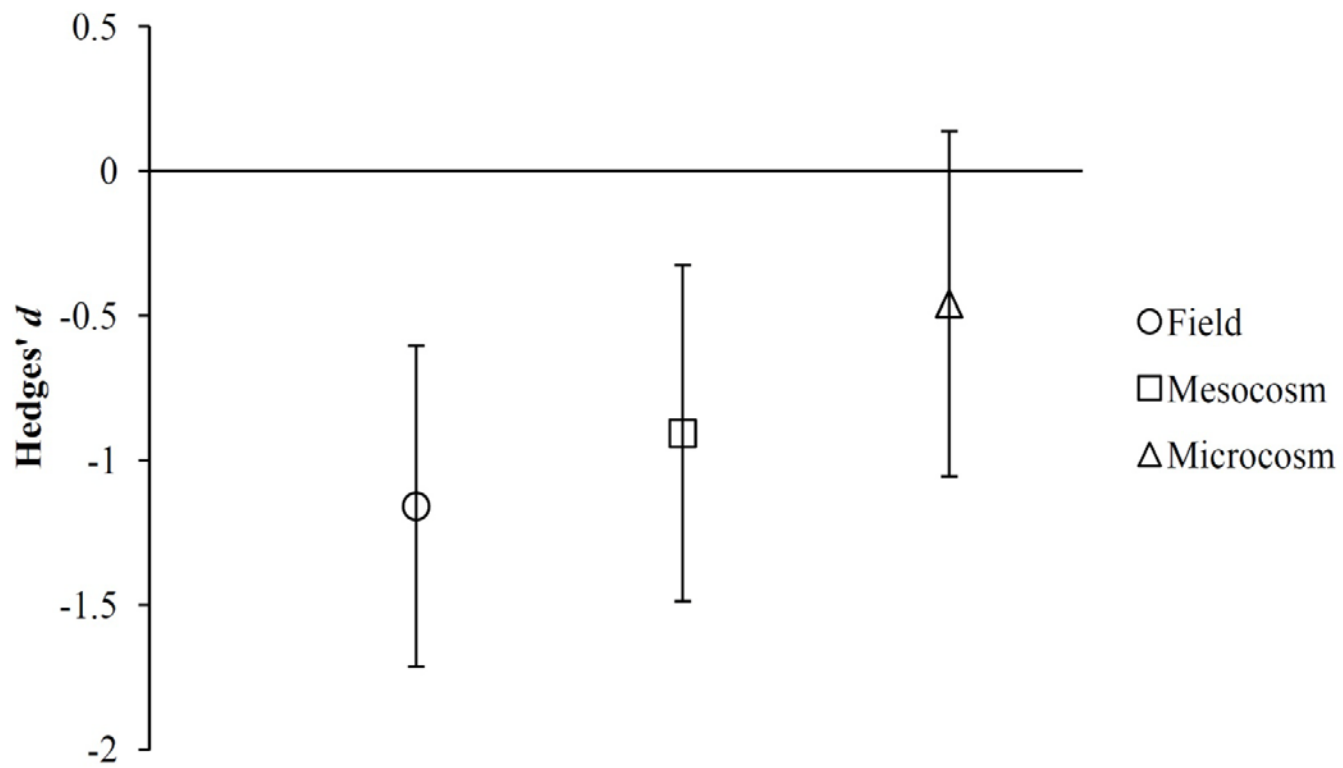
Fig. 6.3: Mean effect size (d++) and 95% CI for experimental venue and the strength of competitive interactions.
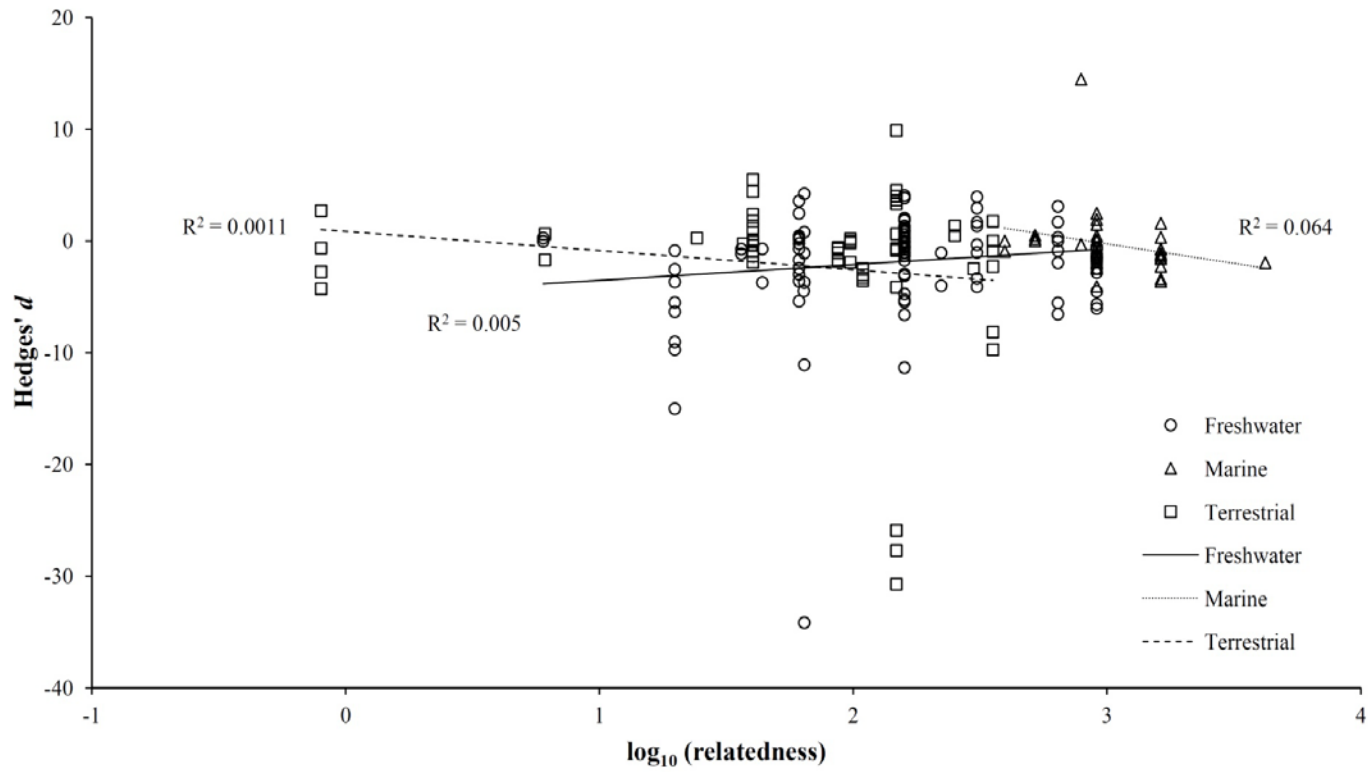
Fig. 6.4: Meta-regression of the interaction between habitat type, phylogenetic relatedness and the strength of competitive interactions.
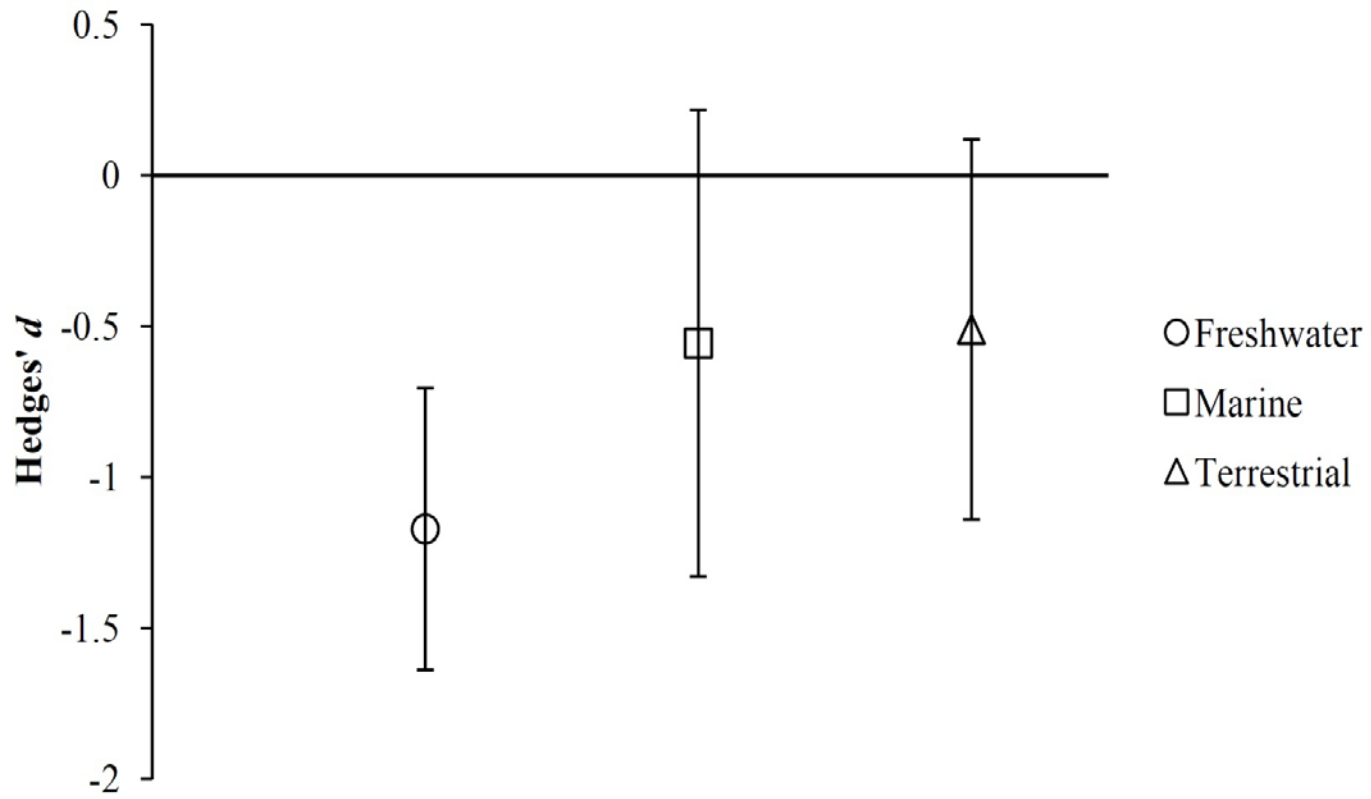
Fig. 6.5: Mean effect size (d++) and 95% CI for habitat type and the strength of competitive interactions.
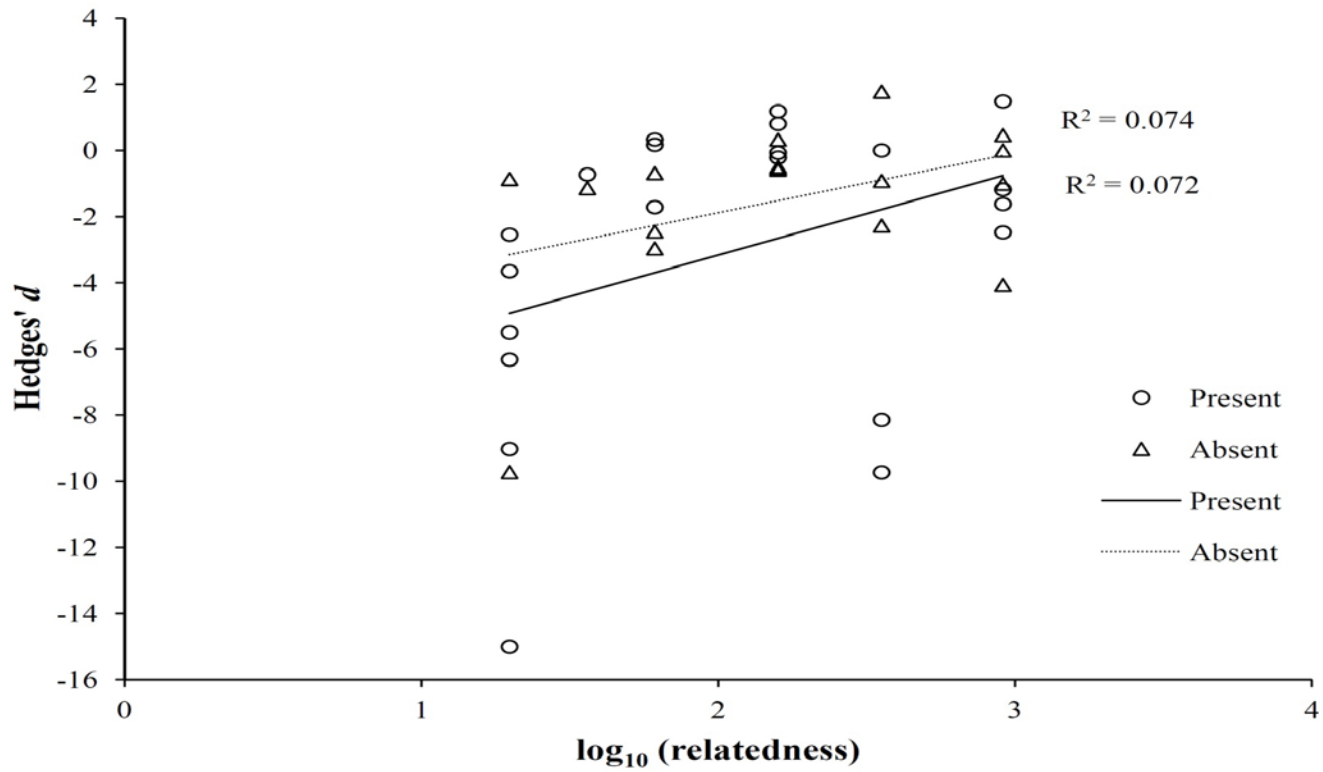
Fig. 6.6: Meta-regression of the interaction between predation presence/absence, phylogenetic relatedness and the strength of competitive interactions.
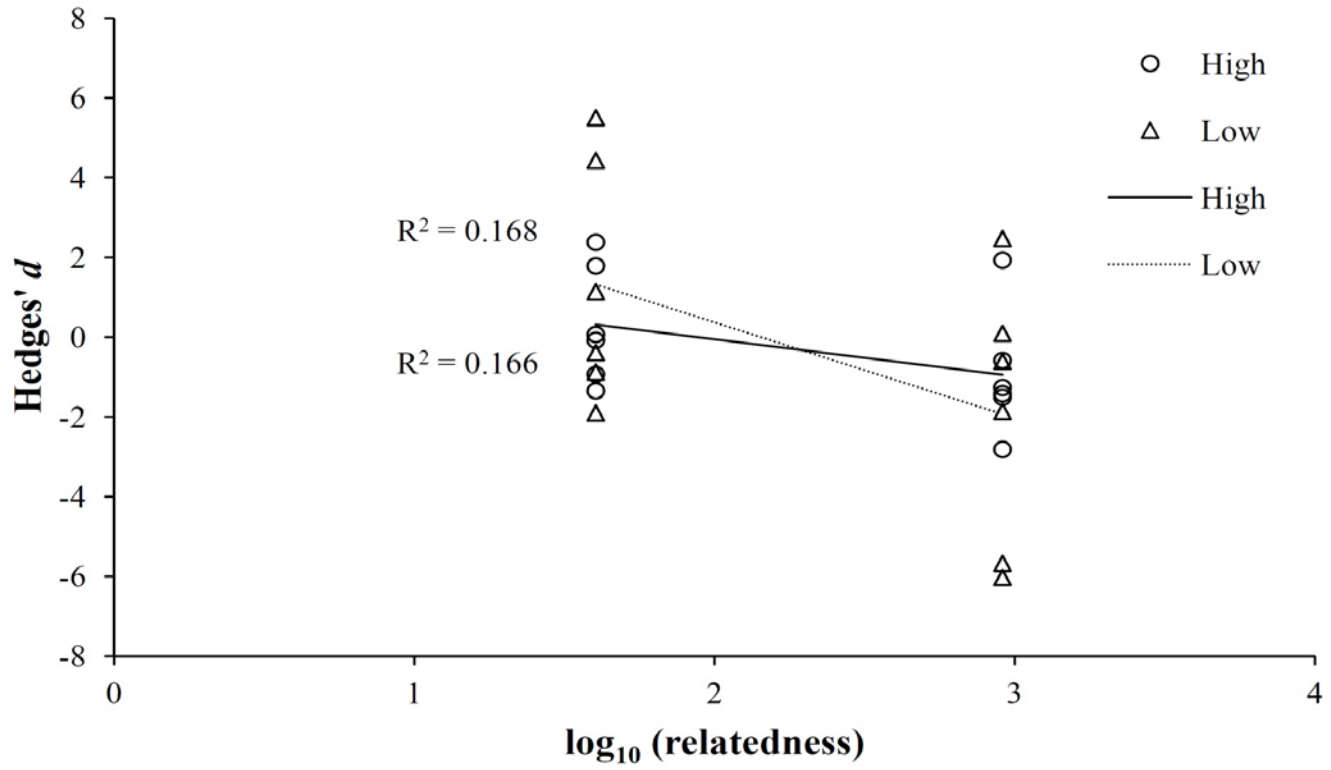
Fig. 6.7: Meta-regression of the interaction between resource level, phylogenetic relatedness and the strength of competitive interactions.
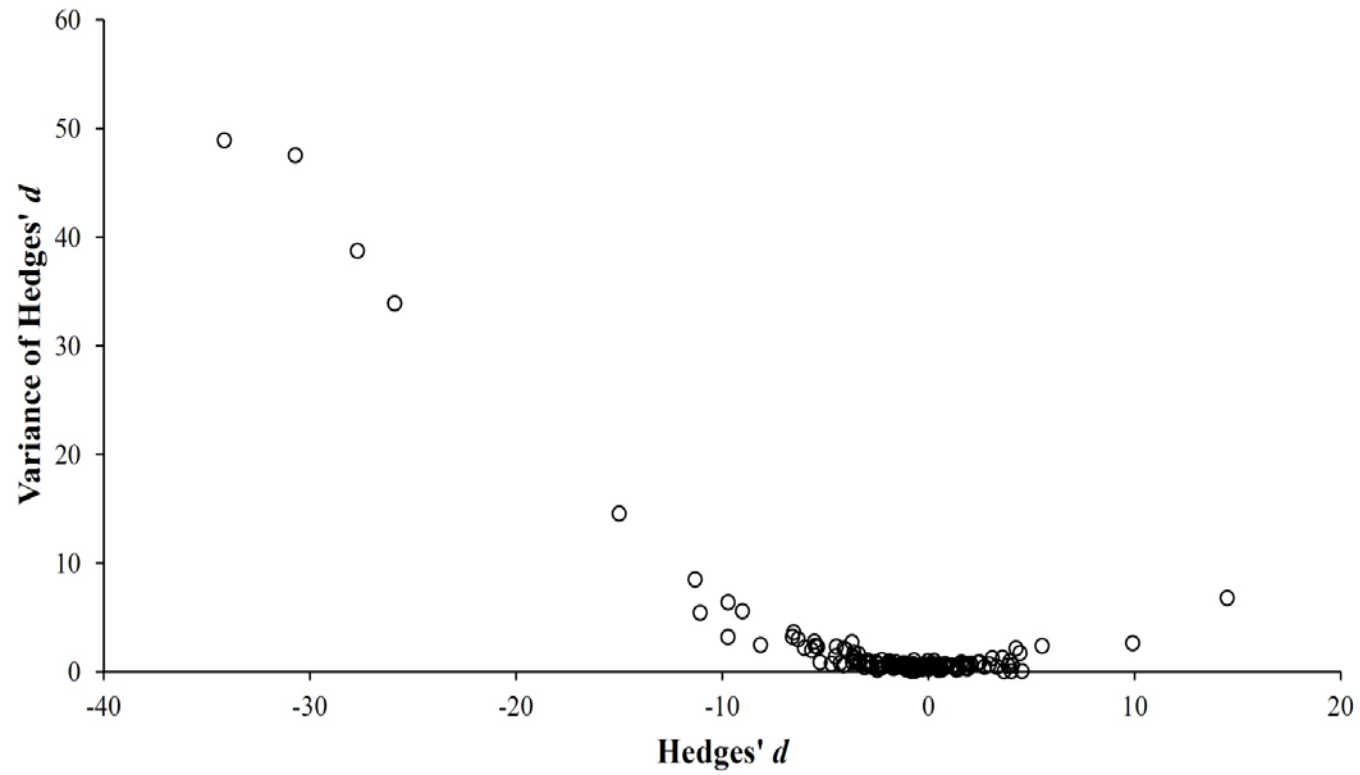
Fig. 6.8: Funnel plot of effect size versus the variance of the effect size.

Appendices

Appendix A: List of Papers Included in Meta-Analysis

Blanchet, S., Loot, G., Bernatchez, L. & Dodson, J. J. 2007 The disruption of dominance hierarchies by a non-native species: an individual-based analysis. *Oecologia* **152**, 569-581.

Bystrom, P. & Garcia-Berthou, E. 1999 Density dependent growth and size specific competitive interactions in young fish. *Oikos* **86**, 217-232.

Cross, R. E. & Stiven, A. E. 1997 Experimental studies of competition in salt marsh juvenile fish (*Fundulus heteroclitus* Linnaeus) and shrimp (*Palaemonetes pugio* Holthuis) in laboratory microcosms. *Journal of Experimental Marine Biology and Ecology* **212**, 133-146.

de Montaudouin, X., Audemard, C. & Labourg, P. J. 1999 Does the slipper limpet (*Crepidula fornicata*, L.) impair oyster growth and zoobenthos biodiversity? A revisited hypothesis. *Journal of Experimental Marine Biology and Ecology* **235**, 105-124.

Eccard, J. A. & Ylonen, H. 2003 Who bears the costs of interspecific competition in an age-structured population? *Ecology* **84**, 3284-3293.

Galbraith-Kent, S. L. & Handel, S. N. 2008 Invasive *Acer* platanoides inhibits native sapling growth in forest understorey communities. *Journal of Ecology* **96**, 293-302.

Hamilton, D. J. 2000 Direct and indirect effects of predation by common eiders and abiotic disturbance in an intertidal community. *Ecological Monographs* **70**, 21-43.

Harris, D. B. & Macdonald, D. W. 2007 Interference competition between introduced black rats and endemic Galapagos rice rats. *Ecology* **88**, 2330-2344.

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Holway, D. A., Suarez, A. V. & Case, T. J. 2002 Role of abiotic factors in governing susceptibility to invasion: a test with argentine ants. *Ecology* **83**, 1610-1619.

Jiang, L. & Morin, P. J. 2007 Temperature fluctuation facilitates coexistence of competing species in experimental microbial communities. *Journal of Animal Ecology* **76**, 660-668.

Jompa, J. & McCook, L. J. 2002 Effects of competition and herbivory on interactions between a hard coral and a brown alga. *Journal of Experimental Marine Biology and Ecology* **271**, 25-39.

Kaplan, I., Lynch, M. E., Dively, G. P. & Denno, R. F. 2007 Leafhopper-induced plant resistance enhances predation risk in a phytophagous beetle. *Oecologia* **152**, 665-675.

Katano, O., Aonuma, Y., Nakamura, T. & Yamamoto, S. 2003 Indirect contramensalism through trophic cascades between two omnivorous fishes. *Ecology* **84**, 1311-1323.

Kawai, T. & Tokeshi, M. 2006 Asymmetric coexistence: bidirectional abiotic and biotic effects between goose barnacles and mussels. *Journal of Animal Ecology* **75**, 928-941.

Kiesecker, J. M. & Blaustein, A. R. 1999 Pathogen reverses competition between larval amphibians. *Ecology* **80**, 2442-2448.

Koivisto, E., Huitu, O. & Korpimaki, E. 2007 Smaller *Microtus* vole species competitively superior in the absence of predators. *Oikos* **116**, 156-162.

Marler, M. J., Zabinski, C. A. & Callaway, R. M. 1999 Mycorrhizae indirectly enhance competitive effects of an invasive forb on a native bunchgrass. *Ecology* **80**, 1180-1186.

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Pfeifer-Meister, L., Cole, E. M., Roy, B. A. & Bridgham, S. D. 2008 Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. *Oecologia* **155**, 357-366.

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Smith, K. G. 2006 Keystone predators (eastern newts, *Notophthalmus viridescens*) reduce the impacts of an aquatic invasive species. *Oecologia* **148**, 342-349.

Steen, H., Mysterud, A. & Austrheim, G. 2005 Sheep grazing and rodent populations: evidence of negative interactions from a landscape scale experiment. *Oecologia* **143**, 357-364.

Titlyanov, E. A., Yakovleva, I. M. & Titlyanova, T. V. 2007 Interaction between benthic algae (*Lyngbya bouillonii*, *Dictyota dichotoma*) and scleractinian coral *Porites lutea* in direct contact. *Journal of Experimental Marine Biology and Ecology* **342**, 282-291.

Van Buskirk, J. 2007 Body size, competitive interactions, and the local distribution of *Triturus newts*. *Journal of Animal Ecology* **76**, 559-567.

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Volkenborn, N. & Reise, K. 2006 Lugworm exclusion experiment: responses by deposit feeding worms to biogenic habitat transformations. *Journal of Experimental Marine Biology and Ecology* **330**, 169-179.