# DIRECT AND INDIRECT EFFECTS OF DROUGHT ON COMMUNITY STRUCTURE AND ECOSYSTEM PROCESSES IN AN AQUATIC ECOSYSTEM

by

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# Abstract

A major challenge of ecologists is to discover general mechanisms that explain how climate shapes ecological communities and ecosystems. Efforts have traditionally focused on direct effects, but a growing body of evidence suggests that indirect effects of climate, via altering species interactions, may be more important. Predators are often particularly vulnerable to environmental stress, thus effects of climate may cascade through ecosystems by altering topdown trophic interactions.

In Costa Rica, where climate change is predicted to decrease the amount of precipitation, bromeliads contain aquatic insect food-webs largely controlled by the top predator, damselfly nymphs. Community composition varies with bromeliad size. Notably, top predators occur only in large bromeliads, possibly because the probability of drought stress decreases with bromeliad size. Thus, bromeliads are ideal systems to study the relative importance of direct and indirect effects of climate on community and ecosystem responses.

To determine whether climate governs community composition directly, I regressed insect drought sensitivity, which I obtained experimentally, against insect habitat size sensitivity, which I calculated from observational data. To examine the importance of indirect drought effects from altered trophic interactions, I experimentally manipulated trophic composition and drought in mesocosms mimicking a single bromeliad leaf well and measured changes in community composition, decomposition, and water quality.

Climate directly governed community composition at the scale of the bromeliad, as drought sensitivity strongly predicted habitat size sensitivity. At the scale of the leaf well, drought altered community composition and ecosystem properties indirectly by reducing topdown control from the top predator. Moreover, indirect effects of drought cascaded through the food-web to affect ecosystem functioning (decomposition) and state (water quality).

These findings suggest that in complex habitats, such as bromeliads, direct (physiological) effects of climate may sufficiently explain community composition. However, in isolated habitats, such as a single leaf well in which dispersal is hindered, indirect effects of climate, via altered trophic interactions, may emerge and cascade through the ecosystem. The relative importance of direct and indirect effects of climate may thus depend on habitat scale.

# Preface

All chapters of this thesis are original works by S. L. Amundrud. The questions underlying the research projects were conceptualized by Diane S. Srivastava, with input from John Richardson and Simon Donner. The development of the experimental design, as well as the performance of all data analyses for both data chapters (2 and 3) were by S.L.A in conjunction with D.S.S. All data were collected by S.L.A except for the bromeliad survey in Chapter 2, which was collected by D.S.S. and has been made available to S.L.A. as part of a data sharing initiative within the Bromeliad Working Group. Versions of Chapter 2 and 3 will be submitted for publication and co-authored by D.S.S.

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# **Chapter 1: General Introduction**

Ecologists have long attempted to understand the factors that govern community composition, species interactions, and ecosystem functions. A deeper knowledge of these processes will not only aid in explaining current ecological patterns, but is also crucial in predicting ecological responses to contemporary ecological change, such as habitat loss and fragmentation, species extinctions, and climate change. Efforts to understand the effects of climate change on ecological communities and ecosystems have traditionally focused on direct, physiological effects of altered temperature (e.g. McKechnie and Wolf 2010) and precipitation (e.g. Ernest et al. 2000, Báez et al. 2006, Ledger et al. 2008) on species. However, there is increasing evidence that the indirect effects of climate change, mediated by altered species interactions, are at least as important (e.g. Brown et al. 2001, Stenseth et al. 2002, Walther et al. 2002, Schmitz et al. 2003, Chase and Knight 2003, Montova et al. 2009, Brodie et al. 2012, McCluney et al. 2012, Blois et al. 2013, Barton and Ives 2014a). As higher trophic levels are often disproportionately vulnerable to environmental stressors (Petchey et al. 1999, Woodward et al. 2010, Ledger et al. 2011, Zarnetske et al. 2012), climate change has the potential to alter topdown trophic interactions. However, empirical studies of the relative importance of physiological responses to climate and altered trophic interactions on community and ecosystem responses are still rare, especially for whole ecosystems.

Neotropical bromeliads (Fig. 1.1) are ideal study systems to examine the relative importance of direct and indirect effects of climate on community and ecosystem responses because they are a repeatable unit of a relatively contained aquatic ecosystem. Bromeliads collect

rainwater and fallen detritus in their leaf axils and support diverse aquatic communities of bacteria, fungi, and macroinvertebrates. The macroinvertebrate community largely consists of insects of several functional feeding groups, including detritivores, filter feeders, and predators. A generalist top predator damselfly nymph controls this food web from the top-down. Bromeliads vary in size, ranging from a few milliliters to over three liters in total tank water volume. As drought probability is negatively related to bromeliad size (Zotz and Thomas 1999), this bromeliad size gradient also represents a desiccation stress gradient. Currently, bromeliads in northwestern Costa Rica experience seasonal droughts ranging from 5 to 33 consecutive days (Fig. 1.2).



Figure 1. 1. Bromeliad near Estación Biológica Pitilla, Costa Rica.



Longest continuous Drought (Days)

**Figure 1. 2. Longest continuous drought interval between October 2012 and October 2013 for 30 bromeliads surrounding Estación Biológica Pitilla, Costa Rica.** Three leaf wells (1 central and 2 peripheral) were measured every second day, and drought was defined as all three leaf wells simultaneously containing no water. For all bromeliads, the longest continuous drought interval occurred sometime between early April to late May 2013. More detailed descriptions of the water dynamics in bromeliads will be published elsewhere.

The purpose of this work is to determine the relative importance of direct and indirect effects of drought on community structure and ecosystem processes for the bromeliad ecosystem. I conducted two experiments and used observational species occupancy data (collected by Diane Srivastava) to examine

- whether insect drought resistance depends on trophic level and predicts habitat occupancy with respect to bromeliad size, and
- 2. how indirect effects of drought (via altered trophic interactions) affect food-web structure, ecosystem processes and habitat quality.

To answer the first question, I quantified differences in drought sensitivities between bromeliad insects by experimentally subjecting individual insects to drought in artificial mesocosms. I then examined whether physiological drought sensitivity predicts the observed differences in habitat size sensitivity in bromeliad-dwelling insects (Chapter 2). To answer the second question, I experimentally contrasted the importance of direct and indirect effects of drought on community structure, decomposition, and water quality by manipulating drought length and community structure in artificial mesocosms (Chapter 3). The relationships among the results of these chapters are discussed in the General Conclusions (Chapter 4).

## Study site and system

I performed both experiments at Estación Biológica Pitilla (10°59'N, 85°26'W) within the Área de Conservación Guanacaste, northwestern Costa Rica. The field station is located at an elevation of 700 m in secondary montane rainforest, with temperatures ranging from 13-35°C (mean = 23°C) and precipitation at approximately 4000 mm per year, falling mostly between May and February (LeCraw 2014). In northwestern Costa Rica, climate change predictions are a decrease in rainfall by up to 30%, and there is already evidence of reduced precipitation on mountains as a result of elevated cloud cover (Karmalkar et al. 2008).

Tank bromeliads (*Vriesea gladioliflora* H. Wendl, *Guzmania scherzeriana* Mez, and *Vriesea sanguinolenta* Cogn. and Marchal) are common in primary and secondary mid-elevation tropical rainforest surrounding the station (Melnychuk and Srivastava 2002, Srivastava et al. 2005). These miniature aquatic ecosystems contain food webs consisting of both macroinvertebrates and micro-organisms (metazoans, protozoans, bacteria, algae and fungi), and are largely fuelled by detritus that falls into bromeliads from the surrounding trees (Fig. 1.3). I

focus on the macroinvertebrates, many of which are aquatic insect larvae which become winged and terrestrial during adult stages. Individual bromeliads contain a subset (ranging from 5 to 20 species) of the approximately 60 invertebrate species ( $\pm 15$  species 95% CI, Chao estimator: D.S.S unpublished results) in the regional pool.



**Figure 1. 3. Diagram of simplified bromeliad macroinvertebrate food web**. Only species used in studies in Chapter 2 and 3 are included in diagram. Solid arrows represent flow of energy between trophic levels (via consumption), dashed arrow represents facilitative effect of processors on collectors via a processing chain.

The dominant detritivores in the system are Tipulidae (*Trentepholia* spp., undescribed: Diptera, functional group: shredder), Scirtidae (*Scirtes* sp.: Coleoptera, functional group: scraper), and Chironomidae (especially *Polypedilum* sp.: Diptera, *Chironomus* sp.: Diptera, and Orthocladiinae: Diptera, functional group: collector). By processing detritus into fine particles, shredder and scraper larvae (collectively called processors) have been shown to facilitate collector emergence in the absence of predators, presumably by converting detritus into suitable feeding and building material for collectors (Starzomski et al. 2010). Dominant filter feeders in the system are mosquito larvae (*Anopheles* spp., *Culex* spp., and *Wyeomyia* spp., Culicidae: Diptera), which feed on microscopic bacteriovores such as flagellates and rotifers (Starzomski et al. 2010). The damselfly larva *Mecistogaster modesta* Selys. (Pseudostigmatidae: Odonata) represents the top predator in the system, accounting for 85–90% of total predator biomass in bromeliads where it occurs (mainly bromeliads > 100 ml in capacity: Srivastava et al. 2005, Srivastava 2006). The remainder of the predator biomass is composed of piercing predators including Tanypodinae chironomids, Ceratopogonidae, tabanids and Dytiscidae beetles, and small engulfing predators such as Corethrellidae (Srivastava 2006).

#### Mesocosms

Mesocosms were necessary to allow for the precise manipulation of water level and drought length (Chapter 2 and 3), as well as for the assembly of replicate insect communities (Chapter 3). I constructed mesocosms that mimicked a single bromeliad leaf well using 50 ml centrifuge tubes, cutting off the tapered bottoms and drilling three holes into the side (d = 7 mm), which I covered with Nitex screen (80  $\mu$ m mesh size) to prevent passage of insect larvae, but allow for unrestricted water flow. I placed these tubes into 207 ml plastic cups, which allowed me to manipulate water levels inside the tubes by modifying water levels in the cups, without disturbing their contents (Fig. 1.4A). In natural bromeliads, invertebrates may use the crevices formed by the overlapping of adjacent bromeliad leaves to escape predators or survive drought, similar to the use of physical refugia in dry streams (Boulton 1989) and treeholes (Srivastava

2005). To replicate this structure in the mesocosms, I glued together one of the long sides of two pieces of 2 cm x 6 cm green polyethylene, and bent the other long edge outwards to form the opening of the crevice (Fig. 1.4). Mesocosm detrital input consisted of two to three leaves of *Conostegia xalapensis* Bonpl. (Melastomataceae), [mean dry weight of 508 mg  $\pm$  6 (SE)], which I first dried and weighed, and then rehydrated for 24 hours prior to adding to mesocosms. Mesocosm cups were filled with stream water to a volume of 15 ml inside the tubes, which I calculated to be a typical volume per bromeliad leaf well [survey data show that on average a *Vriesea* spp. bromeliad at the study site has leaf wells of 32.8 ml  $\pm$  9.90 (SE) capacity which are 44% full of water between September and December, n = 11]. Mesocosm tubes also received 3 ml of filtered (through 80 µm mesh) bromeliad water as a microbial inoculant, as well as detrital particles [80 to 850 µm diameter; 25.28 mg  $\pm$  0.14 (SE)] obtained from bromeliads. Mesocosms were placed on an outdoor veranda with ambient conditions similar to those of the adjacent rainforest (Fig. 1.5).



**Figure 1. 4. (A) Diagram of mesocosm and leaf crevice.** Ambient water level represents 15 ml inside the mesocosm tube. The water level inside the mesocosm tube was manipulated by changing the water level in the mesocosm cup, which entered the tube through Nitex mesh. A "leaf crevice" was placed inside the mesocosm to mimic the natural bromeliad leaf structure. **(B) Photo of mesocosms.** 



**Figure 1. 5. Setup of experiment in Chapter 2.** Mesocosms were placed randomly in one of four grids on an outdoor veranda adjacent to the forest. Picture shows water change procedure.

# Chapter 2: Drought Sensitivity Predicts Habitat Size Sensitivity in a Bromeliad Insect System

# **INTRODUCTION**

A major goal in ecology is to understand which factors determine the association of species with certain habitats. As environmental tolerance largely influences whether a species can persist in a given habitat, there is an increasing recognition of the significance of traitenvironment relationships in structuring communities (Chown 2012). In addition to explaining current ecological patterns of community assemblage, physiological ecology has also been used in forecasting the ecological consequences of environmental change (Chown and Gaston 1999, Pörtner and Farrell 2008, Tewksbury et al. 2008, Kearney and Porter 2009). Physiological responses to temperature (Bernardo and Spotila 2006, Pörtner and Farrell 2008, Tewksbury et al. 2011, Freeman and Class Freeman 2014) and desiccation (Arad et al. 1992, 1993, Lindo et al. 2012) may be particularly useful in developing niche models, as those traits should be strongly linked to a species performance in a given environment. Although trait-based approaches ignore dispersal and biotic interactions, they may be valuable when environmental conditions are the dominant limiting factors, such as in harsh, stressful environments.

Environmental tolerances may be relevant to understanding one of the most pervasive patterns in ecology – the increase in species and trophic diversity with habitat size (Williams 1943, Schoener 1989, Rosenzweig 1995, Holt et al. 1999, Spencer et al. 1999). Specifically, when the intensity of environmental stress negatively correlates with habitat size (Worthen et al. 1998), species that are more vulnerable to environmental stress should require larger habitats than those with a broad environmental tolerance. Consequently, larger habitats may contain more species simply because their environmental conditions are within the fundamental niche of more species (Worthen et al. 1998, Finn and Giller 2000). Such stress mechanisms may also be complemented by other explanations for species-area relationships, such as increased resource availability (Wright 1983) and greater habitat heterogeneity (Kohn and Walsh 1994, Ricklefs and Lovette 1999) in large habitats, and sampling effects (Connor and McCoy 1979, Hill et al. 1994).

Frequently, higher trophic levels require larger habitats than lower trophic levels (Roth and Jackson 1987, Schoener 1989, Pearman 1995, Wellborn et al. 1996, Holt et al. 1999, Spencer et al. 1999, Brashares et al. 2001, Srivastava et al. 2008, Petermann et al. 2014). This may be due to predators' increased vulnerability to disturbances and stressors, as those often negatively correlate with habitat size (Worthen et al. 1998, Finn and Giller 2000, Schoener et al. 2001, Spiller and Schoener 2007). For instance, predatory damselfly nymphs occur only in relatively large bromeliads (Srivastava et al. 2005), and this has been hypothesized to be due to a high drought vulnerability of this top predator (Srivastava et al. 2008). A high sensitivity to habitat size may be linked to certain traits that are often exhibited by predators, such as long generation times (Peters 1983) and large body sizes (Warren and Lawton 1987, Cohen et al. 1993), as these traits are associated with increased vulnerability to environmental stress (Petchey et al. 1999, Brashares et al. 2001, Chadwick and Huryn 2007, Ledger et al. 2011).

Nevertheless, factors other than high stress vulnerability may explain the correlation of trophic level with habitat size. Generally, predators have lower population densities (Silva and Downing 1994), resulting in fewer colonizing individuals and higher extinction rates (Warren

and Gaston 1992) and therefore stronger species-area relationships. The higher per capita energy needs of predators (McNab 1963), as well as the loss of energy from the transfer between trophic levels (Lindeman 1942) may limit predators to large areas, as energy availability (i.e. resource production) generally increases with area size (Wright 1983). Besides, predators can only exist in habitats containing prey. As the probability of any species occurring in a habitat increases with habitat size, specialist predators may require larger habitats because of the trophic dependencies on their prey, representing an additional indirect constraint of area on their persistence (trophic rank hypothesis: Holt et al. 1999). An alternative explanation for the disproportionate habitat sensitivity observed in predators is sampling effects (Srivastava et al. 2008), as predators are generally rare and thus less likely to be found in small habitats.

Aquatic ecosystems may show strong relationships between habitat size and environmental conditions, as key processes such as nutrient entry, evaporation and heat retention often scale with, respectively, perimeter (Polis et al. 1997), surface area and volume. However, it is difficult to predict whether such effects of habitat size on environmental conditions result in changes in community structure. Not only are niche models still rare for aquatic species (but see Poff 1997 for stream systems), but such models assume rather than directly test whether environmental tolerances primarily determine the occurrence of species.

Here, we use an important aquatic habitat in the Neotropics to establish whether differences in drought tolerance between species explain changes in community composition over a gradient of habitat size. Tank bromeliads are discrete habitats for aquatic insect larvae, with a large range in habitat size (i.e. water-holding capacity), ranging from a few milliliters up to more than three liters (Srivastava et al. 2008). Importantly, bromeliad size correlates with drought likelihood, with small bromeliads drying out more frequently than large bromeliads (Zotz and Thomas 1999). Bromeliad communities include several functional feeding groups amongst the macroinvertebrates (Chapter 1). It has been hypothesized that communities in temporary waters, such as bromeliads, will be primarily limited by environmental factors rather than biotic interactions (Poff and Ward 1989). Thus, bromeliads are ideal study systems to examine whether a species' physiological tolerance width is useful in predicting habitat occupancy. We hypothesized that drought sensitivity (1) differs between species and increases with trophic level, and (2) explains natural patterns in species occurrence over a gradient in bromeliad size.

# **METHODS**

#### Determination of habitat size sensitivity indices for bromeliad insects

#### Bromeliad survey

To determine whether bromeliad species and trophic levels differ in habitat size sensitivity, we used survey data from 68 forest bromeliads collected by Diane Srivastava in 1997, 2000, and 2004 in the forest surrounding the study area. The data consisted of all organisms > 1 mm in length (mainly insect larvae) found inside bromeliads, as well as the maximum water holding capacity of each bromeliad (see Srivastava et al. 2008 for detailed survey methods).

### Statistical analysis to obtain habitat size sensitivity indices

For each of the 10 insect species used in the drought manipulation experiment (see below), we calculated the mean volume of all bromeliads containing at least one individual of the focal species (1997, 2000, 2004 surveys pooled). To examine whether trophic levels differ in habitat occupancy with respect to habitat size, we compared the observed mean habitat size of occurrence of predators to that of detritivores using a Mann-Whitney U test (due to non-normality and unequal variances of the response variable).

Because of sampling effects, the mean observed bromeliad size will be higher for rare species than for common species if species assemble in bromeliads randomly (Srivastava et al. 2008). Thus, mean habitat size of occurrence is not an unbiased measure of habitat sensitivity, as it does not allow us to directly compare between species of different regional abundances. In order to determine whether insects actually differ in habitat size sensitivity, we compared the scaled deviations of observed mean habitat sizes to those expected from a random assembly null model. For each insect species and each surveyed bromeliad, we calculated the bromeliad's probability of containing at least one individual of a given species as  $1 - (1 - \frac{x(i)}{N})^{n(j)}$ , where x(i) is the total abundance of species i in all bromeliads combined (i.e. the regional abundance of species i). N is the total number of all individuals in all bromeliads combined, and n(j) is the total abundance of all individuals in bromeliads) than rare species, null expectations predict that the mean bromeliad size of species occurrence will be negatively correlated with species regional abundance.

To obtain confidence intervals for the null expectations of mean habitat size of insect occurrence, we generated a sampling distribution of the expected mean habitat size of insect occurrence by re-sampling (10000 x with replacement) from the bromeliad pool. We randomly sampled individuals of each species from bromeliads, with the probability of sampling at least one individual of that species as described above. For each sample, we calculated the mean habitat size of occurrence as the average bromeliad maximum volume. We then generated 95% confidence intervals of the null mean habitat size of occurrence for each species by obtaining the 2.5% and 97.5% quantiles of the sampling distribution of means.

The above analysis allowed us to determine whether insect species differ in their habitat occurrence from null expectations. However, it does not allow for direct comparisons of insect species to each other, because of differences between species in relative abundances, and thus differences in null habitat size expectations. In order to obtain indices for habitat size sensitivity for the various species, we calculated Z scores from the observed mean habitat size, the expected mean habitat size, and standard deviation from the sampling distribution described above. We then used these Z scores as proxy for habitat size sensitivity to determine whether predators require larger habitats than detritivores (after correcting for differences in regional abundances), by performing a Mann-Whitney U test.

#### Determination of drought sensitivity indices for bromeliad insects

#### *Experimental manipulation of drought*

To determine whether drought sensitivity differed among bromeliad insects, we subjected the ten most common bromeliad insect species to an experimental drought and measured the response in terms of the relative growth rate of each species. We chose drought effects on relative growth rate as a proxy for drought sensitivity, as it allowed us to directly compare drought sensitivity between insect species, before effects on survival are seen. Insect larvae in our experiment belonged to one of three functional feeding groups: predators, filter feeders, or detritivores. Predators comprised the top predator *Mecistogaster modesta* Selys. (Pseudostigmatidae: Odonata), as well as the intermediate predators Ceratopogonidae (Diptera) and the chironomid Tanypodinae (Diptera). Filter feeders comprised the mosquito larvae Anopheles spp., Culex spp., and Wyeomyia spp. (Culicidae: Diptera), and detritivores consisted of the chironomids Polypedilum sp. (Diptera) and Orthocladiinae (Diptera), as well as Scirtidae beetle larvae (*Scirtes* sp.: Coleoptera) and Tipulidae (*Trentepholia* spp., undescribed: Diptera). Individual insect larvae were subjected to a factorial manipulation of two drought levels (full and partial drought: 0% and 10% of ambient water level, respectively) crossed with drought length (0, 2, 4, 7, 11, and 18 days), representing a drought length that is well within current conditions (Fig. 1.2). We chose a regression design because of its increased power over ANOVA designs, and its ability to capture nonlinear responses to continuous factors (Cottingham et al. 2005). We tested for effects of both full and partial droughts, as forest bromeliads often reach low water levels without complete desiccation, and such low water levels may reduce insect growth through effects on water temperature and chemistry. For Tipulidae, growth rate was obtained from a separate experiment with identical methods, except that it only consisted of one drought level (full drought), and that drought length ranged from 0 to 30 days, with five day intervals. For all insects, we converted drought effects to relative growth rate per day, by dividing the relative change in insect length (in %) over the time of the experiment by the length of the experiment (in days). For all insects except Tipulidae, the length of the experiment was 23 days; for Tipulidae, it was 34 days because Tipulidae data were obtained from a separate experiment.

Mesocosms (Chapter 1) were necessary for the precise manipulation of water level and drought length. To prevent any unwanted biotic effects on growth rate resulting from the interaction with other species or conspecifics, each mesocosm received only one individual insect. In order to quantify the effects of drought on relative insect growth rate, we used digital imaging technology to measure insect length before and after the experiment using the software ImageJ (www.imagej.net). We set up the experiment for most insects on 8 October 2012, but the experiment for *Polypedilum* sp. and Tipulidae were set up on 23 October and 6 November, respectively. Three days after setup, we initiated drought in all mesocosms, except the treatments with a drought length of zero days, by removing all water from the outer cup of the mesocosms (so as not to disturb insects in the tubes) for full drought treatments, and removing all but to a level of 1.5 ml inside the mesocosm tubes for partial drought treatments. At completion of drought length treatments, we added filtered stream water to cups until a volume of 15 ml inside the mesocosms was reached. Every second day throughout the experiment, we replaced 50% of the water inside mesocosms (except for mesocosms under the full drought treatment) to prevent hypoxia. Throughout the experiment, predators were fed live bromeliad insects, such as small mosquitoes or chironomids, so as not to confound effects of starvation on relative growth rate. Predators of the same species received identical amounts and types of prey, irrespective of drought treatment.

Two days after the last drought treatment was completed, mesocosms were emptied and the body length of surviving insects was measured via digital imaging. By sampling all mesocosms at the end of the experiment, rather than each after the completion of its drought period, we eliminated time as a covariate affecting insect growth rate.

#### Statistical analysis to determine drought sensitivity indices

For each insect species, we used the effect (negative slope from linear models) of drought length on relative growth rate as a proxy for drought sensitivity. Thus, a higher value (i.e. a more negative slope) represents a greater drought sensitivity than a lower value. To obtain these drought sensitivity indices, we started with a full model that included drought length, drought level, and their interaction as explanatory variables, as well as initial insect length as covariate. For insects with models in which drought level and the interaction term were not significant (p > 0.05), we simplified the model by removing drought level as explanatory factor, therefore only including drought length and initial insect length as covariate. For insects with models in which drought level was significant (*Anopheles* spp., *Mecistogaster modesta*, Tanypodinae), we proceeded by employing separate linear models for the two drought levels, to examine if drought length affected the relative growth rate for only one of the drought levels.

Due to high mortality rates for *Culex* spp. under full drought, the relative growth rate of this species could only be obtained for five individuals (with only 2 individuals surviving past two days of full drought). Thus, we were not able to reliably obtain a change in growth rate under full drought for this species, nor assess whether drought sensitivity differed between full and partial droughts. Consequently, we used the negative slope from the model for partial drought as drought sensitivity index for *Culex* spp. in further analyses. For Tipulidae, data were obtained from a separate experiment that only included the complete drought level, so we could not test for effects of partial drought on this species.

When models contained outliers (defined as Cook's distance > 1), these were removed and the analysis was repeated without them to examine if results changed qualitatively. This was only necessary for Tipulidae and Ceratopogonidae. For Tipulidae the removal of an outlier made no difference qualitatively, but for Ceratopogonidae, the results changed from significant to not significant when a single outlier was removed. Thus, we only report the non-significant results without the outlier for Ceratopogonidae.

To examine whether differences in sensitivity to drought between insects could be explained by functional feeding group, we employed a linear model on drought sensitivity indices obtained from the analyses explained above, with functional group (predators, filter feeders, and detritivores) as the explanatory variable. For insects that exhibited a significant effect of drought level (*Anopheles* spp., *Mecistogaster modesta*, Tanypodinae), the negative slope for full drought was used; otherwise the negative slope from the complete model was used as drought sensitivity index. For *Culex* spp., we used the negative slope from the partial drought model, as not enough data was available to reliably obtain a slope estimate for the full drought model. As drought sensitivity indices were estimates, we used a weighed regression (R Core Team 2014), where weights were defined as 1/(standard error of slope<sup>2</sup>).

#### Does drought sensitivity predict habitat size sensitivity?

To examine whether insect habitat size sensitivity can be predicted from insect drought sensitivity, we employed a linear model with habitat size sensitivity index (see above) as response and drought sensitivity index (see above) as explanatory variable. We used the negative slope from models for full drought for insects that exhibited a significant effect of drought level (*Anopheles* spp., *Mecistogaster modesta*, Tanypodinae), from models for partial drought for *Culex* spp. (due to a lack of data for full drought), and from simplified models (with no drought level) for all other insects as index for drought sensitivity. Because insect drought sensitivity indices were estimates, we included weights in the model, defined as 1/(standard error of slope<sup>2</sup>). All analyses were carried out in R statistical software (version 3.1.0: R Core Team, 2014).

# RESULTS

## Bromeliad insects differ in habitat size sensitivity

Bromeliad insects differed in the mean habitat size they occupied, as well as in their sensitivity to habitat size after accounting for differences in regional abundances between insects

(Fig. 2.1). Detritivores exhibited the smallest mean habitat size of occurrence at 321.9 ml (± 5.7SE), followed by filter feeders at 361.2 ml (± 52.1 SE). Predators occurred in the largest habitats (mean = 398.4 ml ± 39.0 SE). Although predators tended to occur in larger habitats than detritivores (W = 0, p = 0.057, Fig. 2.1), this was mainly because predators had low regional abundances; the effect of trophic level on habitat size disappeared once we accounted for variations in regional abundances among insect species (W = 7, p = 0.857, Fig. 2.1). Insects whose observed mean habitat size of occurrence was significantly larger than null expectations (i.e. who were sensitive to habitat size) were the top predator *Mecistogaster modesta* (Z = 5.71, p < 0.001), the filter feeding *Culex* spp. (Z = 7.34, p < 0.001), and the detritivores *Polypedilum* sp. (Z = 11.39, p < 0.001) and Scirtidae (Z = 2.11, p = 0.035). The observed habitat size of occurrence of the filter feeding *Anopheles* spp., the predators Tanypodinae and Ceratopogonidae, and the detritivores Orthocladiinae and Tipulidae did not differ from null expectations (p > 0.3 for all). Only one genus of insects, the filter feeding *Wyeomyia* spp., occurred in significantly smaller bromeliads than expected (Z = -6.24, p < 0.001).



**Figure 2. 1. Observed and expected mean habitat size of occurrence for bromeliad insect**. \* indicates the mean observed habitat size of occurrence. • represents the expected mean habitat size of occurrence based on random assembly from a regional pool. Error bars represent 95% confidence interval obtained from the null model sampling distribution of expected means (with 10000 x resampling). Black: predators; dark grey: detritivores; light grey: filter feeders; "other" represents all other species combined.

## Bromeliad insects differ in drought sensitivity

Drought length and level affected relative insect growth rates (Fig. 2.2), but species responses to drought were unrelated to feeding group and thus trophic level ( $F_{2,7} = 0.32$ , p = 0.738). For species whose growth rates were not affected by drought level, we only report the effects of drought length for simplified models with combined drought levels. Drought length significantly decreased the relative growth rate of the detritivore *Polypedilum* sp. ( $F_{1,32} = 22.86$ , p < 0.001), and marginally decreased the relative growth rate of the intermediate predator Ceratopogonidae ( $F_{1,11} = 4.24$ , p = 0.064). Moreover, drought length significantly decreased the

relative growth rate of filter feeding *Culex* spp. for partial drought ( $F_{1,10} = 14.43$ , p = 0.003; data for full drought was not available). The effects of drought length on the remaining predators *Mecistogaster modesta* and Tanypodinae depended on drought level ( $F_{1,20} = 5.06$ , p = 0.036;  $F_{1,11} = 6.23$ , p = 0.030; respectively). Drought length significantly decreased the relative growth rate of *M. modesta* only in full drought treatments ( $F_{1,9} = 12.06$ , p = 0.007), and slightly and marginally significantly increased Tanypodinae growth rate in partial drought treatments ( $F_{1,4} = 7.61$ , p = 0.051). The full drought level also decreased the relative growth rate of the filter feeding *Anopheles* spp. relative to the partial drought level ( $F_{1,19} = 4.789$ , p = 0.042; Fig. 2.2).



**Figure 2. 2. Drought sensitivities of bromeliad insects.** Drought sensitivity was measured as the negative slope of relative growth rate (%) regressed against drought length (days). Thus, a higher value represents a higher sensitivity to drought (i.e. a more negative effect on relative growth rate). Black: full drought (no water), white: partial drought (10% of ambient water), grey: the two drought levels combined (when model resulted in no significant effect of drought levels). P < 0.05 indicated by \*, p < 0.1 indicated by x. Error bars show standard error of slope.

## Drought sensitivity predicts habitat size sensitivity in bromeliad insects



**Figure 2. 3. Drought sensitivity predicts habitat size sensitivity in bromeliad insects.** Habitat size sensitivity was measured as Z score of observed vs expected mean habitat size of insect occurrence. Drought sensitivity was measured as the negative slope of relative growth rate (%) regressed against drought length (days). For insects for which drought level was significant (*Mecistogaster modesta*, Tanypodinae, *Anopheles* spp.), as well as for Tipulidae, drought sensitivity indices were obtained from full drought models. For *Culex* spp., the partial drought model was used, and when drought level had no effect (all other insects), the simplified models (with no drought level factor) were used to obtain drought sensitivity indices. Black: predators; dark grey: detritivores; light grey: filter feeders. Error bars represent standard errors. Solid line: linear model prediction without outlier (*Wyeomyia* spp.) in model ( $R^2 = 0.92$ ,  $F_{1,8} = 84.74$ , p < 0.001); dashed line: linear model prediction with outlier included in model ( $R^2 = 0.65$ ,  $F_{1,8} = 14.53$ , p = 0.005).

Insect drought sensitivity predicts their habitat sensitivity, as insect species with a high drought sensitivity occurred in larger habitats than species with a low sensitivity to drought ( $R^2 = 0.65$ ,  $F_{1,8} = 14.53$ , p = 0.005; Fig. 2.3). However, filter-feeding *Wyeomyia* mosquitoes deviated significantly from the otherwise strong relationship. When *Wyeomyia* spp. were removed from the model, drought sensitivity was an even better predictor of insect habitat size sensitivity ( $R^2 = 0.92$ ,  $F_{1,8} = 84.74$ , p < 0.001; Fig. 2.3), suggesting that habitat size preference of *Wyeomyia* mosquitoes may depend on factors other than drought sensitivity.

# DISCUSSION

Drought sensitivity, not trophic level, predicts habitat size sensitivity in bromeliad insect larvae. Although predators occurred in larger habitats than detritivores, once we accounted for differences in regional abundances between insect species, the apparent preference of predators as a trophic level for larger habitats disappeared. As with habitat size sensitivity, we found no evidence that drought sensitivity was related to trophic level. However, drought sensitivity predicted habitat size sensitivity in bromeliad insects, as insects that exhibited high drought sensitivities occurred in significantly larger habitats than expected by chance. Thus, physiological tolerance is a good predictor of habitat size preference in this aquatic ecosystem, but trophic level is not.

#### Trophic level does not predict drought sensitivity or habitat size sensitivity

Contrary to our expectations, higher trophic levels were not more sensitive to drought than lower trophic levels (Fig. 2.2). Thus, our study does not support the common assertion that predators are more vulnerable to environmental stressors than prey (Menge and Sutherland 1987, Petchey et al. 1999, Brashares et al. 2001, Spiller and Schoener 2007, Woodward et al. 2010, Ledger et al. 2011, Zarnetske et al. 2012). Our results also do not support a greater sensitivity of predators to habitat size, for example as predicted by the trophic rank hypothesis (Holt et al. 1999). Instead, our null model approach confirms previous analyses of this system which concluded that most predators occur in larger habitats than detritivores due to sampling effects (Srivastava et al. 2008). Generally, predators are rarer than their prey (Silva and Downing 1994), so sampling effects may be a major reason why predators are mostly found in larger habitats. An important exception in bromeliads is the top predator Mecistogaster modesta, which did occur in larger habitats than predicted by null expectations (Fig. 2.1). Our study now confirms an earlier conjecture (Srivastava et al. 2008) that the habitat preference of *M. modesta* reflects a relatively high drought sensitivity of this top predator. It is difficult to ascribe the drought sensitivity of M. *modesta*, or indeed any other species we examined, to a specific ecological trait. Drought vulnerable taxa (M. modesta, Culex spp., Polypedilum sp.) included a diverse range of taxonomic classifications, trophic levels, evolutionary histories, feeding groups, body sizes, longevities, regional abundances, etc. We therefore conclude that in bromeliad insects, drought sensitivity cannot be predicted from traits other than physiological tolerance to drought.

Interestingly, only three taxa (*M. modesta*, Tanypodinae, and *Anopheles* spp.) responded to the level of drought. For these insects, when there was some moisture, the negative effects of drought on growth rate disappeared. In the case of the predators *M. modesta* and Tanypodinae, it is conceivable that a small amount of water did allow them to continue feeding, but no water prevented them from feeding. If this is true, their vulnerability to drought may not be based on physiological processes, but by preventing them from physically ingesting prey. Alternatively, for *M. modesta* some moisture may have been sufficient to keep their caudal gills moist for gas exchange.

#### Drought sensitivity determines habitat size sensitivity in bromeliad insects

Except for the filter feeding Wyeomvia spp., drought sensitivity was an exceptionally strong predictor of habitat size sensitivity for bromeliad insects ( $R^2 = 0.92$  in model excluding Wyeomyia spp., Fig. 2.3). Thus, other factors that are typically considered important determinants of community composition, such as dispersal and biotic interactions, do not seem to be significant in determining the realized niches of bromeliad insects. It has been argued that in systems with demanding physiochemical environments, biotic interactions contribute relatively little to community structure (Poff and Ward 1989). Although biotic interactions are important in determining energy flow and abundances in bromeliad communities (Srivastava 2006, Srivastava et al. 2008, Srivastava and Bell 2009, Starzomski et al. 2010), their significance may be overshadowed by environmental stress in this hydrologically dynamic system. Moreover, all bromeliad insects under investigation in this study are winged adults, and thus good dispersers. Thus, in systems where environmental stressors are pronounced (e.g. temporary waters, arid environments, alpine elevations), and where species are good dispersers, physiological resistance to environmental stressors may be the dominant driver of community structure, and a trait-based approach to niche modeling may be appropriate. The notable exception to the predictive ability of drought sensitivity for habitat size sensitivity was the filter feeding Wyeomyia spp. This mosquito deviated from the otherwise strong relationship by selecting much smaller habitats than expected based on its drought sensitivity. Thus, this species likely experiences other pressures that force it to occupy smaller, more drought-prone habitats. Recent experiments have shown

bromeliad-dwelling *Wyeomyia* mosquitoes to be more susceptible to odonate predation than other species (Hammill et al. 2014). Since small bromeliads are largely predator-free (Fig. 2.1), habitat preference in *Wyeomyia* spp. may reflect a trade-off between drought sensitivity and predator vulnerability (Gilbert et al. 2008, Hammill et al. 2014).

## Conclusions

Our study showed that physiological tolerance to environmental stress is an exceptionally strong predictor for habitat size sensitivity of bromeliad-dwelling insects, as species that were more sensitive to drought required significantly larger, less drought prone habitats than species that were less affected by drought (Fig. 2.3). Consistent with the common prediction that predators require larger habitats than their prey (Holt et al. 1999, Srivastava et al. 2008, Petermann et al. 2014), we found that predators tended to occur in larger bromeliads than detritivores. However, the observed increase in habitat size with trophic level was due to differences in regional abundances between predators and detritivores, and not due to differences in sensitivity to environmental stress, as predators were rarer than detritivores.

Nevertheless, drought sensitivity did not predict habitat size sensitivity for all species, as *Wyeomyia* spp. significantly deviated from this relationship (Fig. 2.3). Consequently, we suggest that physiological tolerance to environmental stress must be used cautiously as a predictor of species occurrence, as species interactions and dispersal limitation can complicate responses to environmental stress, for instance by changing behaviour and predation risk (Chapter 3). However, in systems where environmental conditions are the main limiting agents of species (e.g. in stressful environments), physiological trait-based approaches may be especially useful in making niche predictions.
Climate forecasts predict that precipitation will decrease and become more variable in northwestern Costa Rica (Giorgi 2006, Karmalkar et al. 2008), leading to increased frequencies and severities of drought. Therefore, drought vulnerable species (*M. modesta, Culex* spp., *Polypedilum* sp.) will likely require larger bromeliads in the future. Because bromeliad abundance negatively correlates with bromeliad size (Melnychuk and Srivastava 2002), we predict that the number of suitable habitats for drought vulnerable species will decrease as climate change progresses, with potentially detrimental effects on the populations of these drought sensitive species.

## **Chapter 3: Species Interactions Determine Effects of Drought on a Contained Aquatic Ecosystem**

### **INTRODUCTION**

Efforts to understand the effects of climate change on ecological communities and ecosystems have traditionally focused on direct, physiological effects of altered temperature (e.g. McKechnie and Wolf 2010) or precipitation (e.g. Ernest et al. 2000, Báez et al. 2006, Ledger et al. 2008) on species. However, there is increasing evidence that the indirect effects of climate change, mediated by altered species interactions, are at least as important (e.g. Brown et al. 2001, Walther et al. 2002, Stenseth et al. 2002, Schmitz et al. 2003, Chase and Knight 2003, Montoya et al. 2009, Brodie et al. 2012, McCluney et al. 2012, Blois et al. 2013, Barton and Ives 2014a, Ockendon et al. 2014). Because species are intimately connected by trophic links, the response of food webs to climate change will not only consist of the direct response of each species, but also of the cascading effects of shifts in species abundance on other species within the network. Interspecific interactions, such as interactions with consumers (e.g. Barton 2010), competitors (e.g. Ledger et al. 2008), mutualists (e.g. Barton and Ives 2014b) and resources (e.g. Báez et al. 2006), may be sensitive to environmental change (McCluney et al. 2012). A complete understanding of the effects of climate change on ecological systems therefore requires quantification of the direct responses of individual species to altered environmental conditions, as well as indirect responses due to altered interactions with other species and resources. This is especially important as indirect effects of climate change can lead to opposite outcomes as those that would be expected from direct effects alone, such as a species benefitting from climate

change due to adverse effects on their predator (Chase and Knight 2003, Barton 2010) or competitor (Chase and Knight 2003).

The response of food webs to climate change can have consequences for the entire ecosystem. Species are active agents in determining the flux and transformation of carbon and nutrients in ecosystems (Hobbie 1992, Spooner and Vaughn 2008, Carrera et al. 2009, Hicke et al. 2012, Cardinale et al. 2012), so any shift in species composition and abundances, such as from altered environmental conditions, can alter these processes. For instance, changes in community trophic structure as a result of warming can lead to increases in decomposition rates in microbial systems (Petchey et al. 1999), therefore affecting ecosystem functioning. Similarly, community shifts are predicted to drive a shift in ecosystem state in temperate lakes from clearwater to eutrophic (Meerhoff et al. 2007). Thus far, most studies that have included indirect effects of environmental change on food webs and ecosystems have largely focused on modeling efforts (e.g. Montoya et al. 2009), or have inferred indirect effects from correlations (e.g. Ledger et al. 2011, Luczak et al. 2011) and therefore lack a verified mechanistic basis (Ings et al. 2009). Few manipulative experiments have been conducted, and those that have are largely in simplified systems (e.g. Petchey et al. 1999). As direct physiological responses and indirect effects of climate change, via altered species interactions, occur in synchrony, the manipulation of both abiotic conditions and biological communities is required to tease apart the underlying mechanisms.

Given the complexity of ecological networks, a major challenge for ecologists today is to find general patterns that predict how effects of climate change cascade through ecosystems. The trophic level and traits of species may be useful in predicting both the direct and indirect responses to climate change. In terms of direct responses, certain traits are linked to sensitivity to changes in temperature (e.g. large body size, low abundance: Petchey et al. 1999, Woodward et al. 2010) and precipitation (e.g. long generation time: Chadwick and Huryn 2007, longevity, large body size: Ledger et al. 2011). Thus, in food webs where body size and generation time correlate with trophic level (Rooney et al. 2008), higher trophic levels are generally more sensitive to environmental change than lower trophic levels (Petchey et al. 1999, Woodward et al. 2010, Ledger et al. 2011, Zarnetske et al. 2012). Indeed, predators can be disproportionally affected by experimental increases in temperature (Petchey et al. 1999, Marquis et al. 2014) and drought (Ledger et al. 2011, Chapter 2), and carnivores are expected to exhibit a disproportionally high climate sensitivity (Voigt et al. 2007).

Not only are predators expected to be particularly sensitive to climate change, but climate-related shifts in their abundance can have profound effects on communities and ecosystems (Estes et al. 2011, Zarnetske et al. 2012, Sanders et al. 2013). For example, predatory sea stars (*Pisaster ochraceus*) govern intertidal community structure by preventing the competitive exclusion of invertebrates and benthic algae by mussels (Paine 1974). Similarly, predators such as sea otters prevent overgrazing of kelp by sea urchins via a three-tier trophic cascade (Estes and Duggins 1995), whereas piscivorous fishes prevent phytoplankton blooms via a four-tier trophic cascade (Carpenter et al. 2001). Thus, direct negative effects of climate change on predators may indirectly affect food webs and ecosystems by altering top-down trophic interactions.

Climate change may not only indirectly affect species by altering negative species interactions, such as predation, but also by altering positive interactions, such as mutualism or

facilitation. Thus, species benefitting from mutualism or facilitation may be particularly vulnerable to climate change if the benefactor species is negatively affected by climate change (Stachowicz 2001, Bascompte and Stouffer 2009, Kiers et al. 2010, Marquis et al. 2014). Indeed, warming has been shown to negatively affect aphids indirectly via adverse effects on their protectors, ants (Barton and Ives 2014b).

Here, we experimentally assess the relative importance of direct and indirect effects of increases in drought - as predicted by climate change - on community composition, ecosystem functioning, and habitat quality for a Neotropical aquatic insect food web. Because of their relative isolation, freshwater ecosystems are particularly vulnerable to climate change (Woodward et al. 2010), and precipitation change is predicted to be important for the Neotropics (Karmalkar et al. 2008). For example, in northwestern Costa Rica, rainfall may decrease by up to 30% and there is already evidence of reduced precipitation on mountains as a result of elevated cloud cover (Karmalkar et al. 2008). Within the Neotropics, water-filled bromeliads are an ideal system to assess the direct and indirect effects of drought on food webs as they are a repeatable unit of a relatively contained ecosystem. The macroinvertebrate food webs within these detritalbased, miniature ecosystems are known to include both strong top-down effects of apex predators on detritivores (Srivastava 2006, Srivastava et al. 2008, Srivastava and Bell 2009), and facilitative effects of shredder and scraper detritivores (collectively called processors) on collector species (Starzomski et al. 2010). These species interactions have also been shown to affect rates of carbon (Atwood et al. 2013, 2014) and nutrient (Ngai and Srivastava 2006) cycling within the aquatic ecosystem.

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We used manipulations of predatory and facilitative taxa, crossed with an experimental drought, to separate the direct and indirect effects of drought on food web structure and ecosystem process. We hypothesized that (1) the direct negative effects of drought will be strongest for predators, that (2) drought will shift the trophic structure towards detritivores as a result of reduced top-down control, therefore (3) increasing the rate of decomposition and (4) shifting habitat quality to a more eutrophic state, as a result of increased decomposer activity. We also hypothesized that (5) drought will enhance the processing chain due to processor release from predation, therefore benefitting collector species.

#### METHODS

#### Experimental manipulation of drought and trophic structure

The aim of our experiment was to determine the direct and indirect effects of drought on macroinvertebrate community composition, decomposition (an ecosystem function) and water quality (an ecosystem state). If the effects of drought on a response variable are primarily mediated indirectly, via species interactions, we would expect the effect of drought to depend on community structure. To test for such drought x community structure interactions, we crossed four distinct insect communities that differed in functional composition with 12 drought treatments. The four insect communities consisted of all combinations of predator presence/absence and processor presence/absence, allowing us to further compare the effects of top-down (predator presence vs. absence) versus facilitative effects (processor presence vs. absence) as well as their interaction. The 12 drought treatments consisted of a range from 0 to 22 days of drought length (with 2 day intervals between treatments), representing a drought length

that is well within current conditions (Fig. 1.2). We chose a regression design because of its increased power over ANOVA designs, and its ability to capture nonlinear responses to continuous factors (Cottingham et al. 2005). Insect communities consisted of up to nine of the most regionally common insect taxa including detritivores, filter feeders, and a top predator (Table 3.1), with abundances of each species based on field observations spanning 7 years (Srivastava 2006, Srivastava et al. 2008, D.S. Srivastava unpubl. data).

 Table 3. 1. Initial community composition in mesocosms. Communities were assembled with (P+) and without

 (P-) predators, and with (S+) and without (S-) processors (shredders and scrapers) in a full factorial design. Numbers represent numbers of individuals per replicate.

		Community					
Functional Group	Taxon	P-/S-	<b>P-/S</b> +	P+/S-	<b>P</b> +/ <b>S</b> +		
Predator	Pseudostigmatidae: Odonata (Mecistogaster modesta)	-	-	1	1		
Processors: Shredder	Tipulidae: Diptera (Trentepholia sp.)	- 2 -					
Scraper	Scirtidae: Coleoptera (Scirtes sp.)	-	6	-	6		
	Chironomidae: Diptera (Polypedilum sp.)	5	5	5	5		
Collectors	Chironomidae: Diptera (Chironomus sp.)	2	2	2	2		
	Chironomidae: Diptera (Orthocladiinae)	2	2	2	2		
	Culicidae: Diptera ( <i>Culex</i> sp.)	2	2	2	2		
Filter feeders	Culicidae: Diptera (Wyeomyia sp.)	2	2	2	2		
	Culicidae: Diptera (Anopheles sp.)	1	1	1	1		

The experiment was set up on 20 November 2012. Mesocosms (Chapter 1) were necessary to allow for the assembly of replicate insect communities, as well as for the precise manipulation of water level and drought length. Once communities (Table 3.1) were assembled, we sealed the top of the mesocosm tubes with emergence traps (mesh bag:  $d = 80 \ \mu m$ ) to prevent insect oviposition and monitor emergences. We placed mesocosms randomly on a shaded outdoor veranda, with ambient conditions similar to those in the adjacent forest, but without the confounding natural inputs of precipitation, detritus, and insects.

On 22 November, we initiated drought in all mesocosms except in the four mesocosms that had a drought length of 0 days, by removing all water from the cups. At completion of drought (after 2 to 22 days depending on treatment), we added filtered stream water to cups until a volume of 15 ml inside the tube was reached. Every day until and including 15 December, we replaced 50% of the water inside mesocosms (except for mesocosms without water due to drought treatment) to simulate the natural flushing of bromeliad water by rain and to prevent hypoxia, and we monitored insect emergences using the emergence traps attached to the tubes. On 16 December, two days after the 22 day drought treatment was over, we measured pH, O<sub>2</sub>, chlorophyll a, and turbidity in each mesocosm to quantify treatment effects on water quality. On 17 December, we emptied mesocosms to quantify surviving insects. We oven dried and weighed intact leaves and fragments > 2 mm<sup>2</sup> to determine decomposition rates as the difference in dry weight before and after the experiment.

#### **Statistical analyses**

We used linear models to quantify the effects of drought, predators, processors, as well as their possible interactions, on insect survival, decomposition, and habitat quality. We calculated the fraction of insects that survived in each mesocosm until the end of the experiment for each functional feeding group (i.e. predators, shredders, scrapers, filter feeders, and collectors) as response variables. We excluded insects that emerged from this calculation (e.g. if 2 out of 6 original scraper larvae were alive as larvae at the end of the experiment and 1 additional larva emerged as an adult, then survival was calculated as 2/5 or 40%), because most insects that emerged did so during or before drought and could therefore not be considered as drought survivors. In order to obtain a single response variable for water quality, we performed a Principle Component Analysis (PCA) on water quality measurements (i.e. pH, O<sub>2</sub> and chlorophyll a concentrations, and turbidity), as they were likely correlated. We used Quantile-Quantile, residual and outlier plots to check for model suitability. Many relationships with drought length were non-linear, or exhibited heteroscedasticity, requiring transformation (see Appendix). For filter feeder survival, no transformation was able to adequately describe the drought x predator interaction, so we employed two separate models: one where predators were present, and one where they were absent. To statistically quantify the effect of predators on filter feeders, we used the non-parametric Wilcoxon rank sum test.

To explore the mechanisms of indirect effects of drought on community composition, ecosystem function and habitat quality, we employed linear models in combination with orthogonal contrasts, if appropriate, as *post hoc* analysis for responses that showed a significant drought x community treatment interaction. We also used this approach to determine whether the two processor species differ in their effect on predators. This time, instead of using initial community treatment as an explanatory factor in the model, we modified the levels of the explanatory variables to account for insects that perished during the experiment, such as from drought. The insect explanatory variables were modified as follows: predator variable (3 levels: not added, added and died, added and survived), scrapers (3 levels: not added, added and < 50% survived, added and > 50% survived), shredders (4 levels: not added, added and none survived, added and one survived, added and both survived), and collectors (3 levels: all dead, < 20% survived, > 20% survived). Levels were chosen in order to ensure enough data points in each level for analysis. We will refer to these *post hoc* variables as "taxa fate" (e.g. predator fate) from hereon in. We used stepwise regression (as determined by the lowest AIC), to select taxa fates that best explained insect survival, decomposition, and eutrophication, respectively. By following the fate of particular taxa and employing orthogonal contrasts, we could decompose the effect of that taxon on a response into the effect of the taxon being initially added or not, as opposed to the effect of the number of surviving individuals or the presence of dead individuals in the mesocosm. To determine the relationship between decomposition and water quality, we used a Pearson's product-moment correlation.

Again, model assumptions were checked with Quantile-Quantile and residual plots. Transformations were necessary for water quality to meet model assumptions (see Appendix). All analyses were carried out in R statistical software (version 3.1.0: R Core Team, 2014).

#### RESULTS

#### Direct and indirect effects of drought and community manipulations on insect survival

The effects of drought on insect survival depended on functional group, and included direct reductions of survival (especially for predators, shredders and filter feeders), indirect increases in survival via drought-induced reductions in predation (shredders), and neither direct nor indirect changes in survival (scrapers, collectors; Table 3.2A, Fig. 3.1). In some cases, insect survival was also affected by community composition irrespective of drought (predators, filter feeders, collectors).

Table 3. 2. F ratios and p-values for effects from linear models for (A) insect survival and (B) ecosystem responses for drought and community treatment and their interactions. Treatment variables: drought = drought length (days), pred = predator treatment, proc = processor treatment. Dashes indicated absence of dependent variable in one or more treatments, for example predator survival cannot be assessed in treatments without predators and neither can processor survival be assessed in treatments without processors. Filter feeder survival was modelled separately in treatments with predators (P+) and without predators (P-), due to the near zero survival in the former. PC1 is first principle component obtained from the principle component analysis (PCA).

A Response		drought	pred	proc	drought:pred	drought:proc	pred:proc	drought:pred:proc	$\mathbf{R}^2$
Predator	F <sub>1,20</sub>	4.908	-	5.289	-	0.055	-	-	
(Mecistogaster modesta)	р	0.039	-	0.032	-	0.816	-	-	0.339
Shredder	F <sub>1,20</sub>	0.009	0.074	-	6.437	-	-	-	
(Trentepholia sp.)	р	0.925	0.789	-	0.020	-	-	-	0.246
Scraper	F <sub>1.20</sub>	2.185	2.252	-	1.511	-	-	-	
(Scirtes sp.)	р	0.155	0.149	-	0.233	-	-	-	0.229
Collectors	F <sub>1.40</sub>	0.010	1.542	2.192	0.547	1.373	4.517	1.255	
(Chironomidae)	p	0.922	0.222	0.147	0.464	0.248	0.040	0.269	0.222
Filter Feeders (P+)	F <sub>1.20</sub>	0.524	-	0.000	-	1.052	-	-	
(Culicidae)	р	0.478	-	1.000	-	0.317	-	-	0.073
Filter Feeders (P-)	$F_{1,20}$	35.385	-	4.221	-	0.500	-	-	
(Culicidae)	p	<0.001	-	0.053	-	0.488	-	-	0.667

B Response		drought	pred	proc	drought:pred	drought:proc	pred:proc	drought:pred:proc	$\mathbb{R}^2$
Decomposition	F <sub>1,40</sub>	0.205	0.315	2.463	5.657	0.016	1.445	0.017	
(Leaf loss (mg))	р	0.653	0.578	0.124	0.022	0.900	0.236	0.898	0.202
Water quality	F <sub>1,40</sub>	13.614	0.578	3.586	4.691	5.149	0.014	0.078	
(PC1)	р	<0.001	0.452	0.066	0.036	0.029	0.906	0.782	0.409



**Figure 3. 1. Fraction of insects survived (points) with linear model predictions (lines) vs. drought length for the four community compositions**. Community treatments are initial predator addition (added: black, not added: gray) crossed with initial processor addition (added: solid, not added: dashed/empty). Points are jittered slightly along x-axes for clarity of the display. Two separate linear models were used for filter feeder survival for the two predator addition treatments.

#### Drought and shredders decreased predator survival

Predatory damselflies were adversely affected by drought, with less than half of individuals surviving when there were more than ten consecutive days of drought (Table 3.2A, Fig. 3.1). Contrary to our initial predictions, predator survival was also reduced by processor presence, on average 34% irrespective of drought length (Table 3.2A, Fig. 3.1). Processors include both shredders and scrapers, either of which could underlie the observed negative effects on predators. We used *post hoc* regression analyses to determine that shredders, but not scrapers, were the best predictor of decreased predator survival (shredders:  $F_{3,20} = 6.21$ , p = 0.004; scrapers were removed from model by stepwise regression). Further, predator survival was significantly reduced when any shredders survived in the community, regardless of how many survived (orthogonal contrasts in Fig. 3.4A).

#### Drought had indirect positive effects on shredders by reducing predation

Because increased drought length reduced predator survival, the strength of top-down effects on other insects diminished with increased drought length, and particularly benefitted shredders. In predator-free mesocosms, shredders were strongly negatively affected by drought, but in mesocosms with predators, shredder survival instead increased with drought length (Table 3.2A, Fig. 3.1). We were able to attribute this drought x predator interaction to drought-induced changes in predator survival as follows. First, when we modelled shredder survival in our *post hoc* analysis with predator fate as explanatory factor and drought length a covariate, shredder survival was significantly affected by predator fate ( $F_{2,20} = 3.79$ , p = 0.040) but not by drought length ( $F_{1,20} = 1.34$ , p = 0.260), suggesting that predators are the proximate determinant of shedder survival. Second, orthogonal contrast analyses showed that shredder survival was

significantly reduced in communities where predators survived, but not in communities where predators were initially present but perished (orthogonal contrast in Fig. 3.4B). Thus, in the presence of predators, the indirect positive effects of drought on shredders (via reducing predation) outweighed its direct negative effects.

#### Drought and predators decreased filter feeder survival

For filter feeders, drought also had strong negative effects on survival when predators were absent (Table 3.2A, Fig. 3.1), but these effects were masked when predators were present, possibly because predators consumed filter feeders before drought could affect filter feeder survival. In communities with predators, only two out of 120 filter feeders survived (Wilcoxon rank sum test: W = 403, p = 0.003). Thus predation reduced the numbers of surviving filter feeders to such low levels that there were essentially no surviving individuals to respond either directly or indirectly to drought.

#### Predators and processors interacted to affect collector survival

Although collector survival was not directly or indirectly reduced by drought, predators and processors interacted to affect collector survival (Table 3.2A, Fig. 3.1). Collector survival was highest in communities without predators and processors, and the presence of either predator or processors reduced mean survival by 54.7% and 58.5%, respectively. The reduction in collector survival by processors is contrary to our initial predictions of a processing chain facilitation between processors and collectors. Interestingly, when both predators and processors were present simultaneously, mean survival was only reduced by 44.2% (predator x processor interaction, Table 3.2A), suggesting that the negative effects of processors and predators on each other benefitted collectors indirectly.

# Direct and indirect effects of drought and community manipulations on decomposition and water quality

By decreasing top-down control on shredders, drought interacted with predators to indirectly increase the rate of decomposition, which led to eutrophication inside the mesocosms (Table 3.2B, Figs 3.2, 3.3 and 3.6).

#### Drought increased decomposition indirectly by releasing shredders from predation

The effects of drought on decomposition depended on predator presence in the community, and positive effects of drought on decomposition were at least partially mediated via predator effects on shredders. In communities with predators, drought increased decomposition, but in communities without predators, decomposition decreased slightly with drought length (drought x predator interaction: Table 3.2B, Fig. 3.2). We hypothesized that the previously shown indirect positive effect of drought on shredders (due to reduced predation) likely resulted in an indirect positive effect of drought on decomposition. We were able to support this mechanism by *post hoc* regression analysis, as decomposition was only affected by shredder fate ( $F_{3,38} = 3.07$ , p = 0.039), not the fate of scrapers ( $F_{1,38} = 0.07$ , p = 0.791), collectors ( $F_{2,38} = 0.83$ , p = 0.445), or predators ( $F_{2,38} = 0.15$ , p = 0.861), nor the covariate drought ( $F_{1,38} = 0.14$ , p = 0.706). Moreover, orthogonal contrast analysis on the reduced model, which only included shredder fate as an explanatory factor, revealed that the presence of at least one shredder individual significantly increased decomposition (Fig. 3.4C). These results suggest that drought

indirectly increased decomposition by releasing shredders, a keystone decomposer, from predation (Fig 3.6). However, this top-down mechanism cannot fully explain the positive effects of drought on decomposition, as drought also increased decomposition in communities with predators but without processors (Fig. 3.2). We will elaborate on this point further in the Discussion.



**Figure 3. 2. Decomposition, measured as loss of dried leaves (points) with linear model predictions (lines) vs. drought length for the four different community compositions**. Community treatments are initial predator addition (added: black, not added: gray) crossed with initial processor addition (added: solid, not added: dashed/empty). Points are jittered slightly along x-axes for clarity of the display.

#### Drought increased eutrophication by indirectly increasing decomposition

By reducing top-down control on shredders, drought indirectly increased decomposition, shifting water quality to a more eutrophic state (Figs 3.5 and 3.6). Communities differed in water

quality at the end of the experiment, and were distributed along an eutrophication gradient, ranging from low eutrophication levels (relatively high  $O_2$  concentration, high pH, low turbidity, and low chlorophyll a concentration) to high eutrophication levels (reverse of the former; Fig. 3.3A). Because of this evident eutrophication gradient (PC1 in Fig. 3.3A), we proceeded to use the first principle component (PC1) as an index of water quality in our analysis.

The effects of drought on water quality depended on predator and processor presence in the community (Table 3.2B, Fig. 3.3B). In mesocosms with either the presence of predators or the absence of processors, eutrophication increased as drought length increased. The significant drought x predator interaction for water quality suggests that drought may either indirectly alter water quality by increasing the rate of detrital decomposition (via releasing shredders from predation: Fig. 3.6), or by increasing predator mortality and thus necrophilic microbes, or both. The first mechanisms is supported both by the significant positive correlation between decomposition and eutrophication (Pearson's correlation: r = 0.405,  $t_{46} = 3.00$ , p = 0.004; Fig. 3.5) and by our post hoc analysis; stepwise regression analysis on water quality using a full model with predator fate, shredder fate, scraper fate, collector fate, decomposition and drought length as explanatory variables only kept decomposition, drought length, and scraper fate in the reduced model (decomposition:  $F_{1,43} = 7.30$ , p = 0.010; drought length:  $F_{1,43} = 17.58$ , p < 0.001; scraper fate:  $F_{2,43} = 4.60$ , p = 0.015). Thus, the predator-shredder-decomposition mechanism (Fig. 3.6) is partially responsible for increased eutrophication with drought. However, the *post* hoc analysis also demonstrates that scrapers and drought also had additional positive effects on eutrophication other than by affecting decomposition.



Figure 3. 3. (A) Principle Component Analysis of ecosystem responses (final concentrations of O<sub>2</sub> and chlorophyll a, pH, and turbidity). The first principle component (PC1) explains 49.5% of the variation and represents an eutrophication gradient, where a higher score on the PC1 axis corresponds to a more eutrophic state.
(B) Eutrophication (PC1) vs. drought length for the four community compositions. Community treatments are initial predator addition (added: black, not added: gray) crossed with initial processor addition (added: solid, not added: dashed/empty). Points are jittered slightly along x-axes for clarity of the display.



**Figure 3. 4. Orthogonal contrast results (t and p values) for** *post hoc* **orthogonal contrast analyses**. Different letters (A or B) indicate statistical significant difference (at alpha = 0.05). Error bars represent standard errors. Numbers represent sample size. **(A) Predator survival as response to shredder fate**. When at least one shredder survived, predator survival was significantly reduced (not added and both dead vs. one alive and both alive: t =-4.21, p < 0.001). There was no effect of dead shredders (not added vs. both dead: t = -0.99, p = 0.336) nor the number of shredders that survived in the community (one alive vs. both alive: t = -0.60, p = 0.555) on predator survival. **(B) Shredder survival as response to predator fate**. There was no effect of initial predator presence in the community (not added vs. dead and alive: t = 0.97, p = 0.344), but shredder survival significantly decreased when the predator survived (dead vs. alive: t = 2.74, p = 0.013). **(C) Decomposition (dry leaf loss) as response to shredder fate**. When at least one shredder **fate**. There was no effect of dead shredder **s** and both dead vs. one alive and both alive: t = 3.52, p = 0.001). There was no effect of dead shredders (not added vs. both dead: t = 1.17, p = 0.247) nor the number of shredders that survived in the community (one alive vs. both alive: t = 0.27, p = 0.786) on decomposition.



Figure 3. 5. Correlation of eutrophication (PC1) with decomposition (dry leaf loss). Eutrophication increases exponentially as decomposition increases (r = 0.405,  $t_{46} = 3.00$ , p = 0.004).



Figure 3. 6. Mechanism of indirect positive effects of drought on shredder survival, decomposition, and eutrophication. Drought indirectly benefitted shredders by decreasing predator survival. Increased shredder survival in turn increased decomposition, which increased eutrophication in the mesocosms. Solid arrows represent direct effects, dashed arrows represent indirect effects,  $\bigcirc$  represents positive effect,  $\bigcirc$  represents negative effect.

#### DISCUSSION

Drought and community manipulations had both direct and indirect effects on community structure, ecosystem function and ecosystem state (Fig. 3.6). The effects of drought on insect survival differed among functional feeding groups and ranged from no effects on collectors and scrapers, to direct negative effects on predators, shredders, and filter feeders, to indirect positive effects on shredders by reducing predation. By altering community composition and trophic structure, the effects of drought cascaded through the food web and ultimately affected ecosystem functioning and habitat quality, increasing decomposition and shifting water quality to a more eutrophic state.

#### Direct effects of drought on insect survival differ between bromeliad insects

Predator, shredder, and filter feeder survival decreased as drought length increased, while scrapers and collectors were unaffected by drought (Table 3.2A, Figs 3.1 and 3.6). These results agree with the hypothesis that species at higher trophic levels or with larger body sizes are often more sensitive to climate (Voigt et al. 2007), and are disproportionally affected by altered environmental conditions (Petchey et al. 1999, Joern et al. 2006, Woodward et al. 2010, Ledger et al. 2011, Gingold et al. 2013, Marquis et al. 2014). Differences in insect traits, such as physiology, morphology, and behaviour, may explain the variation in drought vulnerability between these taxa. The fact that scrapers and collectors were not affected by drought may be related to their breathing mechanisms, as the respiration methods of both groups involve direct absorption of oxygen against their bodies: Chironomidae collectors exhibit cutaneous respiration (Gordh and Headrick 2001), and Scirtidae scrapers exhibit both plastrons and spiracular

respiration (Stehr 1987). On the other hand, insects that were sensitive to drought in our study (odonate predators, Tipulidae shredders and Culicidae filter feeders) are insects that require submersion in water for gas exchange during their larval stages. The siphons or tubercules of Culicidae and Tipulidae, respectively, are respiratory structures that are supported in part by water (Christopher 1960), and the caudal gills of odonate nymphs (Eriksen 1986) require moisture for gas exchange. Behavioural traits to resist or avoid drought may also explain some of the differences in drought resistance we observed. *Polypedilum* and *Chironomus* chironomids (both collectors) build tubes to avoid predation, which may also help in preventing desiccation during drought (Kikawada et al. 2005). By contrast, odonates (predators) may avoid drought by choosing to oviposit in large bromeliads above 100 ml (Srivastava et al. 2005, Srivastava 2006), which are less likely to dry out (Zotz and Thomas 1999), a strategy that was of course circumvented by our experimental assembly of species.

# Drought had indirect positive effects on shredders and decomposition, which increased eutrophication

By decreasing predator survival, drought had indirect positive effects on shredder survival, resulting in increased decomposition and a shift in habitat quality to a more eutrophic state (Fig. 3.6). Although shredders responded negatively to drought in predator-free communities, an indirect positive effect of drought length arose because the positive effect of reduced predation exceeded the direct negative effect of drought on shredder survival (Table 3.2A, Fig. 3.1). In fact, shredder survival was higher in communities with predators than without predators for droughts exceeding ten days (Fig. 3.1), possibly due to the extra protein shredders obtained from consuming dead predators. Consequently, long droughts allowed shredders to increase their processing of detritus, which partially explained the increase in decomposition with drought in communities with predators (Table 3.2B, Fig. 3.2). Increased decomposition, in turn, correlated with a shift in water quality to a more eutrophic state (Fig. 3.5). Such changes in top-down effects have been observed in various systems undergoing simulated climate change (e.g. wetlands: Chase and Knight 2003, grasslands: Barton 2010, streams: Ledger et al. 2011) and may be common in systems with vulnerable predators and strong predator-prey interactions. Nevertheless, reduced top-down control of shredders cannot completely explain the ecosystem responses in our study. Notably, (1) decomposition and eutrophication also increased in communities with predators but without processors, and (2) drought increased decomposition and eutrophication in communities with predators to levels above what could be explained solely by the increased shredder survival (Figs 3.3 and 3.3B). Although we cannot definitively explain either of these two patterns relating to predator x drought interactions, it is possible that droughtinduced predator mortality fertilizes microbial communities and so increases decomposition and eutrophication. Indirect effects of drought on resource stoichiometry would be a promising area of further research. Nevertheless, this study shows that drought alters ecosystem functioning and state at least partially via releasing shredders from predation, and supports the growing consensus of the importance of indirect effects of climate in altering community structure and ecosystem functions (Brown et al. 2001, Stenseth et al. 2002, Walther et al. 2002, Suttle et al. 2007, Montoya et al. 2009, Brodie et al. 2012, McCluney et al. 2012, Blois et al. 2013, Barton and Ives 2014a, Ockendon et al. 2014).

#### Processors had negative effects on bromeliad insects independent of drought

Contrary to our expectations, processors did not facilitate other insects via a processing chain, nor did they benefit predators by increasing their food supply. On the contrary, the survival of predators, collectors, and filter feeders decreased in communities with processors (Table 3.2A, Fig. 3.1). Odonate survival was particularly reduced by shredders (Fig. 3.4A). The paradox of shredders being heavily consumed by predators, yet predator survival being decreased by shredders, may be due to the odonate's sensitivity to tactile stimulation (Atwood et al. 2014). Tipulidae shredders are relatively large and mobile, and opportunistically bite into whatever they come across (personal observation, D. Srivastava). Such physical interactions between shredders and odonates may have caused a stress response in the odonates, leading to decreased survival. In nature, *M. modesta* nymphs leave the bromeliad when another large insect, such as another odonate or a diving beetle (*Copelatus* sp.) is present, and this behaviour occurs in response to tactile cues (Atwood et al. 2014). In our experiment, however, such emigration was not possible as mesocosms were sealed. Only when predators were able to eat both shredders, and thus removed the tactile stimuli completely, did they have 100% survival (Fig. 3.4A).

Likewise, our results do not support a facilitative effect of processors on collectors via a processing chain found previously in the system (Starzomski et al. 2010). On the contrary, collector survival was negatively affected by processor treatment (Table 3.2A, Fig. 3.1). These contradictory findings may reflect differences in methodology between our study and that of Starzomski *et al.* (2010), such as the use of mesocosms in real bromeliads instead of mesocosms in cups, or the use of emergence of Orthocladiinae chironomids, instead of survival of a variety of chironomid species, as the response. In our study, any positive effects of processing were likely outweighed by negative effects of omnivory by shredders, and collectors exhibited the

highest survival in the absence of both predators and shredders, with otherwise poor survival rates (Fig. 3.1).

# The effects of drought on ecosystem function and state were largely mediated by altered top-down control

In our study, the effects of drought on ecosystem function and state can partially be explained via the top-down chain: drought  $\rightarrow$  predators  $\rightarrow$  shredders  $\rightarrow$  decomposition  $\rightarrow$  water quality. The indirect positive effect of drought on shredders, and the resulting increase in decomposition and shift in water quality to a eutrophic state, are opposite to what would have been expected from direct effects alone, and agree with the growing consensus that indirect effects of climate change can lead to counterintuitive outcomes (e.g. Stenseth et al. 2002, Schmitz et al. 2003, Chase and Knight 2003, Montoya et al. 2009, Brodie et al. 2012, McCluney et al. 2012, Blois et al. 2013, Barton and Ives 2014a). Thus, our results demonstrate that the consideration of species interactions is essential when attempting to predict climate change effects on communities and ecosystems.

For climate change effects to cascade through the food web, trophic levels have to be connected to one another by strong links. Here, the strong indirect effect of drought on decomposition and water quality via negative effects on predators are a result of shredders. Shredders exhibit a disproportionally high functional importance as decomposer, as well as a high susceptibility to predation as preferred prey item of *M. modesta* (LeCraw 2014). This covariance between functional importance and predation susceptibility in shredders, coupled with predator sensitivity to climate change, at least partially underlies the observed strong indirect effects of drought on function. This covariance of functional importance with predation

susceptibility may be key in transferring changes in predators through food webs in other ecosystems as well, for example, sea urchins that link sea otters to kelp (Estes and Duggins 1995), grasshoppers that link predatory spiders to herbs (Barton 2010), planktivore fish that link piscivore fish to zooplankton, and zooplankton who in turn link planktivores to phytoplankton (Carpenter et al. 2001).

#### Conclusions

It is becoming increasingly clear that species interactions cannot be ignored when predicting community and ecosystem responses to climate change. However, research has not yet focused on understanding general mechanisms underlying indirect effects of climate change, especially for drought, in altering ecosystem processes and states. Here, we show that by adversely affecting the top predator, climate change can cascade through the food web to alter community composition, decomposition, and habitat quality. This climate-induced cascade depended on shredders exhibiting both high predation susceptibility and high functional importance as decomposer, therefore forming a strong link between predator and detritus. This covariance of predation susceptibility and functional importance may be common in nature, and is essential for the effects of climate change to be transmitted through the food web. Apart from altering decomposition and habitat quality, it is likely that drought will also indirectly alter other ecosystem functions via adverse effects on the top predator. Bromeliads depend on insect communities and water in their wells for the absorption of nutrients. Since odonates retain nitrogen in the system by preying on detritivores and releasing waste back into the bromeliad, therefore preventing nutrients from being exported in the bodies of terrestrial adult insects (Ngai

and Srivastava 2006), drought may also have indirect negative effects on nutrient cycling in this ecosystem.

### **Chapter 4: General Conclusions**

Drought affects the bromeliad-dwelling insect community directly by governing habitat suitability, and indirectly by altering species interactions. The indirect effects of drought on community structure further affect ecosystem functioning and habitat quality. When examining what factors determine differences in habitat size sensitivity between species, I found physiological sensitivity to drought, but not trophic level, to be an exceptionally strong predictor (Chapter 2). Although predators tended to occur in larger habitats than detritivores, this trophic effect largely disappeared once I accounted for differences in regional insect abundances. Contrary to the premise that predators are more sensitive to environmental stressors (Worthen et al. 1998, Finn and Giller 2000, Schoener et al. 2001), I found no evidence that drought resistance was related to trophic level in bromeliad insects. Except for the top predator Mecistogaster *modesta*, most predators occurred in larger habitats because they were rare, not because they were more sensitive to drought. M. modesta was additionally physiologically sensitive to drought, displaying greater decreases in growth and survivorship than many other macroinvertebrate species in the system. When I examined the relative importance of indirect effects of drought on the bromeliad ecosystem, I found that drought-induced mortality of the keystone predator *M. modesta* reduced top-down control, altering community composition. These changes in macroinvertebrate composition cascaded through the food web to affect ecosystem functioning and habitat quality (Chapter 3). Specifically, the release of the Tipulidae larvae – disproportionately important as decomposers – from predation increased decomposition and shifted the ecosystem to a more eutrophic state. This result agrees with the growing

consensus that species interactions cannot be ignored when predicting ecological responses to climate change (Brown et al. 2001, Stenseth et al. 2002, Walther et al. 2002, Schmitz et al. 2003, Chase and Knight 2003, Montoya et al. 2009, Brodie et al. 2012, McCluney et al. 2012, Blois et al. 2013, Barton and Ives 2014a). Overall, this work suggests that variation between species in physiological tolerance to environmental stress can govern ecological responses to climate change. An understanding of the differences in drought sensitivities between species, especially the disproportionately high sensitivity of the top predator, allowed me to predict community and ecosystem responses in the bromeliad system. Thus, physiological ecology may not only be useful in predicting direct effects of climate change on species, but it may also be valuable in predicting the indirect effects if interactions among species in the system are known.

There are several caveats of this work that need to be addressed, such as the difference in scale and in response metrics between the two studies, and the use of mesocosms. Although species interactions were important in governing the insect food web at the scale of a single leaf well (Chapter 3), the habitat distribution of all insects except the filter feeding *Wyeomyia* mosquito at the scale of the whole bromeliad could be explained solely by species' regional abundances and physiological tolerances to drought (Chapter 2). These seemingly inconsistent results may reflect a diminishing importance of trophic interactions as a consequence of habitat complexity (Grabowski 2004) at the scale of whole bromeliads. Prey species may persist in actual bromeliads because increased habitat complexity reduces the probability of predators and prey co-occurring in the same leaf well (Srivastava 2006). Adult insects may also be highly selective in their oviposition behaviour, avoiding bromeliads of certain sizes because of risk of drought (e.g. *M. modesta*, Chapter 2) or predation (e.g. *Wyeomyia* mosquitoes, Hammill et al.

2014). Such oviposition decisions may reduce the indirect effect of drought in whole bromeliads by removing links in the drought-odonate-prey pathway.

The finding that direct effects govern habitat occupancy patterns in Chapter 2, but indirect effects are more important than direct effects in governing community and ecosystem responses in Chapter 3, may also reflect the different metrics used to quantify species responses. The presence or absence of a species may be sufficiently explained by direct effects of climate (Chapter 2), while species abundances may be more likely to respond to trophic interactions, and thus indirect effects of climate.

The use of mesocosms has considerable advantages, such as replicate communities and the precise manipulation of drought. However, there are several disadvantages of employing these oversimplified systems. Mesocosms only mimic a single leaf well with little habitat complexity. Further, mesocosms remove the normal interactions of the living bromeliad with the insect community, for example through nutrient uptake and water oxygenation. I attempted to mimic these properties of natural bromeliads in mesocosms as truthfully as possible, by providing a mimic for a leaf crevice to enhance complexity, by changing water to prevent hypoxia, and by adding microbial inoculants from real bromeliad water.

In conclusion, this work sheds light on the relative importance of direct and indirect effects of drought on community structure and ecosystem processes for freshwater ecosystems. Empirical studies of the relative importance of physiological responses to climate and the potential of climate change to alter trophic interactions to affect community and ecosystem responses are still rare, particularly for aquatic systems and precipitation. Thus, this work presents important insights into factors that not only govern contemporary ecosystems, but that can also be used to predict ecological responses to environmental change. Future work could repeat the community experiment at the scale of the whole bromeliad, to determine if drought still alters species interactions at this larger scale. The contrast between the mesocosm and a whole bromeliad experiment would provide insight on the importance of environmental heterogeneity in buffering for the effects of climate change on species interactions. Moreover, similar experiments could be conducted in other ecosystems, such as freshwater ponds or terrestrial systems, to test for the generality of these findings and broaden their applicability. Ultimately, these findings could aid in predicting the responses of communities and ecosystems to climate change, and inform conservation decisions.

### References

- Arad, Z., S. Goldenberg, and J. Heller. 1992. Intraspecific variation in resistance to desiccation and climatic gradients in the distribution of the land snail Xeropicta-vestalis. Journal of Zoology 226:643–56.
- Arad, Z., S. Goldenberg, and J. Heller. 1993. Intraspecific variation in resistance to desiccation and climatic gradients in the distribution of the bush-dwelling land snail Trochoideasimulata. Journal of Zoology 229:249–65.
- Atwood, T. B., E. Hammill, H. S. Greig, P. Kratina, J. B. Shurin, D. S. Srivastava, and J. S. Richardson. 2013. Predator-induced reduction of freshwater carbon dioxide emissions. Nature Geoscience 6:191–194.
- Atwood, T. B., E. Hammill, D. S. Srivastava, and J. S. Richardson. 2014. Competitive displacement alters top-down effects on carbon dioxide concentrations in a freshwater ecosystem. Oecologia 175:353–61.
- Báez, S., S. L. Collins, D. Lightfoot, and T. L. Koontz. 2006. Bottom-up regulation of plant community structure in an aridland ecosystem. Ecology 87:2746–54.
- Barton, B. T. 2010. Climate warming and predation risk during herbivore ontogeny. Ecology 91:2811–2818.
- Barton, B. T., and A. R. Ives. 2014a. Species interactions and a chain of indirect effects driven by reduced precipitation. Ecology 95:486–494.

- Barton, B. T., and A. R. Ives. 2014b. Direct and indirect effects of warming on aphids, their predators, and ant mutualists. Ecology 95:1479–1484.
- Bascompte, J., and D. B. Stouffer. 2009. The assembly and disassembly of ecological networks. Philosophical Transactions: Biological Sciences 364:1781–7.
- Bernardo, J., and J. R. Spotila. 2006. Physiological constraints on organismal response to global warming: mechanistic insights from clinally varying populations and implications for assessing endangerment. Biology Letters 2:135–9.
- Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. Science 341:499–504.
- Boulton, A. J. 1989. Over-summering refuges of aquatic macroinvertebrates in two intermittent streams in central Victoria. Transactions of the Royal Society of South Australia 113:23–34.
- Brashares, J. S., P. Arcese, and M. K. Sam. 2001. Human demography and reserve size predict wildlife extinction in West Africa. Proceedings: Biological Sciences 268:2473–8.
- Brodie, J., E. Post, F. Watson, and J. Berger. 2012. Climate change intensification of herbivore impacts on tree recruitment. Proceedings of the Royal Society B: Biological Sciences 279:1366–70.
- Brown, J. H., T. G. Whitham, S. K. M. Ernest, and C. A. Gehring. 2001. Complex species interactions and the dynamics of ecological systems: long-term experiments. Science 293:643–650.

- Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, A. P. Kinzig, G. C. Daily, M. Loreau, J. B. Grace, A. Larigauderie, D. S. Srivastava, and S. Naeem. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.
- Carpenter, S., J. Cole, J. Hodgson, J. Kitchell, M. Pace, D. Bade, K. Cottingham, T. Essington, J. Houser, and D. Schindler. 2001. Trophic cascades, nutrients, and lake productivity: whole-lake experiments. Ecological Monographs 71:163–186.
- Carrera, A. L., M. J. Mazzarino, M. B. Bertiller, H. F. del Valle, and E. M. Carretero. 2009. Plant impacts on nitrogen and carbon cycling in the Monte Phytogeographical Province, Argentina. Journal of Arid Environments 73:192–201.
- Chadwick, M. A., and A. D. Huryn. 2007. Role of habitat in determining macroinvertebrate production in an intermittent-stream system. Freshwater Biology 52:240–251.
- Chase, J. M., and T. M. Knight. 2003. Drought-induced mosquito outbreaks in wetlands. Ecology Letters 6:1017–1024.
- Chown, S., and K. Gaston. 1999. Exploring links between physiology and ecology at macroscales: the role of respiratory metabolism in insects. Biological Reviews of the Cambridge Philosophical Society 74:87–120.
- Chown, S. L. 2012. Trait-based approaches to conservation physiology: forecasting environmental change risks from the bottom up. Philosophical Transactions of the Royal Society B: Biological Sciences 367:1615–1627.

- Christopher, S. 1960. Aedes aegypti (L.) the Yellow Fever Mosquito. Pages 153–5. Cambridge University Press, Cambridge.
- Cohen, J. E., S. L. Pimm, P. Yodzis, and J. Saldaña. 1993. Body sizes of animal predators and animal prey in food webs. Journal of Animal Ecology 62:67–78.
- Connor, E. F., and E. D. McCoy. 1979. The statistics and biology of the species-area relationship. The American Naturalist 113:791–833.
- Cottingham, K. L., J. T. Lennon, and B. L. Brown. 2005. Knowing when to draw the line: designing more informative ecological experiments. Frontiers in Ecology and the Environment 3:145–152.
- Eliason, E. J., T. D. Clark, M. J. Hague, L. M. Hanson, Z. S. Gallagher, K. M. Jeffries, M. K. Gale, D. a Patterson, S. G. Hinch, and A. P. Farrell. 2011. Differences in thermal tolerance among sockeye salmon populations. Science 332:109–12.
- Eriksen, C. 1986. Respiratory roles of caudal lamellae (gills) in a lestid damselfly (Odonata: Zygoptera). Journal of the North American Benthological Society 5:16–27.
- Ernest, S. K., J. H. Brown, and R. R. Parmenter. 2000. Rodents, plants, and precipitation: spatial and temporal dynamics of consumers and resources. Oikos 88:470–482.
- Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T.E. Essington, R. D. Holt, J. B. C. Jackson, R. J. Marquis, L. Oksanen, T. Oksanen, R. T.Paine, E. K. Pikitch, W. J. Ripple, S. A. Sandin, M. Scheffer, T. W. Schoener, J. B. Shurin,
A. R. E. Sinclair, M. E. Soulé, R. Virtanen, and D. A. Wardle. 2011. Trophic downgrading of planet Earth. Science 333:301–306.

- Estes, J., and D. Duggins. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. Ecological Monographs 65:75–100.
- Finn, J. A., and P. S. Giller. 2000. Patch size and colonisation patterns : an experimental analysis using north temperate coprophagous dung beetles. Ecography 23:315–327.
- Freeman, B. G., and A. M. Class Freeman. 2014. Rapid upslope shifts in New Guinean birds illustrate strong distributional responses of tropical montane species to global warming.
  Proceedings of the National Academy of Sciences of the United States of America 111:4490–4.
- Gilbert, B., D. S. Srivastava, and K. R. Kirby. 2008. Niche partitioning at multiple scales facilitates coexistence among mosquito larvae. Oikos 117:944–50.
- Gingold, R., T. Moens, and A. Rocha-Olivares. 2013. Assessing the response of namatode communities to climate change-driven warming: a microcosm experiment. PloS ONE 8:e66653.
- Giorgi, F. 2006. Climate change hot-spots. Geophysical Research Letters 33:L08707.
- Gordh, H., and D. H. Headrick. 2001. A Dictionary of Entomology. Page 398. Second edition. CABI Publishing, New York.

- Grabowski, J. H. 2004. Habitat complexity disrupts predator-prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004.
- Hammill, E., T. B. Atwood, P. Corvalan, and D. Srivastava. 2014. Behavioural responses to predation may explain shifts in community structure. In review.
- Hicke, J. A., C. D. Allen, A. R. Desai, M. C. Dietze, R. J. Hall, E. H. Ted Hogg, D. M. Kashian,
  D. Moore, K. F. Raffa, R. N. Sturrock, and J. Vogelmann. 2012. Effects of biotic
  disturbances on forest carbon cycling in the United States and Canada. Global Change
  Biology 18:7–34.
- Hill, J. L., P. J. Curran, and G. M. Foody. 1994. The effect of sampling on the species-area curve. Global Ecology and Biogeography 4:97–106.
- Hobbie, S. E. 1992. Effects of plant species on nutrient cycling. Trends in Ecology and Evolution 7:336–9.
- Holt, R., J. Lawton, G. Polis, and N. Martinez. 1999. Trophic rank and the species-area relationship. Ecology 80:1495–1504.
- Ings, T. C., J. M. Montoya, J. Bascompte, N. Blüthgen, L. Brown, C. F. Dormann, F. Edwards,
  D. Figueroa, U. Jacob, J. I. Jones, R. B. Lauridsen, M. E. Ledger, H. M. Lewis, J. M.
  Olesen, F. J. F. van Veen, P. H. Warren, and G. Woodward. 2009. Ecological networks beyond food webs. The Journal of Animal Ecology 78:253–69.

- Joern, A., B. Danner, J. Logan, and W. Wolesensky. 2006. Natural history of mass-action in predator-prey models: A case study from wolf spiders and grasshoppers. The American Midland Naturalist 156:52–64.
- Karmalkar, A. V., R. S. Bradley, and H. F. Diaz. 2008. Climate change scenario for Costa Rican montane forests. Geophysical Research Letters 35:L11702.
- Kearney, M., and W. Porter. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology Letters 12:334–50.
- Kiers, T. E., T. M. Palmer, A. R. Ives, J. F. Bruno, and J. L. Bronstein. 2010. Mutualisms in a changing world: an evolutionary perspective. Ecology Letters 13:1459–74.
- Kikawada, T., N. Minakawa, M. Watanabe, and T. Okuda. 2005. Factors inducing successful anhydrobiosis in the African chironomid Polypedilum vanderplanki: Significance of the larval tubular nest. Integrative and Comparative Biology 45:710–4.
- Kohn, D., and D. Walsh. 1994. Plant species richness the effect of island size and habitat diversity. Journal of Ecology 82:367–377.
- LeCraw, R. M. 2014. The influences of spatial processes at multiple scales on local community structure and function. University of British Columbia.
- Ledger, M. E., F. K. Edwards, L. E. Brown, A. M. Milner, and G. Woodward. 2011. Impact of simulated drought on ecosystem biomass production: an experimental test in stream mesocosms. Global Change Biology 17:2288–2297.

Ledger, M. E., R. M. L. Harris, P. D. Armitage, and A. M. Milner. 2008. Disturbance frequency influences patch dynamics in stream benthic algal communities. Oecologia 155:809–19.

Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–417.

- Lindo, Z., J. Whiteley, and A. Gonzalez. 2012. Traits explain community disassembly and trophic contraction following experimental environmental change. Global Change Biology 18:2448–2457.
- Luczak, C., G. Beaugrand, M. Jaffré, and S. Lenoir. 2011. Climate change impact on Balearic shearwater through a trophic cascade. Biology Letters 7:702–5.
- Marquis, M., I. Del Toro, and S. L. Pelini. 2014. Insect mutualisms buffer warming effects on multiple trophic levels. Ecology 95:9–13.
- McCluney, K. E., J. Belnap, S. L. Collins, A. L. González, E. M. Hagen, J. Nathaniel Holland, B.
  P. Kotler, F. T. Maestre, S. D. Smith, and B. O. Wolf. 2012. Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change.
  Biological Reviews of the Cambridge Philosophical Society 87:563–82.
- McKechnie, A. E., and B. O. Wolf. 2010. Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. Biology Letters 6:253–6.
- McNab, B. 1963. Bioenergetics and the determination of home range size. The American Naturalist 97:133–140.

- Meerhoff, M., J. M. Clemente, F. T. de Mello, C. Iglesias, A. R. Pedersen, and E. Jeppesen. 2007. Can warm climate-related structure of littoral predator assemblies weaken the clear water state in shallow lakes? Global Change Biology 13:1888–1897.
- Melnychuk, M. C., and D. S. Srivastava. 2002. Abundance and vertical distribution of a bromeliad-dwelling zygopteran larva, Mecistogaster modesta, in a Costa Rican rainforest (Odonata: Pseudostigmatidae). International Journal of Odonatology 5:81–97.
- Menge, B., and J. Sutherland. 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. American Naturalist 130:730–757.
- Montoya, J. M., G. Woodward, M. C. Emmerson, and R. V Solé. 2009. Press perturbations and indirect effects in real food webs. Ecology 90:2426–33.
- Ngai, J. T., and D. S. Srivastava. 2006. Predators accelerate nutrient cycling in a bromeliad ecosystem. Science 314:963.
- Ockendon, N., D. J. Baker, J. A. Carr, E. C. White, R. E. A. Almond, T. Amano, E. Bertram, R.
  B. Bradbury, C. Bradley, S. H. M. Butchart, N. Doswald, W. Foden, D. J. C. Gill, R. E.
  Green, W. J. Sutherland, E. V. J. Tanner, and J. W. Pearce-Higgins. 2014. Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. Global Change Biology 20:2221–9.
- Paine, R. T. 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15:93–120.

- Pearman, P. B. 1995. Effect of pond size and consequent predator density on two species of tadpoles. Oecologia 102:1–8.
- Petchey, O. L., P. T. McPhearson, T. M. Casey, and P. J. Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:69–72.
- Petermann, J. S., V. F. Farjalla, M. Jocque, P. Kratina, A. A. M. MacDonald, N. A. C. Marino, P. D. de Omena, G. C. O. Piccoli, B. A. Richardson, M. J. Richardson, G. Q. Romero, M. Videla, and D. Srivastava. 2014. Dominant predators mediate the impact of habitat size on trophic structure in bromeliad invertebrate communities. Ecology:In press.
- Peters, R. 1983. The Ecological Implications of body size. Cambridge University Press, Cambridge.
- Poff, N. L. 1997. Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. Journal of the North American Benthological Society 16:391– 409.
- Poff, N. L., and J. V Ward. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Canadian Journal of Fisheries and Aquatic Sciences 46:1805–18.
- Polis, G., W. Anderson, and R. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics 28:289–316.

Pörtner, H. O., and A. P. Farrell. 2008. Physiology and climate change. Science 322:690–692.

- R Core Team. 2014. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ricklefs, R., and I. Lovette. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. Journal of Animal Ecology 68:1142–1160.
- Rooney, N., K. S. McCann, and J. C. Moore. 2008. A landscape theory for food web architecture. Ecology Letters 11:867–81.
- Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, Cambridge, UK.
- Roth, A. H., and J. F. Jackson. 1987. The effect of pool size on recruitment of predatory insects and on mortality in a larval Anuran. Herpetologica 43:224–232.
- Sanders, D., L. Sutter, and F. J. F. van Veen. 2013. The loss of indirect interactions leads to cascading extinctions of carnivores. Ecology Letters 16:664–9.
- Schmitz, O. J., E. Post, C. E. Burns, and K. M. Johnston. 2003. Ecosystem responses to global climate change: moving beyond color mapping. BioScience 53:1199–1205.
- Schoener, T. W. 1989. Food webs from the small to the large: the Robert H. MacArthur Award Lecture. Ecology 70:1559–1589.

- Schoener, T. W., D. A. Spiller, and J. B. Losos. 2001. Natural restoration of the species-area relation for a lizard after a hurricane. Science 294:1525–1528.
- Silva, M., and J. A. Downing. 1994. Allometric scaling of minimal mammal densities. Conservation Biology 8:732–743.
- Spencer, M., L. Blaustein, S. S. Schwartz, and J. E. Cohen. 1999. Species richness and the proportion of predatory animal species in temporary freshwater pools: relationships with habitat size and permanence. Ecology Letters 2:157–166.
- Spiller, D. A., and T. W. Schoener. 2007. Alteration of island food-web dynamics following major disturbance by hurricanes. Ecology 88:37–41.
- Spooner, D. E., and C. C. Vaughn. 2008. A trait-based approach to species' roles in stream ecosystems: climate change, community structure, and material cycling. Oecologia 158:307–17.
- Srivastava, D. S. 2005. Do local processes scale to global patterns? The role of drought and the species pool in determining treehole insect diversity. Oecologia 145:205–215.
- Srivastava, D. S. 2006. Habitat structure, trophic structure and ecosystem function: interactive effects in a bromeliad-insect community. Oecologia 149:493–504.
- Srivastava, D. S., and T. Bell. 2009. Reducing horizontal and vertical diversity in a foodweb triggers extinctions and impacts functions. Ecology Letters 12:1016–28.

- Srivastava, D. S., M. C. Melnychuk, and J. T. Ngai. 2005. Landscape variation in the larval density of a bromeliad-dwelling zygopteran, Mecistogaster modesta (Odonata: Pseudostigmatidae). International Journal of Odonatology 8:67–79.
- Srivastava, D. S., M. K. Trzcinski, B. A. Richardson, and B. Gilbert. 2008. Why are predators more sensitive to habitat size than their prey? Insights from bromeliad insect food webs. The American Naturalist 172:761–71.
- Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience 51:235–246.
- Starzomski, B. M., D. Suen, and D. S. Srivastava. 2010. Predation and facilitation determine chironomid emergence in a bromeliad-insect food web. Ecological Entomology 35:53–60.
- Stehr, F. W. 1987. Immature Insects. Page 754 (F. W. Stehr, Ed.). First edition. Kendall/Hunt Pub. Co.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. Science 297:1292–1296.
- Stillman, J. H., and A. Tagmount. 2009. Seasonal and latitudinal acclimatization of cardiac transcriptome responses to thermal stress in porcelain crabs, Petrolisthes cinctipes. Molecular Ecology 18:4206–26.
- Suttle, A. K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

- Tewksbury, J. J., R. B. Huey, and C. A. Deutsch. 2008. Putting the heat on tropical animals. Science 320:1296–1297.
- Voigt, W., J. Perner, and H. T. Jones. 2007. Using functional groups to investigate community response to environmental changes: two grassland case studies. Global Change Biology 13:1710–1721.
- Walther, G.-R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J.-M. Fromentin,O. Hoegh-Fuldberg, and F. Bairlein. 2002. Ecological responses to recent climate change.Nature 416:389–395.
- Warren, A. P. H., and J. H. Lawton. 1987. Invertebrate predator-prey body size relationships: an explanation for upper triangular food webs and patterns in food web structure? Oecologia 74:231–235.
- Warren, P. H., and K. J. Gaston. 1992. Predator-prey ratios: a special case of a general pattern?Philosophical Transactions: Biological Sciences 338:113–130.
- Wellborn, G. A., D. K. Skelly, and E. E. Werner. 1996. Mechanisms creating community structure across a freshwater habitat gradient. Annual Review of Ecology and Systematics 27:337–363.
- Williams, C. B. 1943. Area and the number of species. Nature 152:264–267.

- Woodward, G., D. M. Perkins, and L. E. Brown. 2010. Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society of London. Series B, Biological sciences 365:2093–2106.
- Worthen, W., M. Jones, and R. Jetton. 1998. Community structure and environmental stress: desiccation promotes nestedness in mycophagous fly communities. Oikos 81:45–54.
- Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos 41:496– 506.
- Zarnetske, P. L., D. K. Skelly, and M. C. Urban. 2012. Biotic multipliers of climate change. Science 336:1516–8.
- Zotz, G., and V. Thomas. 1999. How much water is in the tank? Model calculations for two epiphytic bromeliads. Annals of Botany 83:183–192.

## Appendix

## Transformations for linear models examining effects of drought on community composition and water quality (Chapter 3)

- for scrapers, the fraction of survivors (response) was sqrt(*raw*) transformed
- for shredders and filter-feeders, drought length was ln(raw+1) transformed
- for predators, drought length was  $\ln(raw+1)^2$  transformed
- for scrapers, collectors, decomposition, and water quality, drought length was raw<sup>2</sup> transformed
- for water quality, both decomposition and drought length were  $raw^2$  transformed