

ABIOTIC AND BIOTIC PROCESSES SHAPE SPECIES DISTRIBUTIONS AND
ECOLOGICAL COMMUNITIES ACROSS SPATIAL SCALES

by

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A DISSERTATION SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE AND POSTDOCTORAL STUDIES
(Zoology)

THE UNIVERSITY OF BRITISH COLUMBIA
(Vancouver)

AUGUST 2020

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Abiotic and biotic processes shape species distributions and ecological communities across spatial scales

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ABSTRACT

Species distributions and the composition of ecological communities result from the interplay of three constraints: physical barriers to dispersal, species-specific environmental requirements, and species interactions. However, how spatial scale and environmental context affect the relative importance of these constraints is still poorly understood. I combined manipulative experiments, observational surveys along environmental gradients, and species distribution models to explore the relative importance of abiotic and biotic constraints on aquatic invertebrate communities inside bromeliads across a range of spatial scales. At the geographic scale (Central and South America), the distribution of a bromeliad-specialist damselfly was strongly limited by dispersal barriers and climate, but not by biotic interactions from other bromeliad-dwelling odonates. At the regional scale (along two elevational gradients in Costa Rica), the relative importance of abiotic and biotic constraints on species distributions and community assemblages depended on environmental context: while thermal tolerances (i.e., abiotic effects) explained invertebrate distributions under moist conditions, biotic interactions from crane fly larvae, which became predatory under drought, explained their distributions under dry conditions. At the local scale (the bromeliad), biotic interactions from crane fly larvae were disproportionately important in mediating the effects of drought and warming on community structure and ecosystem functions. This hierarchical set of studies demonstrates the scale-dependence of the interplay of abiotic and biotic processes in affecting species distributions and

community assemblages. While species interactions were the main drivers of community change at the local scale of the habitat, biotic effects were not important at the large geographic scale. Notably, the relative importance of abiotic and biotic processes at the landscape scale depended on environmental context, an important insight given that environmental conditions are already shifting as a result of climate change.

LAY SUMMARY

Species distributions and ecological communities are governed by abiotic factors like climatic constraints and physical barriers to dispersal, as well as biotic effects from other species. However, how spatial scale and environmental context affect the interplay of these constraints is still poorly understood. I combined modeling techniques with observational surveys along environmental gradients and controlled experiments to investigate the relative importance of abiotic and biotic processes on an aquatic invertebrate food web inside bromeliad plants. I found that, while biotic interactions were key drivers of community responses at small and intermediate spatial scales, they were not detectable at the large geographical scale. At the intermediate scale of the landscape, the relative importance of biotic interactions and climatic (i.e., abiotic) effects depended on environmental context, demonstrating that processes that shape ecosystems are dynamic and may shift with climate change.

PREFACE

CHAPTER 2 has been previously published as:

Amundrud, S. L., Videla, M., and Srivastava, D. S. (2018). Dispersal barriers and climate determine the geographic distribution of the helicopter damselfly *Mecistogaster modesta*. *Freshwater Biology* 63: 214-223.

DSS and MV conceived the idea. MV collected the data. I performed the analyses (except the Maxent models of potential competitors in Appendix A1, which was done by MV) and wrote the paper, with comments from DSS and MV.

CHAPTER 3 has been previously published as:

Amundrud, S. L., and Srivastava, D. S. (2020). Thermal tolerances and species interactions determine the elevational distributions of insects. *Global Ecology and Biogeography* 29: 1315-1327

I conceived the idea and designed the study with input from DSS. I and my field assistants Bret Flynn, Megan Reich, Sarina Clay-Smith, Kathleen Higgins, and Derek Wiens conducted the invertebrate survey and CT_{max} experiment. I analyzed the data and wrote the manuscript, with input from DSS.

CHAPTER 4 has been previously published as:

Amundrud, S. L., Clay-Smith, S. A., Flynn, B. L., Higgins, K. E., Reich, M. S., Wiens, D. R. H., and Srivastava, D. S. (2019) Drought alters the trophic role of an opportunistic generalist in an aquatic ecosystem. *Oecologia* 189: 733-744

I conceived and designed Experiment 1, and SCS, BLF and MSR performed Experiment 1. I and DSS conceived and designed Experiment 2, and I, KEH and DRHW performed Experiment 2. I analyzed the data and wrote the manuscript with input from DSS. All authors provided editorial advice.

CHAPTER 5 has been previously published as:

Amundrud, S. L., and Srivastava, D. S. (2019) Disentangling how climate change can affect an aquatic food web by combining multiple experimental approaches. *Global Change Biology* 25: 3528-3538

I conceived and designed the study with input from DSS. I performed the experiment with help from Kathleen Higgins and Derek Wiens. I analysed the data and wrote the manuscript, with input from DSS.

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ACKNOWLEDGEMENTS

This thesis was only possible because of the personal and professional support from many people. A huge thank you to my advisor, Diane Srivastava, for your insight, patience, trust in my abilities, and striking the perfect balance between letting me find my own path and providing guidance and support when needed. Thanks to my committee members Chris Harley, Amy Angert, and Villy Christensen, who have advised me on developing and thinking through my various projects.

A tremendous thank you to my research assistants: Bret Flynn, Kathleen Higgins, Derek Wiens, Megan Reich, and Sarina Clay-Smith, for your tireless efforts hiking up and down the mountain to survey bromeliads, willingness to work long days, care in tending experiments, while still finding the time to appreciate this amazing adventure and the beauty of the wilderness around us. Your help was instrumental to this work. Special thanks also to the current and past members of the Srivastava lab and the Bromeliad Working Group, especially Melissa Guzman, Natalie Westwood, Pierre Rogi, Kurt Trzcinski, Alatheia Lethaw, and Andrew McDonald. I am particularly grateful to Angie Nicolas, who translated my permit applications into Spanish, and to Régis Cereghino, who was an important mentor and funder of this research.

This thesis would not have been possible without the kindness and logistical support of many people in Monteverde and elsewhere in Costa Rica. Mary and Elias Newswanger let us live and work in their own home for four months in 2015 while they “took the opportunity to travel”. Bill Haber provided advice on how to acquire the research permits, suggested study sites, and shared his love of odonates with me. Néstor Guevara and Randall Zamora Castro guided us safely through the Costa Rican wilderness, spotted the most hidden bromeliads, and shared their love and wisdom for the Costa Rican flora and fauna. Alan Pounds provided advice and shared

his knowledge about the natural history and the impacts of climate change on the Monteverde Cloud Forest. Special thanks also to Luis Guillermo Chaverri, who identified my mosquito larvae.

Thank you so much to the wonderful people from the Monteverde Cloud Forest Reserve and the Centro Científico Tropical (especially Yoryineth Mendez Corrales for invaluable help with logistical matters), and the Children's Eternal Rain Forest Reserve (especially Giselle Rodriguez and Lindsay Stallcup). Thank you also to the wonderful hosts at Estación San Gerardo and Estación Pocosol for their Costa Rican hospitality and feeding us the most delicious meals. I am grateful to the land owners that allowed me to collect bromeliad invertebrates on their property: Alicia Mendes near San Luis, as well as Fred Morrison and Bill Calvert at Finca Colibri. Finally, a very big thank you to the Costa Rica Campus of the University of Georgia (especially José Montero and Fabricio Camacho), for hosting us in 2016, going through great lengths to ensure we had all the lab space and research equipment we needed, and making the second field season feel more like an extended vacation.

Last but not least, I want to thank my family. My parents Lisi and Klaus, my siblings Christoph and Laura, and my father in law Greg, thank you for supporting and believing in me. And a huge thank you to my mother in law, Linda, for the countless hours of babysitting so I could work on my PhD. Trevor, words cannot express how grateful I am for the many sacrifices you made so I could take this path, for your endless encouragement, unconditional love, for being at my side to celebrate my successes and to support me through the tough times. I truly could not have done this without you. And finally, to Cleo, for bringing a whole new kind of joy into my life, and for reminding me to once again notice the small things that no doubt sparked my interest in biology a long time ago: the snails, the worms, the dandelions, the “rollie pollies”...

DEDICATION

To Trevor and Cleo

1 INTRODUCTION

Identifying the processes that shape species distributions and community assemblages is fundamental to our understanding of how ecosystems respond to global change. The realized niches of species are broadly defined by the interplay of three processes: dispersal limitation, habitat filtering, and species interactions (Soberón 2007). Yet, most attempts to understand species distributions and the make-up of ecological communities have focused on the effects of abiotic conditions on single species, such as physiological effects of temperature (e.g. McKechnie and Wolf 2010) and precipitation (e.g. Ernest et al. 2000; Báez et al. 2006; Ledger et al. 2008). For instance, species distribution models (SDMs) typically correlate species presence records with climatic variables, but such envelope models assume that species occur in all locations within their climatic tolerance (Kearney and Porter 2009), and thus do not take into account other limitations to species occurrence, such as altered species interactions (however, if biotic interactions systematically covary with climatic variables, climatically based models will be a good proxy for the combined effects of biotic and abiotic factors). Because of the growing amount of evidence that species interactions can be as or more important in shaping the structure of ecological communities than abiotic effects on species' physiologies (Schmitz et al. 2003; Chase and Knight 2003; Montoya et al. 2009; Ockendon et al. 2014; Amundrud and Srivastava 2016), we need to incorporate biotic processes into models predicting the ecological effects of global change.

Abiotic and biotic processes operate at a hierarchy of spatial scales, and their relative impact on ecological communities is likely scale-dependant (Chase and Knight 2013). While biotic processes such as predation and competition often determine the composition of communities at small spatial scales (e.g., Chase and Knight 2003; Amundrud and Srivastava 2016), the relative impact of species interactions can become negligible when considering larger

spatial scales (Eltonian noise hypothesis: Soberón 2007). Nevertheless, even at large geographical scales, biotic interactions can be important in affecting species distributions (e.g., Heikkinen et al. 2007; Boulangeat et al. 2012; De Araújo et al. 2014). Although progress has been made in understanding the scale-dependence of the relative importance of abiotic and biotic constraints on ecological communities, this has yet to be adequately applied to understanding the effects of global change such as climate change.

For my PhD dissertation, I took advantage of the utility of bromeliad-dwelling invertebrate food webs to investigate the relative importance of abiotic and biotic processes in shaping species distributions and the make-up of communities across various spatial scales, ranging from the large continental scale to the small scale of the local habitat. By collecting rainwater and fallen detritus, tank bromeliads provide habitats for diverse communities of aquatic microorganisms and macroinvertebrates (Figure 1.1). These miniature food webs are ideal study systems to investigate how abiotic and biotic processes operate at various spatial scales, as tank bromeliads occur over landscape gradients within a large geographic range (most of the Neotropics). Bromeliad-dwelling faunal communities are relatively self-contained systems that can be easily manipulated at the local scale in order to investigate abiotic and biotic mechanisms. As these food webs have been studied extensively, we already have a detailed understanding of important processes that affect community assemblages locally. For example, I previously showed in my MSc work that a keystone predator (damselfly nymph: *Mecistogaster modesta*, Figure 1.2) mediates the ecological effects of drought (Amundrud and Srivastava 2016), which is expected to increase in montane areas of Costa Rica with climate change (Karmalkar et al. 2008).

Figure 1. 1: Phytothelm bromeliads at Monteverde Mountain, Costa Rica.



Figure 1. 2: Bromeliad dwelling damselfly (*Mecistogaster modesta*) adult (left) and larva (right).



I organized my dissertation chapters by spatial scale, going from the geographic region to the landscape to the local habitat. In **Chapter 2**, I employed SDMs to investigate the relative importance of physical dispersal barriers, climatic constraints, and biotic interactions in determining the distribution of the damselfly *M. modesta*, which spends its larval stage exclusively in bromeliads, at the geographic scale. Most SDMs assume that species occur in habitats that encompass their climatic tolerance range (Kearney and Porter 2009), and do not take into account other limitations to species occurrence, such as dispersal barriers and biotic constraints. In collaboration with Dr. Martin Videla, a former postdoc of my advisor Diane Srivastava, I incorporated dispersal constraints (the potential barriers imposed by the Andes mountain range and oceans) and biotic constraints (the presence of other bromeliad-dwelling odonate species that present potential competitors or intraguild predators) into SDMs. Model predictions suggested that at this large geographic scale, biotic factors were not important in governing the distribution of *M. modesta*. Instead, the distribution of this species seemed to be primarily limited by both climatic constraints (dry conditions and low temperatures) and dispersal barriers.

Next, I investigated the relative importance of abiotic and biotic processes in determining species distributions and community assemblages at the landscape scale, by surveying bromeliad food webs along two elevational gradients on the dry Pacific and wet Atlantic slopes of Monteverde Mountain, Costa Rica, as well as experimentally determining their upper thermal tolerances. These mountain slopes represent an ideal “natural experiment” to tease apart the various abiotic and biotic constraints on species regional distributions. While the ambient temperature increases towards lower elevations on both mountain slopes at roughly equal rates, the Pacific slope is significantly dryer than the Atlantic slope, allowing me to disentangle the

effects of temperature and precipitation on invertebrate elevational distributions. Predatory damselflies occur only at low elevations on the Atlantic slope (consistent with expectations from the SDM in Chapter 2). In **Chapter 3**, I investigated the relative importance of abiotic and biotic processes in driving the elevational distributions of bromeliad invertebrates. While both climate and biotic factors were important in driving invertebrate elevational distributions, their relative influences depended on environmental context. On the wet Atlantic slope, taxon-specific heat tolerances explained invertebrate elevational distributions, while biotic interactions explained their elevational distributions on the dry Pacific slope. Interestingly, it was not the damselfly that drove these biotic effects. Instead, crane fly larvae, which were previously thought to be facultative detritivores, exerted adverse effects on other invertebrates at low elevation sites on the Pacific slope (i.e., the warmest and driest sites), thus affecting their elevational distributions.

Last, I investigated the relative importance of abiotic and biotic factors in shaping bromeliad invertebrate communities at the local scale of the habitat. In **Chapter 4**, I investigated several potential mechanisms that may have caused crane fly larvae to exert negative effects on other invertebrates under dry environmental conditions, thus driving their elevational distributions. Through two controlled experiments, I demonstrated that drought enabled opportunistic predation by crane fly larvae via increasing predator-prey encounter rates, resulting from habitat compression due to a reduction in water volume. In **Chapter 5**, I combined multiple experimental approaches to test the individual and combined effects of drought, warming, and biotic interactions on community structure and ecosystem functioning. I found that adverse effects of crane flies on other invertebrates arose under drought conditions and became stronger with warming. Altered species interactions thus mediated the effects of drought and warming on the invertebrate food web at the scale of the single habitat. Indeed, the relative importance of

these biotic processes far outweighed any direct effects of drought and temperature on the community.

These chapters demonstrate the scale-dependence of the relative importance of abiotic and biotic processes in affecting species distributions and the make-up of ecological communities. A key insight that emerged from all chapters is that climate change will affect invertebrate communities. While indirect effects of environmental change due to altered species interactions mediated community responses at small spatial scales, such biotic effects were not detectable at large scales. Importantly, this dissertation demonstrates that the interplay between abiotic and biotic processes at intermediate spatial scales can depend on environmental context. As such, this research is shedding light on the dynamic nature of the various processes that affect ecological communities across space and time.

2 DISPERSAL BARRIERS AND CLIMATE DETERMINE THE
GEOGRAPHIC DISTRIBUTION OF THE HELICOPTER
DAMSELFLY *MECISTOGASTER MODESTA*¹

¹ Previously published as Amundrud, S. L., Videla, M., and Srivastava, D. S. (2018). Dispersal barriers and climate determine the geographic distribution of the helicopter damselfly *Mecistogaster modesta*. *Freshwater Biology* 63: 214-223.

2.1 CHAPTER SUMMARY

Species' ranges are typically constrained by the interplay of physical barriers to dispersal, environmental requirements such as suitable climatic conditions, and biotic constraints such as from predation or competition. However, teasing apart the relative importance of these constraints in determining species distributions still represents a major challenge for ecologists. The Neotropical damselfly *Mecistogaster modesta* (Coenagrionidae: Odonata) inhabits wet and moist forests in mainland Central America and northwestern South America. This habitat specialist spends its larval development exclusively in tank bromeliads, where it acts as a keystone predator within the aquatic food web. Although tank-forming bromeliads occur from the southern United States throughout most of South America, *M. modesta* is absent from the Caribbean islands and South America southeast of the Andes mountain chain. We employed species distribution models (SDMs) to explore the relative importance of physical barriers (Andes mountain range and oceanic barriers), climate (mean annual temperature and annual precipitation), and biotic interactions (competition from other bromeliad-dwelling odonates) in limiting the geographic distribution of *M. modesta*. We found that dispersal barriers strongly limit the geographic distribution of *M. modesta*. In addition, its range is restricted by low temperatures and low precipitation. Competition from other bromeliad-dwelling odonates was not important in limiting the damselfly's range. Because of the physical barriers to dispersal, *M. modesta* does not occupy its full potential geographic range. Specifically, our model predicted suitable habitat on the Caribbean islands and throughout most of South America, where the species is currently absent. These findings have important conservation implications, particularly as the aridification of rainforests and subsequent localized extinctions due to climate change

continue. On the other hand, the species may respond to warming temperatures by tracking climate to higher elevations, with subsequent effects on naïve high-elevation bromeliad food webs. An upwards migration could also increase the probability of *M. modesta* overcoming the dispersal barrier presented by the Andes, enabling the damselfly to invade large areas of suitable habitat in South America.

2.2 INTRODUCTION

Damselflies and dragonflies (Odonata) are among the most ancient winged insects on Earth (~ 300 MYA: Ingley et al. 2012). As both adults and larvae typically occupy high trophic positions, these insects are often used as indicators of aquatic and terrestrial ecosystem health (Collins and McIntyre 2015). Odonates possess some of the best dispersal capabilities of all insects (Sánchez-Herrera and Ware 2012), yet these acrobatic flyers are not found everywhere. Teasing apart the relative importance of factors that determine the geographic distributions of odonates (Collins and McIntyre 2015), as well as of organisms in general (Endler 1982; De Araújo et al. 2014), still represents a major challenge for ecologists.

Major mountain ranges have led to the isolation and subsequent diversification of plants (e.g., Antonelli et al. 2009) and animals, including invertebrates (e.g., von Oheimb et al. 2013; De-Silva et al. 2016) and birds (e.g., Graham et al. 2009). Similarly, large expanses of water such as oceans and great lakes represent major dispersal barriers to most terrestrial organisms (MacDonald 2003), and can restrict the geographic ranges of even good dispersers, such as

winged insects (e.g., yellow-faced bumble bee: Jha 2015). Such direct physical barriers may limit the geographic distributions of odonates, and indeed, their range edges often coincide with mountain ranges and oceans (Wellenreuther et al. 2012). However, geographic barriers usually do not fully explain the geographic range limits of odonates.

The constrained geographic ranges of odonates may also be a function of their sensitivity to environmental conditions. At large spatial scales, climate, particularly temperature and precipitation, appears to ultimately determine the physiological niche of organisms (Pearson and Dawson 2003), including odonates (Collins and McIntyre 2015). Temperature determines, among other things, thermoregulation proficiency (De Marco et al. 2005), flight performance of adults (Dingemanse and Kalkman 2008; Samejima and Tsubaki 2010), development rates of larvae (Lutz 1968; Pickup and Thompson 1990; Hassall et al. 2007; Braune et al. 2008; Richter et al. 2008), time to emergence (Hassall et al. 2007; Richter et al. 2008), and voltinism (i.e., the number of generations completed within 1 year in the field, Braune *et al.*, 2008). Precipitation, on the other hand, is strongly linked to hydroperiod in lentic waters (Collins et al. 2014) and thus determines environmental suitability for oviposition by odonates. In addition, low precipitation and associated increases in drought lengths and/or frequencies can adversely affect odonate larvae (Ball-Damerow, M'Gonigle & Resh, 2014a b; Amundrud & Srivastava, 2015, 2016).

Apart from dispersal limitation and abiotic constraints, biotic interactions such as predation and competition may also limit the distributions of odonates (Collins and McIntyre 2015). For example, the presence of predatory fish is strongly linked to the occurrence of some odonate species in ponds (McGuffin et al. 2006). In temporary waters where fish are absent, other odonate species represent strong biotic controls (e.g., Benke 1978; Johnson et al. 1985; Fincke 1994). In such systems, intraguild predation (where predators with shared prey kill and

eat each other: Polis, Myers & Holt, 1989), and cannibalism are the main biotic constraints (e.g., Benke 1978; Suutari et al. 2004). Biotic interactions can also limit distributions of odonates through the “ghost of competition past” (Worthen and Horacek 2015), where current geographical limits of species reflect the historical effects of competition with other organisms (Connell 1980). Although important at the local scale, biotic interactions are often considered to be negligible in affecting species distributions at large geographical scales (Eltonian noise hypothesis: Soberón and Nakamura 2009). Nevertheless, recent work suggests that biotic interactions can be important in affecting species distributions even at large spatial scales (e.g., Heikkinen et al. 2007; Boulangeat et al. 2012; De Araújo et al. 2014).

The realized geographic distributions of odonates are likely determined by the interplay of physical barriers limiting their dispersal, environmental requirements, and biotic constraints [see BAM (biotic, abiotic, and migration) diagram in Soberón, 2007]. The BAM model (Soberón 2007) posits that the range that a species fills should represent all areas within the dispersal ability of the species (M) with suitable abiotic (A) and biotic (B) conditions. Species distribution models (SDMs) can be valuable in teasing apart these factors in limiting odonate distributions (Collins and McIntyre 2015), especially if the relative contributions of the main factors conceptualized in the BAM model are well understood, or at least hypothesized (Saupe et al. 2012). However, few, if any, studies have evaluated the combined effects of climate, physical barriers, and biotic constraints on odonate ranges.

Here, we employ SDMs to explore the factors that limit the geographical distribution of the Neotropical damselfly *Mecistogaster modesta* (Coenagrionidae: Odonata). *M. modesta* oviposits its eggs exclusively in epiphytic bromeliads (Ingleby et al. 2012), where the larvae feed on other insect larvae (Srivastava 2006). Adults feed on orb-weaving spiders, which they pluck

from webs (Hedström and Sahlén 2001; Ingleby et al. 2012). Although tank-forming bromeliads occur from the southern United States (latitude ~ 30 °N) to almost the southern tip of South America (latitude ~ 45 °S; Benzing 2000), *M. modesta* is limited to mainland Central America and northwestern South America, inhabiting wet and moist forests from Colombia and Venezuela to Mexico-Belize (Hedström and Sahlén 2001). Throughout much of its range, *M. modesta* is the only odonate species associated with bromeliads, although there may be some overlap with other bromeliad-dwelling odonates in the *Bromeliagrion* genus towards the southern limit of its range (see Figure 2.1 and Appendix A). Within bromeliads, *M. modesta* nymphs have large top-down effects on the bromeliad ecosystem that eclipse the effects of any other invertebrate species. For example, *M. modesta* larvae have been shown to reduce abundances of other invertebrates by 25-90 % (Srivastava 2006; Hammill et al. 2015b) and decomposition by 20-50 % (Srivastava 2006; Atwood et al. 2013), increase nitrogen uptake by the bromeliad by 1200 % (Ngai and Srivastava 2006), and change CO₂ flux by up to 200 % (Atwood et al. 2013; Hammill et al. 2015b). Bromeliads that contain *M. modesta* have fundamentally different biomass pyramids and mosquito communities than bromeliads that do not (Petermann et al. 2015; Hammill et al. 2015a). Determining which factors limit the geographic distribution of this odonate species is therefore essential to understanding spatial patterns in the structure and functioning of bromeliad food webs in Central America, and how these food webs may change under altered climate.

We used SDMs to explore the combined effects of climate, physical barriers, and biotic constraints on *M. modesta*. SDMs have been widely applied for freshwater species, to explore matters as diverse as assessing the impacts of climate change (e.g., benthic stream macroinvertebrates: Domisch et al. 2011), predicting suitable habitat for threatened species (e.g.,

freshwater turtle: Costa et al. 2015), and predicting the spatial distribution of invasive species (e.g., piscivorous chub: Sato et al. 2010). A detailed review on the use of SDMs to model odonate distributions has been conducted by Collins & McIntyre (2015). We employed SDMs to reveal the relative importance of physical barriers (Andes mountain range and oceanic barriers), climate (temperature and precipitation), and biotic interactions (competition from other bromeliad-dwelling damselflies). If our model predicts no or little suitable habitat beyond the physical barriers constraining the range of *M. modesta*, it would indicate that climate and/or biotic constraints are the major factors limiting the damselfly's range. In contrast, if our model predicts suitable habitat on the islands and/or southeast of the Andes, it would suggest that *M. modesta* is limited by dispersal barriers. As there are neither obvious physical barriers nor other bromeliad-dwelling odonates towards the northern range limits of *M. modesta*, we expect climatic constraints to be the limiting factors towards the north.

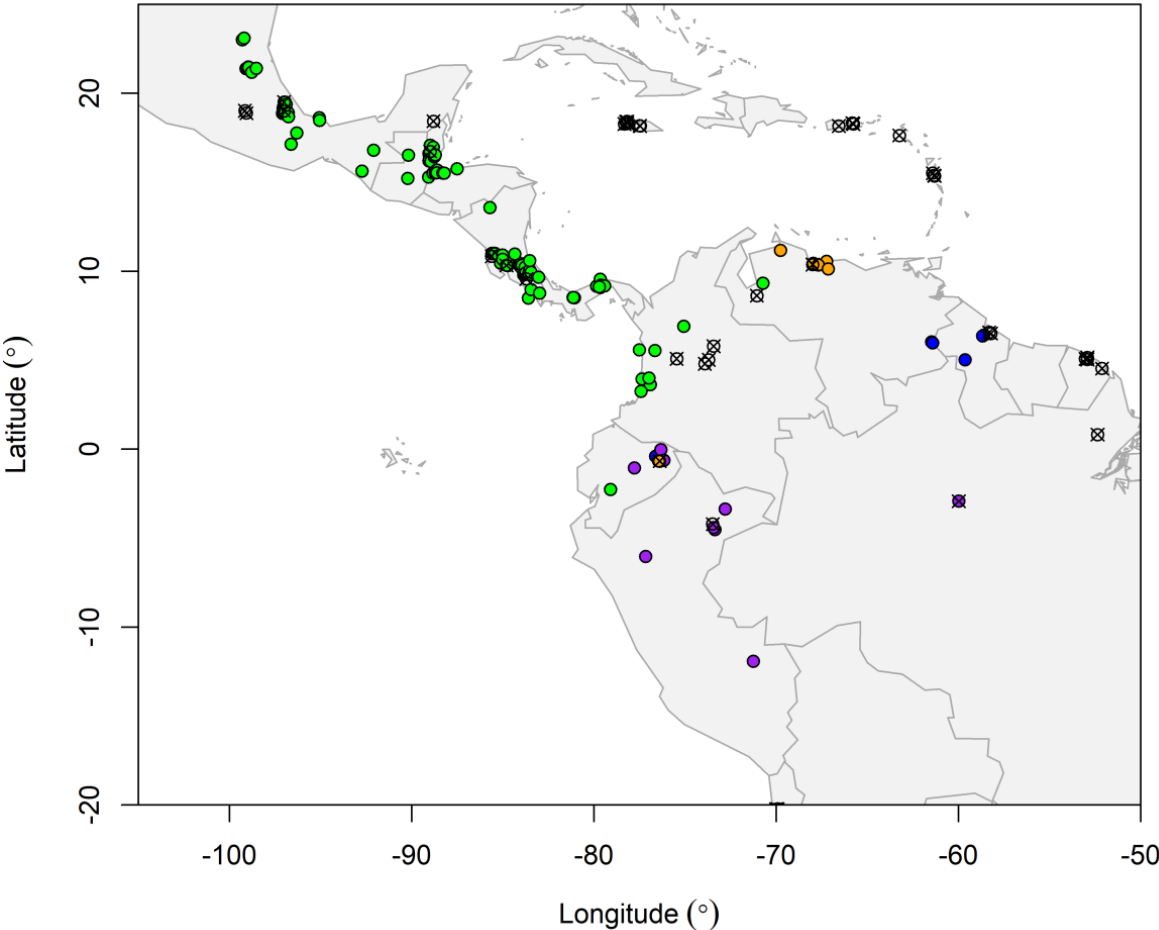
2.3 METHODS

2.3.1 Data Collection

We obtained occurrence records of *M. modesta* from several online databases, including the Global Biodiversity Information Facility (www.gbif.org), Biodiversity and Environmental Resource Data System of Belize (www.biodiversity.bz), Smithsonian National Museum of Natural History (www.mnh.si.edu), and Odonata Central (www.odonatacentral.org). We attained additional records from members of the Bromeliad Working Group

(<http://www.zoology.ubc.ca/~srivast/bwg/researchers.html>), museum curators, known experts of Odonata, and published studies on invertebrates inhabiting bromeliad phytotelmata. We also included absence records as sites where at least 20 bromeliads were inspected and no *M. modesta* larvae were found. When no exact coordinates were available, we estimated the geographic coordinates and the associated error according to the point-radius method (Wieczorek et al. 2004) using an online georeferencing calculator (<http://manisnet.org/gc.html>). We only included records with a geographical uncertainty of radius less than 5 km, resulting in a data set consisting of 101 presence and 52 absence records for *M. modesta* (Figure 2.1).

Figure 2. 1: Map showing location of presence and absence records of *M. modesta*, as well as presence records of the three potential competitor species. Coloured dots show occurrence records of *M. modesta* (green), *Bromeliagrion beebeanum* (blue), *B. rehni* (purple), and *B. fernandezianum* (orange). Empty dots with black crosses show *M. modesta* absence records.



2.3.2 Variable Selection

To examine the importance of dispersal in governing the distribution of *M. modesta*, we created a single binary “barrier” variable that indicated whether a record was collected from within vs. beyond the hypothesized dispersal barriers represented by the Pacific and Atlantic oceans and the Andes mountain range. Specifically, the layer we created defined grid cells as “beyond barriers” (value = 0) when grid cells were southeast of the summit of the Andes or more than 10 km offshore of the mainland, or “within barriers” (value = 1) if in the rest of the terrestrial study area.

To examine the importance of climate, we obtained 19 bioclimatic variables from the WorldClim database at 2.5 arc-minutes resolution (Hijmans et al. 2005), which roughly corresponds to a 5 km resolution near the tropics. To select meaningful climatic predictor variables in our model, we first reduced our data set by removing all absence records from the islands and southeast of the Andes, as we *a priori* hypothesized that *M. modesta* cannot disperse to these areas because of dispersal barriers. Including these absences could lead to erroneous predictions, as absences from habitats due to dispersal barriers, but with suitable climate, would bias a model that predicts species occurrence from climate (Peterson et al. 2011). We then estimated and ranked relative variable importance as deviance explained for the 19 climate variables by predicting *M. modesta* occurrence for each of the climate variables separately using logistic GLMs. Next, we examined the correlation between all possible variables to ensure that variables were not highly correlated ($r > 0.8$). This procedure led us to choose “annual mean temperature” (bio1) and “annual precipitation” (bio12), as these variables exhibited a high importance (they ranked 1st and 4th, respectively) and a low correlation ($r = 0.50$). In addition, this choice is consistent with the known physiological importance of temperature and

precipitation to *M. modesta* (Amundrud and Srivastava, unpublished data). For both climatic variables, we compared the fitted curves of two polynomial logistic models (of 1st and 2nd degree, respectively) to a smooth spline. As the simpler curves (1st degree predictor variable) represented a closer fit to the data in both cases, we used 1st degree predictor variables for bio1 and bio12 as climatic predictors of *M. modesta* occurrence in our final models.

Interacting species have been included as predictor variables in SDMs as either occurrence records, or as an input layer of their estimated occurrence or habitat suitability (Giannini et al. 2013; De Araújo et al. 2014). Here we implemented the latter approach to examine whether competition determines the geographic distribution of *M. modesta* by using the modeled distributions of three of its potential competitors: *Bromeliagrion bebeanum*, *B. fernandezianum*, and *B. rehni*. We focused on those species because they are present in the north of South America, so their ranges may overlap with that of *M. modesta* (Figure 2.1). Other bromeliad-dwelling odonate species have too few records or occur too far from the known range of *M. modesta*, making competition unlikely. Because there are few presence records for these *Bromeliagrion* species (6, 6 and 11, respectively; Figure 2.1), we performed SDMs with Maxent version 3.2.1 (Phillips et al. 2006), a widely used algorithm for presence-only data that performs better than others when the sample size is small (Hernandez et al. 2006; Wisz et al. 2008). For each competitor species, we included the habitat suitability scores obtained from the Maxent model as a continuous variable. In addition, we created variables for all possible combinations of competitor species whereby, for a given grid cell, the highest suitability value among the two (or three) competitor models was kept, resulting in seven possible competitor layers (the three competitor species individually, the three pairwise combination, and all three competitor species combined). The results were qualitatively identical for all seven competitor layers; thus, we only

report the results of the model in which the competition layer represents all three competitor species. This layer estimates the suitability of the habitat for at least one putative competitor of *M. modesta*, even if the identity of this competitor changes geographically. The detailed methods and results of the competitor models are listed in Appendix A.

2.3.3 *Species Distribution Models*

We employed logistic generalized linear models (GLMs) to explore the relative importance of physical dispersal barriers, climate, and competition in determining the geographic distribution of *M. modesta*. We chose GLMs because of their relatively high predictive power relative to other modeling approaches, as our goal was to predict *M. modesta* occurrence from these abiotic and biotic variables. Because it is crucial that the absence data used to train a SDM are limited to geographic areas within the dispersal ability of the species (i.e., within M in BAM model: Peterson et al. 2011), our modeling approach consisted of two steps: (1) to statistically test our expectation that the ocean and Andes represent effective dispersal barriers [and thus the absences on islands and the mainland southeast of the Andes represent records from areas outside of M (migration) in the BAM model but within A (abiotic) \cup B (biotic)]; and, in the case that the model confirms that these absence records lie outside the area of dispersal capacity of *M. modesta*, (2) to predict *M. modesta* occurrence from climate and competition on a model trained on presence/absence records that lie within the area of dispersal capacity of the species (i.e., on the reduced data set excluding absence records on islands and south-east of the Andes, or within M in the BAM model).

To examine whether dispersal barriers limit the distribution of *M. modesta*, we employed an “across barrier” model as a logistic regression on the complete *M. modesta* data set (i.e., including the absence records from the islands and south-east of the Andes). As explanatory variables, we included the two climatic variables (“mean annual temperature” and “annual precipitation”), their interaction, the pooled competition variable, and the binary “barrier” variable. We used the combined competitor variable (generated from all three competitor species) as described earlier. We used stepwise regression [function “step” in R (R Core Team, 2015)] for model simplification.

Because the distribution of *M. modesta* was strongly limited by the oceanic and mountain barriers (see Results), we employed a second “within barrier” model that we trained on presence/absence records within the dispersal area (i.e., within M of BAM) of the damselfly. Training our model using records within M reduced the data set to 101 presences and 18 absences. As above, we used a logistic GLM to predict the probability of *M. modesta* occurrence from the two climatic variables, their interaction, and the combined competition variable, followed by stepwise regression.

We performed a 10-fold cross validation to check for model performance and robustness, using the R package *DAAG* (Maindonald and Braun 2015). To calculate threshold-dependent model performance indices, we chose the threshold to maximize Kappa using the *PresenceAbsence* package (Freeman and Moisen 2008) in R.

2.4 RESULTS

The “across barrier” analysis suggested that dispersal barriers are likely to limit the geographic distribution of *M. modesta*, as the barrier variable, as well as the two climatic variables (bio1 and bio12), were significant predictors of the damselfly’s occurrence (Table 2.1a). The competition variable and the interaction term of bio1 x bio12 were removed from the model by stepwise regression. The total variance explained by the model was 71.6%, and 10-fold cross validation established model robustness (Table 2.1b).

Table 2. 1: Fit of simplified “across barrier model” to the full dataset of presence-absence records. Data to train the model included absences outside the hypothesized area of dispersal. The initial model included dispersal barriers, climatic constraints [annual mean temperature (bio1) and annual precipitation (bio12), as well as their interaction] and biological constraints (competitors). Competition and the bio1 x bio12 interaction terms were removed from the model by stepwise regression. **(a)** ANOVA table after stepwise regression. **(b)** Model performance indices and 10-fold cross validation (CV).

(a)	DF	Deviance	Residual DF	Residual Deviance	p-value
NULL			152	196.13	
bio1	1	13.57	151	182.56	< 0.001
bio12	1	12.89	150	169.67	< 0.001
barrier	1	114.05	149	55.62	< 0.001

(b)	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC	TSS
Model	0.45	0.95	0.99	0.87	0.88	0.97	0.86
10-fold CV	0.45	0.93	0.97	0.85	0.84	0.96	0.82

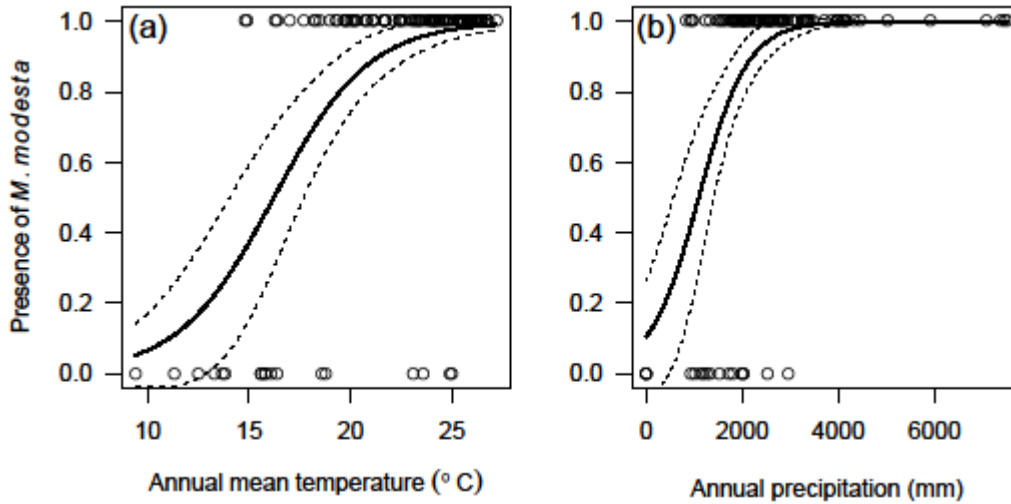
The “within barrier” analysis suggested that climatic constraints are likely important limiting factors of *M. modesta* occurrence within the potential dispersive area of the species (Table 2.2a). As in the “across barrier” model, the interaction of bio1 x bio12 and the competition variable were removed from the model by stepwise regression. The total variance explained by the final model was 45%, and a 10-fold cross validation showed adequate model robustness (Table 2.2b). A closer examination of the climatic constraints on *M. modesta* occurrence revealed that the species is limited by low temperatures and dry conditions, as rises in annual mean temperature (bio1) and annual precipitation (bio12) significantly increase the predicted probability of *M. modesta* occurrence (Figure 2.2). Specifically, the mean annual temperature and precipitation for which our model predicts a 50% probability of *M. modesta* occurrence is 16.22°C (± 0.95 °C SE), and 1091 mm (± 217 mm SE), respectively (Figure 2.2).

Table 2. 2: Fit of simplified “within barrier model” to the reduced dataset of presence-absence records. Data to train the model did not include absences outside the hypothesized area of dispersal. The initial model included climatic constraints [annual mean temperature (bio1) and annual precipitation (bio12), as well as their interaction] and biological constraints (competitors). Competition and the bio1 x bio12 interaction terms were removed from the model by stepwise regression. **(a)** ANOVA table after stepwise regression. **(b)** Model performance indices and 10-fold cross validation (CV).

(a)	DF	Deviance	Residual DF	Residual Deviance	p-value
NULL			118	101.12	
bio1	1	36.44	117	64.69	< 0.001
bio12	1	9.07	116	55.62	0.002

(b)	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC	TSS
Model	0.57	0.92	0.97	0.67	0.68	0.93	0.64
10-fold CV	0.57	0.91	0.96	0.61	0.61	0.85	0.57

Figure 2. 2: Probability of occurrence of *M. modesta* for (a) annual mean temperature (bio1) and (b) annual precipitation (bio12). Empty circles represent presence (at 1) and absence (at 0) records of *M. modesta*. Solid lines represent the predicted probabilities of *M. modesta* occurrence from logistic regression models, and dashed lines represent their 95 % confidence intervals.



The predicted realized geographic distribution of *M. modesta* encompasses most of Central America (except at high elevations) and the northern parts of South America, spanning from southern Mexico below $\sim 20^{\circ}\text{N}$ (and further north at both of Mexico's coasts) to the northeastern side of the Andes mountain range in South America (from east Venezuela to Ecuador and possibly into Peru; Figure 2.3). However, the potential geographic distribution predicted by our model spans far into South America to $\sim 30^{\circ}\text{S}$ and includes the Caribbean islands, suggesting that suitable habitat for *M. modesta* exists beyond the physical barriers represented by the ocean and Andes mountain range (Figure 2.4).

Figure 2. 3: The predicted realized geographic distribution of *M. modesta* (white to green colour scale indicates probability of occurrence of *M. modesta*). This species distribution model is restricted to areas that are within the dispersal ability of the damselfly.

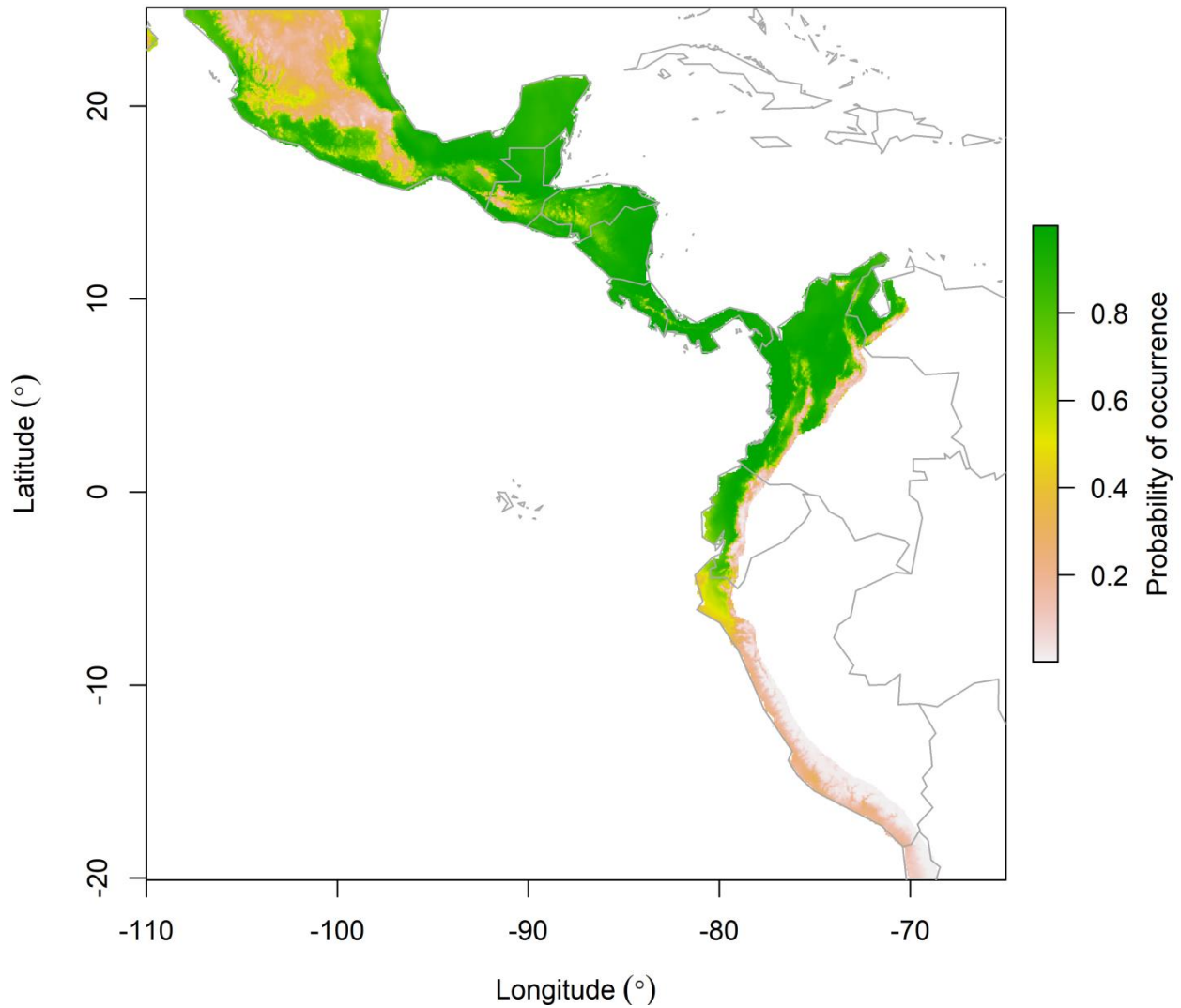
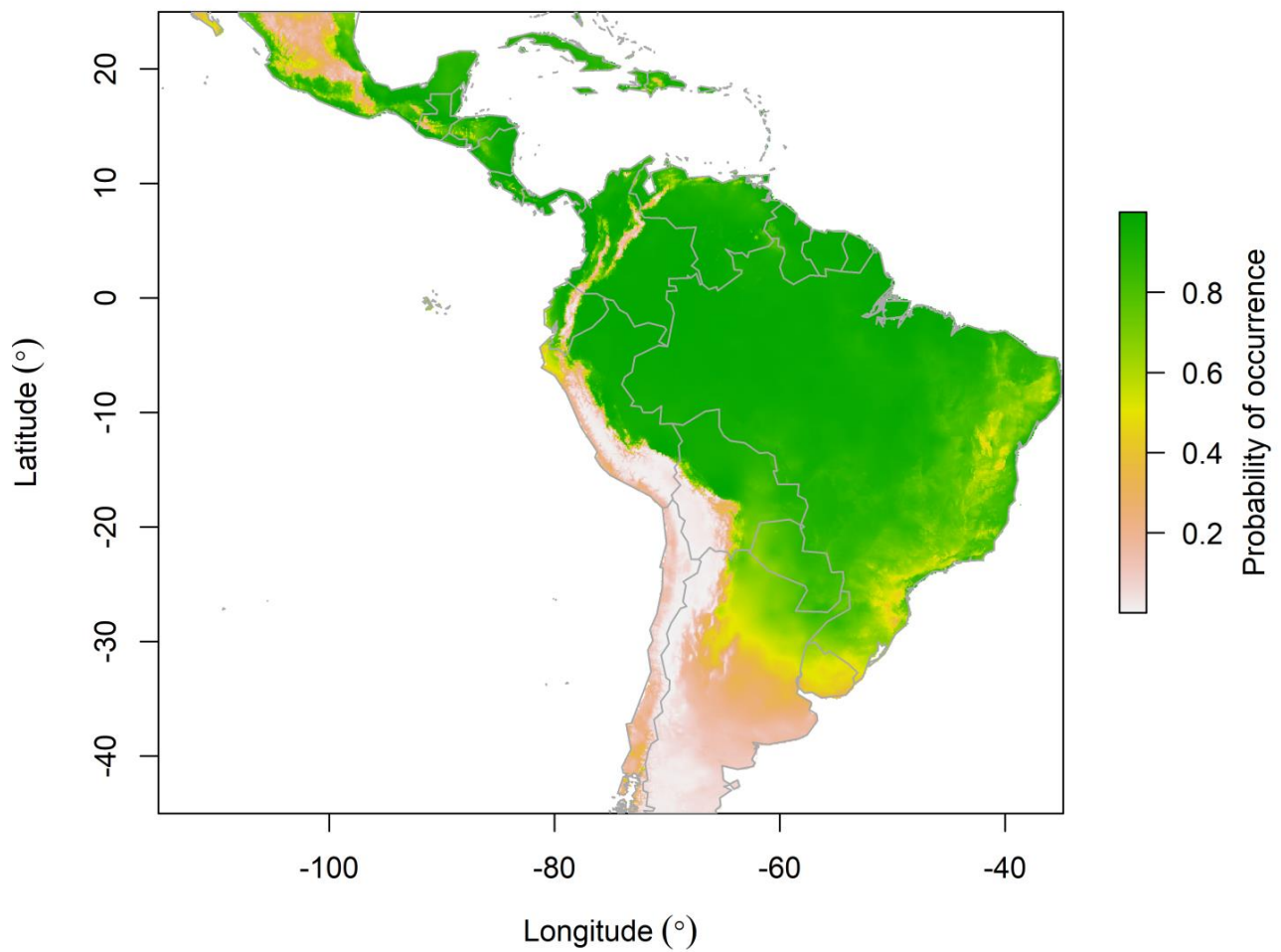


Figure 2. 4: The predicted potential geographic distribution of *M. modesta* (white to green colour scale indicates probability of occurrence of *M. modesta*). Although the damselfly is not currently present on islands and east of the Andes, our model predicts that the climate there is suitable for the damselfly.



2.5 DISCUSSION

Our analysis suggests that physical barriers to dispersal and climatic constraints likely determined the distribution of *M. modesta* in our study, but competition from other bromeliad-dwelling odonates was not important. In particular, we identified two dispersal barriers: oceanic distances in excess of 10 km and the Andes mountain chain, which likely exclude *M. modesta* from the Caribbean islands and from much of South America. In addition, annual mean temperature and annual precipitation were likely also key factors limiting the geographic distribution of *M. modesta*. These climatic constraints excluded *M. modesta* from high elevations (too cold), as well as from latitudes above its northern range edge in Mexico (too dry) and from west of the Andes (too dry and/or too cold; Figure 2.3). As dispersal barriers exclude *M. modesta* from suitable habitat on the Caribbean islands and southeast of the Andes (Figure 2.3), our study indicates that this damselfly does not occupy its full potential geographic distribution (Figure 2.4).

M. modesta is unlikely to occupy its full potential geographic niche, as our “across-barrier” analysis predicted suitable habitat on the Caribbean islands and southeast of the Andes. We conclude that *M. modesta*, like other Neotropical animals (Emmons and Feer 1997), has not been able to cross the ocean expanse between the Central American mainland and the Caribbean islands to fill its potential range, consistent with marine barriers limiting animal distributions (MacDonald 2003; Smith 2009), even for taxa with good dispersal capabilities such as winged insects (Jha 2015). In addition, the geographic distribution of *M. modesta* is constrained by the Andes mountain range, which excludes it from suitable habitat in much of South America (Figure 2.4). This is not surprising, as the Andes represent a significant barrier for many

organisms including plants (e.g., Antonelli et al. 2009; Givnish et al. 2016), insects (e.g., De-Silva et al. 2016), and birds (e.g., Graham et al. 2009). It is likely that this mountain range represents a barrier to *M. modesta* because of unfavourable environmental conditions at high elevations, and indeed, Odonata richness often decreases with increasing elevations (e.g., Ecuadorian Andes: Jacobsen, 2003; Amundrud and Srivastava, pers. obs.). However, our analysis does suggest that potentially suitable habitat corridors exist through the Andes, notably in east-central Columbia and northwest Venezuela (Figure 2.4). It is possible that *M. modesta* has not successfully migrated through these low elevation corridors simply because the habitat conditions there are not suitable despite a suitable climate (e.g., bromeliads or primary forest may be absent). Behavioural tendencies of *M. modesta* to avoid open areas may be more important than its ability to disperse, consistent with the discovery that dispersal behaviour is more important in predicting odonate range size than is dispersal capacity (McCauley et al. 2014). Indeed, biological corridors are also inefficient for the giant tree-hole breeding damselfly *Megaloprepus caerulatus*, a species related to *Mecistogaster modesta*, which is sensitive to habitat fragmentation and does not travel through open areas (Khazan 2014). However, it is important to note that odonates in the *Bromeliagrion* genus that do fulfill the bromeliad niche east of the Andes may occur across these physical barriers (Appendix A), although too few records exist to make accurate predictions of their exact ranges. Any behavioural constraints of *M. modesta* that impede it from passing through such corridors may thus not apply to bromeliad-dwelling odonates in general.

In addition to physical barriers, climatic constraints were important factors limiting the geographic range of *M. modesta*, excluding the species from cold and dry areas. Although temperature and precipitation together affect water levels in bromeliads (i.e., high temperatures

and low precipitation lead to the driest conditions in bromeliads), we did not find a significant interaction of precipitation and temperature (the interaction term was removed from the models by stepwise regression). Furthermore, damselflies were restricted by low temperatures rather than the high temperatures that would be associated with faster evaporation rates. Instead, both annual mean temperature and annual precipitation had strong individual positive effects on the probability of *M. modesta* occurrence (Figure 2.2). Direct positive physiological effects of temperature on *M. modesta* thus appear to be more important than indirect negative effects of temperature by affecting the hydroperiod of bromeliads, consistent with studies showing that odonate occurrence (Ball-Damerow et al. 2014a) and richness (Jacobsen 2003) increases with higher temperatures. Our finding that low precipitation limited *M. modesta* occurrence is also not surprising, as experimental evidence suggests that *M. modesta* larvae are disproportionately affected by drought (Amundrud and Srivastava 2015, 2016), which results from low precipitation in bromeliads (Zotz and Thomas 1999). Other studies have also found negative effects of low precipitation and drought on odonates (e.g., Ball-Damerow et al. 2014a, b), particularly for those species that are habitat specialists (Ball-Damerow et al. 2014a).

Our analysis suggests that biotic factors from potential competitors were likely not important in limiting the distribution of *M. modesta*. However, the competition layer used in our models correlated with the layer representing dispersal barriers, and such correlations can result in biotic interactions being masked (Godsoe et al. 2017a). Still, closely related species of giant damselflies that breed in water-filled tree holes do coexist despite strong intraguild predation, because large larvae kill smaller ones independently of species identity, ensuring that competitive dominance is more a function of larval size than species identity (Fincke 1994). Similarly, our study shows that in South America, the ranges of the three bromeliad-dwelling

damsselfies (*Bromeliagrion bebeanum*, *B. fernandezianum*, and *B. rehni*) do overlap (see Appendix A), suggesting that competition does not constrain the distributions of those species at a large spatial scale.

To summarize, both physical barriers to dispersal and climatic constraints were important limiting factors of the geographic distribution of *M. modesta*, while competition from other bromeliad-dwelling odonates was not. Our finding that the distribution of this damsselfy is strongly linked to climate has important conservation implications, particularly as aridification of rainforests due to climate change continues (Brodie et al. 2012). Conversely, this species may benefit from rising temperatures by tracking climate to higher elevations. The introduction of this novel predator to high elevation systems would have strong effects on naïve high-elevation bromeliad food webs. An upwards migration by *M. modesta* could also increase the probability of this species overcoming the dispersal barrier presented by the Andes, enabling it to invade large areas of suitable habitat in South America which are currently beyond reach. Such a range expansion from climate change has happened, for example, for mountain pine beetles in British Columbia, Canada (Carroll et al. 2003). Future research should consider how simultaneous changes in precipitation and temperature in the Neotropics can alter the constraints on keystone species such as this damsselfy.

3 THERMAL TOLERANCES AND SPECIES INTERACTIONS

DETERMINE THE ELEVATIONAL DISTRIBUTIONS OF

INSECTS²

² Previously published as Amundrud, S. L., and Srivastava, D. S. (2020) Thermal tolerances and species interactions determine the elevational distributions of insects. *Global Ecology and Biogeography* 29: 1315-1327

3.1 CHAPTER SUMMARY

While physiological limits to thermal extremes are often thought to determine the abundance and geographic distribution of species, more recent evidence suggests that species interactions may be equally important. Moreover, the relative importance of these constraints may shift with changing abiotic conditions, such as climate change. Here, we explore the relative importance of physiological tolerances to heat and species interactions in determining the distribution of insects along two elevational gradients. The gradients contrast in precipitation but not temperature, allowing us to separate these two climatic factors. We estimated the elevation preferences of the aquatic larvae of five bromeliad-dwelling insect taxa by surveying 170 bromeliads along the moist Atlantic and the dry Pacific slopes of Monteverde, Costa Rica, and experimentally determined their critical thermal maxima (CT_{max}). We determined if taxon-specific heat tolerances predict their elevation preferences, using Deming regressions, and tested if potential predators mediated elevation effects on insect distributions, using structural equation models. On the moist Atlantic slope, heat tolerances of insects explained their elevational distributions: taxa with high heat tolerances preferred low elevations where conditions are warmest, while taxa with low heat tolerances preferred high elevations where it is coldest. By contrast, on the drier Pacific slope, the elevational abundance pattern of many insects reflected negative interactions from crane fly larvae. These larvae are known to become predatory under drought conditions and were disproportionately abundant at low elevations on the Pacific slope. In summary, we show that under drought, indirect effects mediated by species interactions can override any direct physiological effects of environmental conditions on insect distributions. The relative importance of limits to physiological tolerance and species interactions thus depends on

environmental context, an important insight given that environmental conditions are expected to shift with climate change.

3.2 INTRODUCTION

In a rapidly changing world, understanding how species distributions respond to changes in abiotic and biotic conditions is becoming ever more important. The abiotic niches of species can be broadly defined by their tolerance to climatic conditions such as temperature and precipitation. Species physiological limits to thermal extremes have often been considered to have major controls on their abundances and geographic distributions (e.g., Gaston and Chown 1999; Bozinovic et al. 2011; Kellermann et al. 2012). More recent evidence, however, suggests that species interactions may be at least as important in determining species distributions as physiological constraints of organisms (e.g., Ockendon et al. 2014; Godsoe et al. 2017b). Yet, the interplay of abiotic and biotic factors in shaping species distributions and abundances, and thus spatial variation in the composition of ecological communities, is still poorly understood.

Temperature is one of the most important abiotic constraints on the distribution and abundances of living organisms (Sunday et al. 2011, 2012), resulting from its profound effects on biological functions at all levels of biological organization (Hochachka and Somero 2002). As predicted by the thermal adaptation hypothesis (Sunday et al. 2012), thermal tolerance limits of ectotherms often correlate with species distributions (Addo-Bediako et al. 2000; Kellermann et

al. 2012; Vorhees et al. 2012). Much of the evidence supporting the thermal adaptation hypothesis comes from studies testing thermal tolerance limits in ectotherms along latitudinal (e.g., Addo-Bediako et al. 2000; Hoffmann et al. 2002) and elevational (e.g., Gaston and Chown 1999; Oyen et al. 2016) gradients. Tolerance to extreme heat events is often considered to be the most important predictor of species distributions (Clusella-Trullas et al. 2011; Kellermann et al. 2012; Vorhees et al. 2012; Overgaard et al. 2014; Kaspari et al. 2015), and studies often use measures of “heat tolerance”, which identify the upper bounds of species’ thermal tolerances, as an ecologically relevant method to link the thermal limits of species to their distributions (e.g., Cooper et al. 2008; Jørgensen et al. 2019). However thermal tolerance cannot always adequately explain species distributions (e.g., Nowrouzi et al. 2018).

Species interactions, by affecting local abundance, may also constrain the geographic distributions of species (Ockendon et al. 2014), but there are mixed views on the importance of this constraint (Nicholson 1958; Davis et al. 1998; Silvertown 2004). Species can be influenced by interactions from other species from the same, higher, or lower trophic levels, and interactions can range from inhibitory (Lawton and Hassell 1981) to beneficial (Bruno et al. 2003). Importantly, the strength and overall importance of species interactions can vary with changing abiotic conditions (Chase and Knight 2003; Hein et al. 2013; Blois et al. 2013; Ockendon et al. 2014; Amundrud and Srivastava 2016; Godsoe et al. 2017b; Amundrud and Srivastava 2019; Amundrud et al. 2019). For example, the magnitude of top-down effects exerted by consumers is often temperature dependent (Marino et al. 2018), as temperature affects metabolic rates (Vucic-Pestic et al. 2011) and thus alters consumption rates in aquatic (e.g., damselflies: Thompson 1978; fish: Meerhoff et al. 2007) and terrestrial (e.g., spiders: Barton and Schmitz 2009; beetles: Vucic-Pestic et al. 2011) systems. Similarly, changes in hydrological regimes in aquatic systems,

which depend on rainfall and evaporation rates (Schindler 2001), can impose biomechanical or metabolic constraints on organisms (Woodward et al. 2016) and thus alter species interactions (Chase and Knight 2003; Amundrud and Srivastava 2016, 2019; Amundrud et al. 2019). Due to the mediating role of climate in species interactions, the relative importance of physiological tolerance limits and species interactions in controlling species distributions and abundances likely depends on environmental context.

Surveys of communities along environmental gradients have been critical in developing our mechanistic understanding of the importance of biotic and abiotic regulators of species distributions. Altitudinal gradients in particular have been useful in improving our knowledge of the drivers of species distributions, as considerable climatic variation exists over short distances, diminishing any effects of dispersal limitation that can confound latitudinal gradients (Qian and Ricklefs 2007). As such, any turnover in community composition along altitudinal gradients is likely driven by changing abiotic conditions and biotic factors (Carpenter 2005). Yet, it has been challenging to disentangle which climatic factors are driving distributional limits of species, as multiple climatic factors (such as temperature, precipitation, solar radiation, etc.) change in concert.

Here, we present the results of an observational study exploring the relative importance of heat tolerance and species interactions in determining the elevational distributions of aquatic insects inhabiting phytothelm bromeliads. We contrast two elevation gradients, which span the Pacific and Atlantic slopes of the mountain of Monteverde, Costa Rica, providing us with an ideal opportunity to tease apart the effects of temperature from the effects of precipitation on the communities: while temperature increases at equal rates towards lower elevations on both the Pacific and Atlantic slopes, the Atlantic slope is relatively wet, while the Pacific slope is

relatively dry, especially towards lower elevations (Figure 3.1). Bromeliads and their associated macroinvertebrate communities occur naturally along these gradients, and bromeliad food webs are known to be strongly governed by species interactions. These include positive interactions from detritivorous crane fly (*Trentepohlia* spp.) larvae on other insects through detrital processing (Starzomski et al. 2010), as well as negative top-down effects from predatory damselfly (*Mecistogaster modesta*) nymphs on the communities (Amundrud and Srivastava 2016). Importantly, crane fly larvae have recently been shown to become predatory under drought conditions (Amundrud and Srivastava 2019; Amundrud et al. 2019), while the persistence of damselfly nymphs has been shown to be limited by drought (Amundrud and Srivastava 2016).

A central prediction of the thermal adaptation hypotheses is that tropical insect distributions are tightly linked to their physiological tolerance of thermal extremes (Deutsch et al. 2008; but see Vasseur et al. 2014). We predicted that if thermal tolerance limits are the main drivers of the elevational distributions of insects, then taxa with low tolerances to heat will be distributed towards higher elevations where conditions are coldest, while taxa with high tolerances to heat will be more resistant to warmer conditions and thus can thrive at lower elevations on both mountain slopes (Prediction 1). However, if species interactions are the primary driver of insect elevational distributions, we predicted that top-down effects from damselflies and/or crane flies will explain elevational distributions better than heat tolerance (Prediction 2). Finally, if the relative importance of species interactions depends on environmental context (i.e., drought), the relative influence of species interactions and temperature in driving insect distributions will depend on mountainside (Prediction 3). Such context-dependence could occur if negative interactions from damselflies shape insect

distributions on the Atlantic slope, but not on the Pacific slope, which may be too dry for damselflies to persist (Prediction 3.1). Alternatively, negative interactions from crane flies could shape the elevational distributions of other taxa on the Pacific slope, where drought enables crane flies to become predatory, but not on the Atlantic slope which does not experience drought conditions (Prediction 3.2).

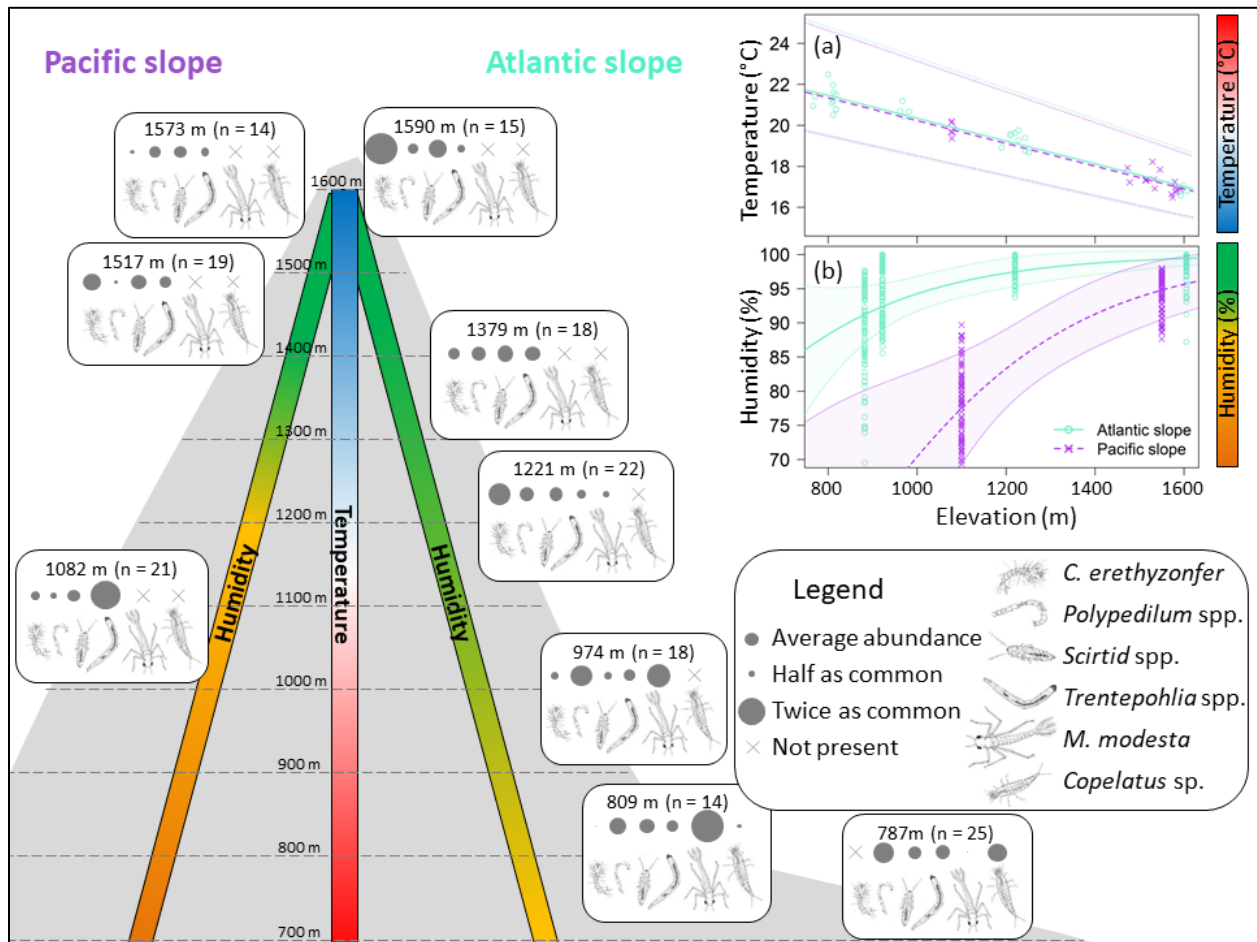
3.3 METHODS

3.3.1 *Study site and system*

The study area extended from the high elevation cloud forest of Monteverde, northwestern Costa Rica (10°18'N 84°46'W, highest elevation ~ 1600 m), and down the Atlantic (10°21'N 84°40'W, lowest elevation ~ 800 m) and Pacific (10°17'N 84°48'W, lowest elevation ~ 1100 m) slopes of the Tilaran mountain range (Figure 3.1). All study sites were in the Monteverde Cloud Forest Reserve and the Children's Eternal Rain Forest Reserve, except for the lowest elevation site on the Pacific slope, which was on private land. Although we attempted an equal sampling effort at both mountainsides, this was not possible, as bromeliads were rare on the dry Pacific slope and much of the forest has been converted to farm land. Elevational gradients in the tropics exhibit particularly high spatial turnover in temperature (Dillon et al. 2006; García-Robledo et al. 2016). While the mean annual temperature increases at roughly equal rates towards lower elevations on both mountain sides, elevations below ~ 600 m on the Pacific slope are experiencing significantly greater temperature variation (defined as Bioclim

1960-1990 estimated temperature annual range) than the same elevations on the Atlantic slope (Baudier et al. 2018). However, over the elevational extent of our study (> 800m), both mountain slopes experienced similar elevation-related temperature changes: mean and maximum daily temperature (recorded by temperature loggers from Sep. 9-30, 2016; see legend of Figure 3.1 for more information) increased by ~ 6°C and ~ 7.5°C, respectively, per 1000 m drop in elevation on both mountain slopes (Figure 3.1a). The two slopes do however differ in humidity, with low elevations on the Pacific slope being significantly drier than low elevations on the Atlantic slope (Figure 3.1b). Bromeliads occur naturally along these elevational gradients and exhibit variation in thermal and hydrological regimes according to local environmental conditions. Tank bromeliads at Monteverde [*Werauhia gladioliflora* (H. Wendl.) Antoine, *Werauhia sanguinolenta* Cogn. and Marchal, and *Guzmania scherzeriana* Mez] contain detrital based food webs consisting of macroinvertebrates and microorganisms. The dominant macroinvertebrates inside bromeliads are the larvae of dipterans (filter-feeding Culicidae: mainly *Culex* spp., *Wyeomyia* spp., and *Anopheles* spp.; detritivorous Chironomidae: especially *Polypedilum* spp. and Orthoclaadiinae; and omnivorous Tipulidae: undescribed *Trentepohlia* spp.), as well as detritivorous coleopteran Scirtidae (*Scirtes* spp.). At elevations below ~ 1300 m on the Atlantic slope, predatory damselfly larvae *Mecistogaster modesta* Selys. (Coenagrionidae: Odonata) occur at low abundances, and predatory larvae and adults of a diving beetle (Dytiscidae: *Copelatus* spp., Coleoptera) are common at the lowest elevation site (Figure 3.1).

Figure 3. 1: Diagram summarizing the study area on Monteverde mountain. The main diagram depicts the elevations and sampling effort (i.e., number of bromeliad sampled: n) of the nine study sites, as well as the species composition at each site. Line drawings represent insect species (i.e., the larvae of the mosquito *Culex erethyazonfer*, the chironomid *Polypedilum* spp., the marsh beetle *Scirtid* spp., the crane fly *Trentepohlia* spp., the damselfly *M. modesta*, and the diving beetle *Copelatus* spp.). Filled circles represent the relative abundances* of the species at each study site. Colour bars along the mountain represent temperature (Atlantic slope = Pacific slope) and humidity (Atlantic slope ≠ Pacific slope) change along elevation. Subset figures on top right show (a) the average daily mean (marks and solid/dashed lines), maximum and minimum (dotted lines) temperature†, and (b) the mean daily humidity (±95% C.I.) obtained from weather stations (Feb. 2 – May 15, 2013) on the Atlantic (green circles and solid line) and Pacific (purple crosses and dashed line) slopes. The lines in (b) were fit with logistic regression models and are for visual purposes only (i.e., these model were not used in further analyses).



*For each species, its average abundance was calculated from sites where at least one individual of that species was present (e.g., for *M. modesta*, only the four lowest elevation sites at the Atlantic slope were included in the calculation, as this species was absent from all other sites).

† We placed iButton™ data loggers (DS1921G-F5# Thermochron, 4K) inside and outside (tied on and shaded by the plant) bromeliads, which recorded the temperature hourly from Sep. 9-30, 2016, the timeframe for which we had overlapping temperature data for all loggers for all sites. Habitat temperature did not depend on mountainside or whether or not temperature loggers were placed inside or outside bromeliads.

3.3.2 *Survey of bromeliad food webs*

We surveyed bromeliad food webs at nine sites along the two elevation gradients (Figure 3.1) from late September to early December in 2015 and 2016 (see Appendix B.1 for names, elevations, exact coordinates and sampling dates of sites). Because sampling time can affect abundance patterns of insects due to seasonal effects, we ensured that sampling was completed in the shortest possible timeframe, and performed non-systematically with respect to mountainside and elevation (see Figure B.1 in Appendix B.1). We quantified the aquatic macroinvertebrate communities inside bromeliads with a water-holding capacity of up to 1000 ml ($n = 14 - 25$ depending on site: Figure 3.1) by rinsing the entire contents of bromeliads, searching bromeliad water and detritus thoroughly for insects and other invertebrates, and recording the identities (finest taxonomic level or morphospecies) and abundances of all organisms > 1 mm in length. We measured the water-holding capacity (in mL) of each bromeliad by adding a known quantity of water to the empty bromeliads until overflowing, and then subtracting the overflow from the volume added. We also quantified the detritus inside bromeliads as the dry weight of leaf fragments retained by a sieve with a mesh size of 850 μm . We transported live insect larvae collected in 2015 back to the laboratory in Santa Elena, where they were maintained at constant room temperature of ~ 20 °C until they were used in further experiments.

3.3.3 Determination of insect heat tolerances

We experimentally determined the heat tolerances of five common macroinvertebrate taxa [$n = 10 - 12$ individuals per taxon per site of the larvae of the mosquito *Culex erethyzonfer* (filter-feeder), the chironomid *Polypedilum* spp. (collector), the marsh beetle *Scirtid* spp. (scraper), the crane fly *Trentepohlia* spp. (shredder), and the damselfly *M. modesta* (predator)]. Larvae were collected in 2015 at two sites on the Atlantic slope (at 1379 m and 1221 m elevation) and two sites on the Pacific slope (at 1517 m and 1082 m elevation; Figure 3.1). We determined heat tolerances as the critical thermal maxima (CT_{max}) of larvae that have been acclimatized at the laboratory for at least 4 days (Brattstrom 1968; Duarte et al. 2012) by subjecting individuals to gradually increasing temperatures ($0.3\text{ }^{\circ}\text{C min}^{-1}$) in an electric water bath. Such dynamic assays of temperature ramping have been found to be suitable in characterizing heat tolerance in insects (Jørgensen et al. 2019). We estimated heat tolerance as the temperature at which the insect first failed to respond to a tactile stimulus (e.g., Buchanan et al. 1988; Kivivuori and Lahdes 1996; Cooper et al. 2008; Jørgensen et al. 2019).

3.3.4 Statistical Analyses

We performed all analyses in R (version 3.6.2: R Core Team 2019). From our total data set of 170 bromeliads, we removed outliers, defined as bromeliads with disproportionately high macroinvertebrate abundances totalling > 400 individuals ($n = 4$), resulting in a final data set consisting of 166 bromeliads (see Figure 3.1 for sample size at each study site). We explored the potential effects of elevation, mountainside, or their interaction on each of bromeliad size and detrital content, using linear models. To quantify the effect of elevation, mountainside, and their

interaction on abundances of focal taxa, we employed generalized linear models (GLMs) with a Poisson error distribution. In these insect abundance models, we included bromeliad capacity as covariate to control for any effects of bromeliad size that could confound effects of elevation and/or mountainside. We examined model suitability by checking for overdispersion in Poisson models, as well as by using quantile–quantile, residual, and outlier plots. We employed the *glm.poisson.disp* function (R package *dispmod*: Scrucca 2018) to correct for overdispersion in Poisson models.

We estimated the elevation preference (EP) of each taxon by extracting the slope from the elevation term of the Poisson model. A positive slope thus indicates a preference for high elevations, while a negative slope indicates a preference for low elevations. When the interaction of mountainside with elevation was not significant (*Scirtid* spp. and *Polypedilum* spp.), we extracted the slope of a simplified model that did not include mountainside. When mountainside interacted with elevation (*C. erethyzofer* and *Trentepohlia* spp.), we fit separate models for the Pacific and Atlantic mountainside, and extracted the slope from each model.

As an alternative measure of insect differences in sensitivity to elevation, we also calculated the mean elevation of occurrence of each taxon for each mountainside as the average elevation of occurrence over all individuals within each taxon. We stress that, while this metric allows us to compare elevation midpoints of various taxa within this survey data, any comparisons to other data sets (or indeed between the two mountainsides) are not appropriate, as this metric is strongly influenced by sampling extent and unequal sampling effort across elevation.

To test Prediction 1 (thermal tolerance limits are the main drivers of elevational insect distributions) and Prediction 3 (the relative importance of thermal tolerance and species interactions depends on environmental context), we investigated the relative importance of heat tolerance on the EP of bromeliad insects for each side of the mountain by employing a Deming regression in the *deming* R package (Therneau 2018). Deming regression is suitable for regressions between variables both measured with error, and both heat tolerance and EP were estimates with standard errors. To test the robustness of results based on EP, we also performed a weighted regression [weights = $1/(CT_{\max}^2)$] in which we used the mean elevation of occurrence instead of EP as response.

To test Prediction 2 (species interactions are the primary driver of insect elevational distributions) and Prediction 3 (the relative importance of thermal tolerance and species interactions depends on environmental context), we employed structural equation models (SEMs), using the *lavaan* package in R (Rosseel 2012), to explore how elevational distributions of insects were related to direct effects of elevation versus indirect effects mediated by the potential predators *M. modesta* (Prediction 3.1) and *Trentepohlia* spp. (Prediction 3.2). Although we do not measure species interactions per se (this would require measurements of per capita interaction strength), we predicted that predation would result in a negative correlation of the relative abundances of potential predators with potential prey species, as both *M. modesta* and *Trentepohlia* spp. have been shown in previous experiments to exert negative per capita interactions on other insects (e.g., Amundrud and Srivastava 2016; Amundrud et al. 2019). However, we do acknowledge that the relative abundance of a co-occurring species could also reflect shared (unmeasured) habitat characteristics (Araújo and Luoto 2007). To meet the assumption of equal variances in SEMs, we recoded the terms in our model by dividing elevation

by 150 and multiplying the relative abundances of our focal taxa by integers ranging from 5 (for *Scirtid* spp. and *Polypedilum* spp., the most common taxa) to 100 (for *M. modesta*, the rarest taxon) so that variances were within one order of magnitude of one another (Rosseel 2012).

3.4 RESULTS

Bromeliads tended to become smaller towards higher elevations ($F_{1,162} = 29.9$, $p < 0.001$), but bromeliad size did not depend on mountainside ($F_{1,162} = 1.77$, $p = 0.18$) or the interaction of elevation with mountainside ($F_{3,162} = 0.88$, $p = 0.35$). Detrital content inside bromeliads did not depend on elevation ($F_{1,160} = 1.04$, $p = 0.31$), mountainside ($F_{1,160} = 3.58$, $p = 0.06$), or their interaction ($F_{1,160} = 0.41$, $p = 0.52$).

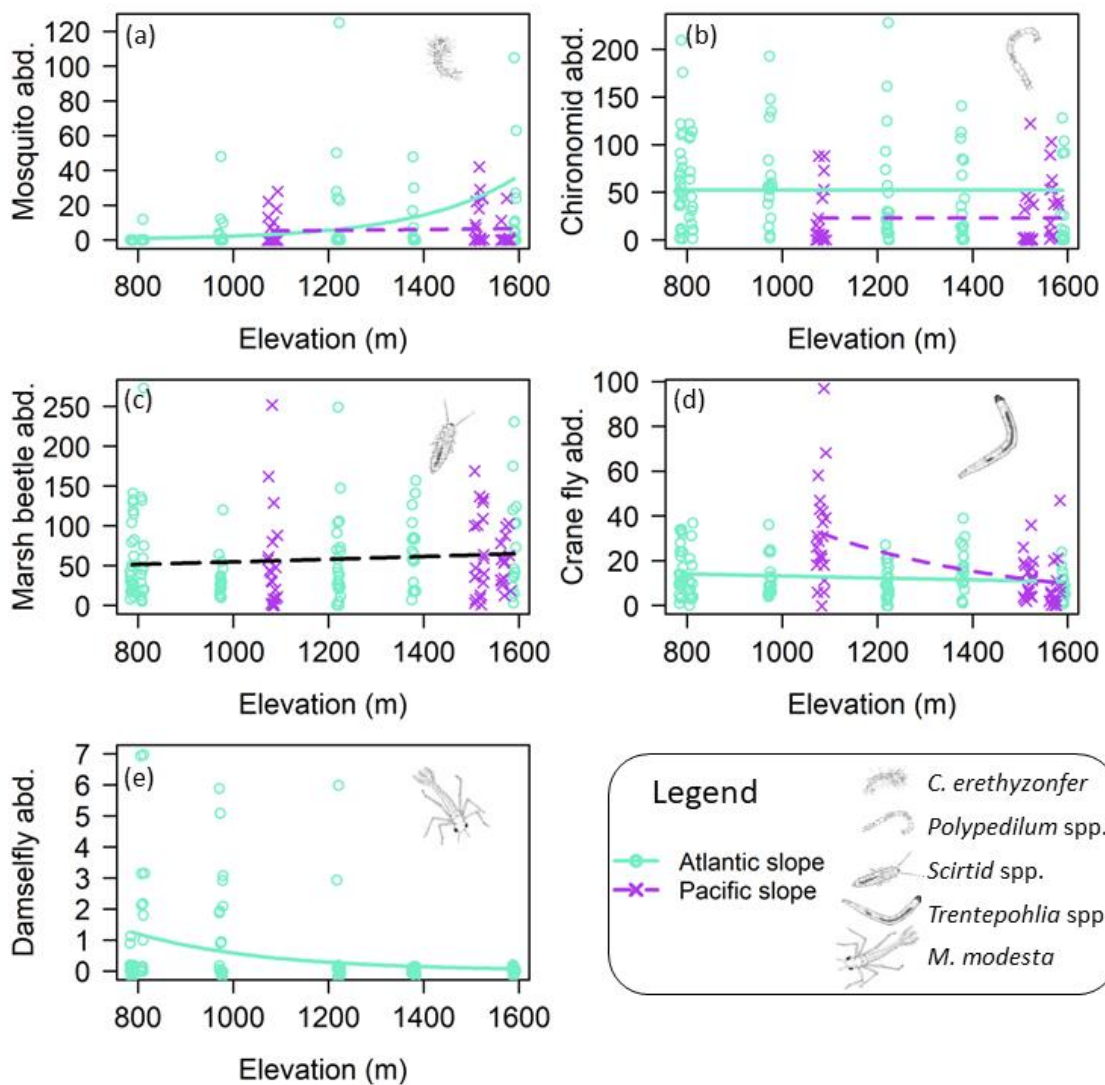
Bromeliad-dwelling insect taxa exhibited distinct elevation preferences (Figure 3.2 and Appendix B.2). The larvae of mosquitoes (*C. erethyzofer*) and marsh beetles (*Scirtid* spp.) both increased in abundance towards higher elevations, although for mosquitoes this preference was only apparent on the Atlantic slope (Table 3.1, Figure 3.2a,c). By contrast, the predatory damselfly nymph (*M. modesta*) and the facultative predatory crane fly larva (*Trentepohlia* spp.) preferred lower elevations; specifically, damselfly abundance increased towards low elevations on the Atlantic slope (this species was absent from the Pacific slope and from elevations $> \sim 1250$ m on the Atlantic slope), whereas crane fly abundance was highest at the low elevation site on the Pacific slope (Table 3.1, Figure 3.2d,e). The chironomid larva (*Polypedilum* spp.) was the only taxa whose abundance was not affected by elevation. However, this insect was twice as

common on the Atlantic slope as on the Pacific slope (Table 3.1, Figure 3.2b). Bromeliad capacity only affected the abundances of two taxa, marsh beetles and chironomids, which both increased in abundance with bromeliad size (Table 3.1). The mean elevation of occurrences of bromeliad insects mirrored their elevation preferences (Appendix B.2).

Table 3. 1: Abundance of five focal insect species (“taxon”) in bromeliads as a function of elevation (continuous), mountainside (categorical: Atlantic vs. Pacific), their interaction, and bromeliad capacity (continuous). For the damselfly *M. modesta*, mountainside is not included, as this species was only found on the Atlantic slope. For each focal taxon, all explanatory variables were fit in a single Poisson generalized linear model, with terms assessed with an ANOVA as indicated by X^2 and p-values.

Taxon	elevation		mountainside		elevation:side		bromeliad capacity	
	X^2	p	X^2	p	X^2	p	X^2	p
<i>C. erethydonfer</i>	13.07	< 0.001	1.27	0.259	4.34	0.037	0.21	0.647
<i>M. modesta</i>	6.13	0.013	-	-	-	-	2.91	0.088
<i>Polypedilum spp.</i>	0.05	0.832	17.43	< 0.001	2.69	0.101	7.24	0.007
<i>Scirtid spp.</i>	14.51	< 0.001	2.07	0.150	0.21	0.646	31.04	< 0.001
<i>Trentepohlia spp.</i>	7.90	0.005	7.37	0.007	13.18	< 0.001	0.56	0.454

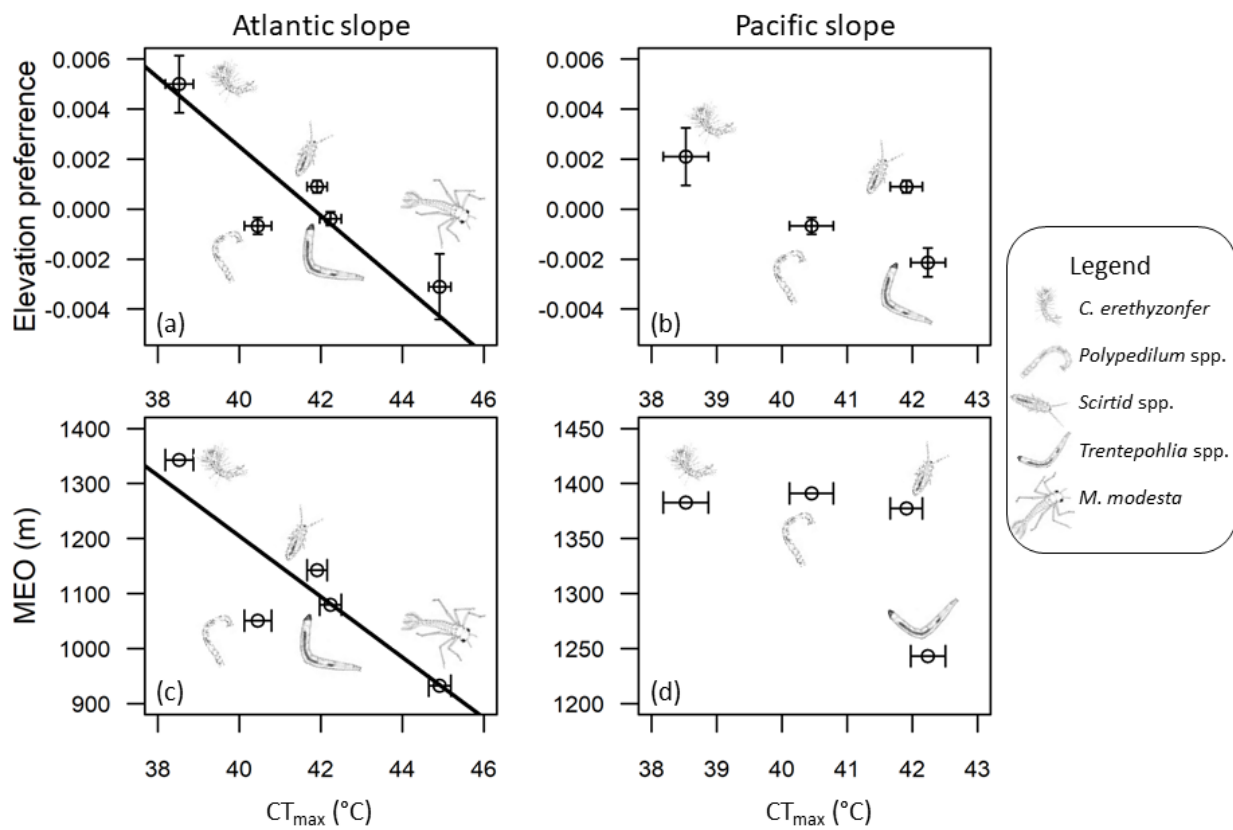
Figure 3. 2: The abundances (abd.) of focal species inside bromeliads surveyed along the elevation gradients on the Atlantic (green circles, solid lines) and Pacific (purple crosses, dashed lines) slopes of Monteverde. Focal species are the larvae of (a) the mosquito *Culex erethyzofer*, (b) the chironomid *Polypedilum* spp., (c) the marsh beetle *Scirtid* spp., (d) the crane fly *Trentepohlia* spp., and (e) the damselfly *M. modesta*. Lines represent best fit from Poisson regressions models. When mountainside interacted with elevation (*C. erethyzofer* and *Trentepohlia* spp.) or when only mountainside was statistically significant (*Polypedilum* spp.), separate lines are shown for the Pacific and Atlantic slopes (purple, dashed or green, solid); otherwise, the regression line from the model without mountainside is shown (*Scirtid* spp.: black, longdashed). *M. modesta* abundance was only modeled on the Atlantic slope, as it was absent from the Pacific slope.



Bromeliad insects also exhibited distinct heat tolerances. Mosquitoes had the lowest tolerance to heat ($CT_{\max} = 38.5^{\circ}\text{C} \pm 0.3$ (SE), $n = 41$), followed by chironomids ($CT_{\max} = 40.5^{\circ}\text{C} \pm 0.3$ (SE), $n = 42$). The heat tolerances of marsh beetles ($CT_{\max} = 41.9^{\circ}\text{C} \pm 0.2$ (SE), $n = 43$) and crane flies ($CT_{\max} = 42.2^{\circ}\text{C} \pm 0.3$ (SE), $n = 40$) were similar, and damselflies exhibited the highest heat tolerance of all bromeliad insects in our study ($CT_{\max} = 44.9^{\circ}\text{C} \pm 0.3$ (SE), $n = 12$). Heat tolerances did not differ between mountainsides, so we only report the combined (i.e., average) CT_{\max} for each taxon.

Taxon-specific heat tolerances were related to elevation preferences and mean elevation of occurrences of bromeliad insects on the Atlantic, but not the Pacific slope of Monteverde (Figure 3.3). On the Atlantic slope, insect taxa that exhibited high heat tolerances tended to disproportionally occur at low elevations - where it is warm - while taxa with low heat tolerances tended to disproportionately occur at high elevations - where it is cold (Deming regression: $p = 0.002$, Figure 3.3a; weighted regression: $F_{1,3} = 10.5$, $p = 0.048$, $R^2 = 0.78$; Figure 3.3c). On the Pacific slope, by contrast, there was no significant relationship of elevation preference (or mean elevation of occurrence) with CT_{\max} (Deming regression: $p = 0.93$, Figure 3.3b; weighted regression: $F_{1,2} = 0.86$, $p = 0.45$, $R^2 = 0.30$; Figure 3.3d). We caution, however, that our analysis on the Pacific slope suffers from very low statistical power ($n = 4$), so the negative results on the Pacific slope should not be interpreted as a lack of effect of heat tolerance on elevation preference and mean elevation of occurrence.

Figure 3. 3: Heat tolerance (CT_{max}) explains elevation preference and mean elevation of occurrence (MEO) on the Atlantic slope (a and c), but not on the Pacific slope (b and d). Elevation preference was measured as the coefficient of the effect of elevation on abundance. Symbols represent the larvae of the mosquito *Culex erethyzonfer*, the chironomid *Polypedilum* spp., the marsh beetle *Scirtid* spp., the crane fly *Trentepohlia* spp., and the damselfly *M. modesta*. Line represents best fit of statistically significant relationship ($\alpha = 0.05$).



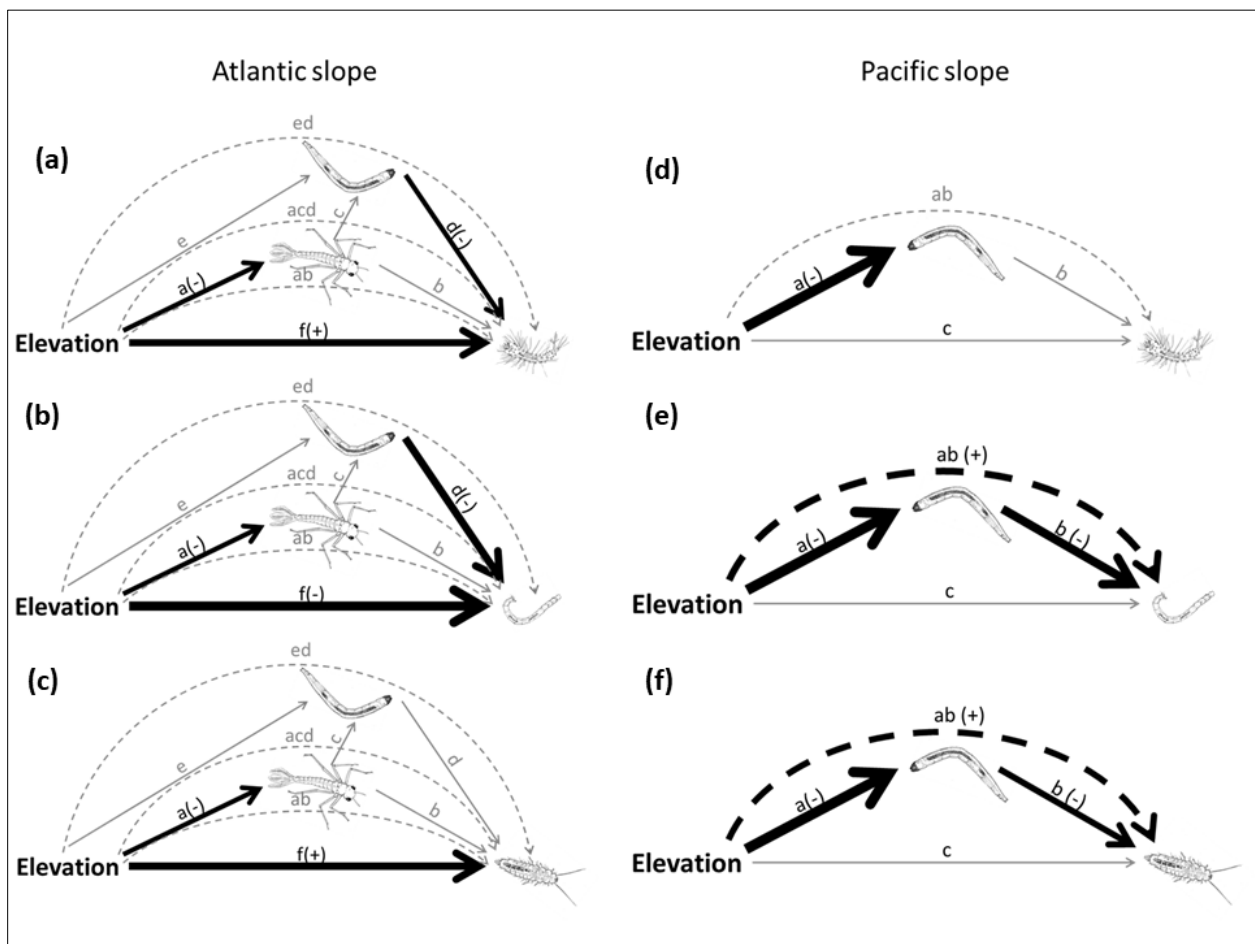
Potential effects of species interactions explained the effects of elevation on insect abundance on the Pacific slope, but not on the Atlantic slope (Table 3.2, Figure 3.4). On the Pacific slope, elevation had indirect positive effects on the relative abundances of the larvae of chironomids (*Polypedilum* spp.) and marsh beetles (*Scirtid* spp.), and for both taxa this indirect effect was mediated by crane fly larvae (*Trentepohlia* spp.; pathway ab: Table 3.2b, Figure 3.4e,f), suggesting that chironomids and marsh beetles become more abundant towards higher elevations because of adverse effects of crane flies at low elevations (pathway b: Table 3.2b, Figure 3.4d-f). In contrast to the Pacific slope, species interactions did not mediate effects of elevation on relative abundance patterns of bromeliad insects on the Atlantic slope (pathways ab, ed, and acd: Table 3.2a, Figure 3.4a-c). Instead, the relative abundances of the larvae of mosquitoes (*C. erethyzonfer*) and marsh beetles were positively affected by elevation, while chironomids and damselflies were negatively affected by elevation (pathways f and a: Table 3.2a, Figure 3.4a-c). Importantly, although crane flies had negative effects on mosquitoes and chironomids on the Atlantic slope (pathway d: Table 3.2a, Figure 3.4a,b), those negative effects of crane fly larvae did not result in any indirect effects of elevation on these insects (pathway ed), presumably because crane flies were not affected by elevation on the Atlantic slope (pathway e: Table 3.2a, Figure 3.4a-c). When we replaced damselfly abundance in analyses with “obligate predator” abundance (i.e., combined abundances of the diving beetle *Copelatus* spp. and the damselfly), the results were qualitatively identical (Appendix B.3).

Table 3. 2: The abundance of each of three focal species (columns) is modelled with structural equation models (SEMs), with each SEM being composed of multiple paths (rows, with letters corresponding to Figure 3.4). The significance (p values) of individual paths is assessed with Z-scores. The SEMs were fit separately for a) the Atlantic slope and b) the Pacific slope.

a) Atlantic slope		<i>C. erethyzonefer</i>		<i>Polypedilum</i> spp.		<i>Scirtid</i> spp.	
path	Z	p	Z	p	Z	p	
a: <i>M. modesta</i> ~ elevation	-2.272	0.023	-2.272	0.023	-2.272	0.023	
b: focal species ~ <i>M. modesta</i>	-0.280	0.775	1.297	0.195	-1.523	0.128	
c: <i>Trentepohlia</i> spp.~ <i>M. modesta</i>	-1.472	0.141	-1.472	0.141	-1.472	0.141	
d: focal species ~ <i>Trentepohlia</i> spp.	-2.227	0.026	-3.404	0.001	-0.612	0.540	
e: <i>Trentepohlia</i> spp.~ elevation	-0.160	0.873	-0.160	0.873	-0.160	0.873	
f: focal species ~ elevation	3.099	0.002	-4.055	< 0.001	3.327	0.001	
ab: indirect effect mediated by <i>M. modesta</i>	0.283	0.777	-1.126	0.260	1.265	0.206	
ed: indirect effect mediated by <i>Trentepohlia</i> spp.	0.160	0.873	0.160	0.873	0.155	0.877	
acd: indirect effect mediated by <i>M. modesta</i> + <i>Trentepohlia</i> spp.	-1.080	0.280	-1.161	0.245	-0.549	0.583	

b) Pacific slope		<i>C. erethyzonefer</i>		<i>Polypedilum</i> spp.		<i>Scirtid</i> spp.	
path	Z	p	Z	p	Z	p	
		<					
a: <i>Trentepohlia</i> spp.~ elevation	-4.223	0.001	-4.223	< 0.001	-4.223	< 0.001	
b: focal species ~ <i>Trentepohlia</i> spp.	1.050	0.294	-3.700	< 0.001	-2.693	0.007	
c: focal species ~ elevation	1.310	0.190	-1.705	0.088	1.297	0.195	
ab: indirect effect mediated by <i>Trentepohlia</i> spp.	-1.019	0.308	2.783	0.005	2.270	0.023	

Figure 3. 4: Path diagram summarizing results of structural equation models for the three focal species on the Atlantic (left panels) and Pacific (right panels) slopes. The three focal species are the larvae of the mosquito *Culex erethyzonfer* (a and c), the chironomid *Polypedilum* spp. (b and e), and the marsh beetle *Scirtid* spp. (c and f). Species that can potentially mediate the effects of elevation on the focal species are the facultative predatory crane fly larva *Trentepohlia* spp. (both Pacific and Atlantic slopes) and the obligatory predatory damselfly nymph *M. modesta* (Atlantic slope only). Color indicates statistically significant (black) or non-significant (grey) path ($\alpha = 0.05$). Thickness of arrow represents magnitude of effect when effect is significant. Direction of effect is indicated by (+) or (-).



3.5 DISCUSSION

Species distributions and the make-up of ecological communities are governed by abiotic conditions and biotic interactions, but the interplay between these two factors is still poorly understood. We showed that the relative importance of temperature and species interactions in determining the elevational distributions of bromeliad-dwelling insect communities can depend on environmental conditions, consistent with Prediction 3. On the moist Atlantic slope of Monteverde, insects with high heat tolerances preferred low elevations where conditions are warmest, while insects with low heat tolerances preferred high elevations where it is coldest. On the drier Pacific slope, by contrast, the elevational abundance patterns of insects reflected potential negative interactions from crane fly larvae, which are known to become predatory under drought conditions (Amundrud and Srivastava 2019; Amundrud et al. 2019), consistent with Prediction 3.2. We stress that our results cannot be interpreted in terms of one factor (heat tolerance) being solely responsible for driving elevational distributions on the Atlantic slope, while another (species interactions) is solely responsible for driving the results on the Pacific slope. Instead, both are important, but the relative importance of (and our ability to detect) these factors depended on mountain side and thus environmental context.

Our conclusion from the Atlantic slope, that the impact of physiological heat tolerance on insect elevational distributions overshadows any effects of species interactions, is consistent with expectations from the thermal adaptation hypothesis (Sunday et al. 2012), and supports the findings of other studies that link species' thermal tolerances with their distributions along gradients in both latitude (Addo-Bediako et al. 2000; Hoffmann et al. 2002) and elevation (Gaston and Chown 1999; Oyen et al. 2016). However, our finding that negative interactions

from crane fly larvae outweighed any physiological effects from high temperatures in driving insect elevational distributions on the Pacific slope underlines that, under certain conditions, factors other than physiological traits can be more important in determining species distribution and abundance patterns.

Indirect effects of climate stressors on entire communities can be driven by “leverage species”, that is, species that are both sensitive to the stressor and dominant in terms of species interactions (Harley et al. 2006). Such species can act as “biotic multipliers” of climate change, resulting in community-level effects that outweigh any direct effects of climate change on individual species (Zarnetske et al. 2012). On the Pacific slope, the crane fly *Trentepohlia* spp. may have acted as leverage species, as it responded both strongly to changes in climatic conditions, while also exerting disproportionate community level effects. The dry and warm conditions on the low elevation Pacific slope resulted in changes in population size as well as potential per capita effects of crane flies, both of which can result in ecosystem level changes (Sanford 1999). Not only were crane fly larvae disproportionately abundant on the low elevation Pacific slope, presumably due to the combined effects of a high heat tolerance and a high drought tolerance (Amundrud and Srivastava 2015), but the warm and dry conditions also facilitated negative effects of crane flies on other bromeliad insects, consistent with recent findings that crane fly larvae become ferocious predators of other insect larvae under drought (Amundrud and Srivastava 2019; Amundrud et al. 2019). The mosquito *C. erethyzofer* was the only potential prey that was not affected by crane flies on the Pacific slope (Table 3.2b, Figure 3.4d). Instead, the preference of this mosquito for high elevations was most likely linked to its low tolerance to heat. On the Atlantic slope, by contrast, no insects acted as leverage species to transmit the effects of altered climatic conditions on the community. Instead, the taxon that

exerted adverse effects on other insects (crane fly) was not affected by elevation, while the taxon that strongly responded to elevation (damselfly) was not common enough to exert significant effects on the community (Table 3.2a, Figure 3.4a-c). Collectively, these results suggest that under certain environmental conditions, indirect effects mediated by species interactions may override any direct physiological effects of environmental conditions on species distributions. Pinpointing these conditions is critical when making predictions about species distributions, particularly in the face of climate change.

Making accurate predictions of how climate change will affect species distributions and communities is ever more important in a rapidly changing world. While species' physiological tolerance limits to abiotic conditions have often been employed to predict ecological responses to climate change, they may not always be the main drivers of species distributions. Not only is it becoming increasingly clear that single species can act as biotic multipliers of climate change (Zarnetske et al. 2012), and that such biotic multipliers can be more important drivers of species distributions than species' physiological limits to abiotic conditions (Ockendon et al. 2014), but we show here that the relative importance of abiotic and biotic effects can depend on environmental context. It is thus likely that the relative importance of physiological and ecological drivers of species distributions will shift with changing abiotic conditions, such as climate change. In our study, insect elevational distributions on the Atlantic slope were related to their physiological tolerance limits to high temperatures. However, with climate change, the effects of species interactions (i.e., from predation) may override the effects of physiological limits to drive insect distribution patterns. Specifically, predatory damselflies are expected to benefit from warmer temperatures and increase locally in abundance. In addition, this predator will likely track climate change to higher elevations, as previous species distribution models

suggest that this species' range is limited by low temperatures found at high elevations (Amundrud et al. 2018). As such, increased predation pressure from this keystone predator on the Atlantic slope will potentially alter insect elevational distributions as the climate warms. Altered top-down effects from climate change are predicted to affect food webs across many ecosystem types (Marino et al. 2018), underlining that predators are particularly likely to mediate the effects of climate change (Urban et al. 2017).

We acknowledge several caveats of our study. First, the decrease in bromeliad size towards higher elevations could have potentially influenced elevational abundance patterns of bromeliad insects. However, we can discount this possibility. The abundances of only two insect taxa were related to bromeliad size: both *Scirtid* spp. and *Polypedilum* spp. increased with bromeliad size. If the elevational abundances of these insects were driven by bromeliad size, we would expect a decrease in their abundances with elevation, along with the decrease in bromeliad size. This was not the case, however, as *Scirtid* spp. abundance increased towards higher elevations, while *Polypedilum* spp. abundance was not affected by elevation. Second, we recognize that there are several obstacles to experimentally determining physiological tolerance limits of insects. We minimized any potential biases that could have affected the results by applying the same strict experimental protocol to all subjects (e.g., constant rates of temperature ramping and close to constant starting temperatures, identical selection of endpoints to estimate heat tolerance, as well as acclimation times of at least 4 days). We stress, however, that while our heat tolerance estimates are comparable within this study, they should not be compared to other studies where the methodology might have differed (Lutterschmidt and Hutchison 1997; Terblanche et al. 2007; Cooper et al. 2008). Third, we acknowledge that, although multiple studies have suggested that the most important predictor of species distributions is their

physiological tolerance to extreme heat events (e.g., Kellermann et al. 2012; Vorhees et al. 2012; Overgaard et al. 2014), tolerance to low temperature may be more important in governing geographic distributions for some species (Lutterschmidt and Hutchison 1997). *M. modesta* damselfly larvae in particular were likely limited by cold temperatures towards higher elevations, based on the results from a species distribution model (Amundrud et al. 2018). Fourth, we showed that the relative importance of physiological tolerance limits and species interactions depended on drought. However, it is likely that the dynamic nature of the relative importance of these two factors also shifts with season, and it would be informative to repeat this study across seasons and years. Finally, our finding that damselflies were very rare at the lowest elevation site on the Atlantic slope, even though this species tended to become more common in other lower elevation sites on the Atlantic slope, was surprising. The low damselfly numbers at this site may be related to the high abundances of diving beetles (Figure 3.1), as *M. modesta* damselflies are known to avoid these predators due to negative effects of intra-guild predation or tactile stimulation (Atwood et al. 2014).

We studied the interplay of thermal tolerance limits and species interactions in shaping aquatic insect food webs inside Neotropical bromeliads along two elevational gradients, and demonstrated that the relative importance of abiotic and biotic drivers of insect distributions can depend on environmental context. While heat tolerance was more important in explaining insect elevational distributions when conditions were wet (Atlantic slope), indirect effects from potential predators were more important in explaining their elevational distributions when conditions were dry (Pacific slope). These two elevation gradients allowed us to examine species occurrence over a broad range of climate parameter space but over a spatial extent small enough that dispersal is not expected to be limiting, enabling us to attribute distributions to the

interactive effects of rainfall, temperature and potential predators. The mechanistic processes inferred from this landscape-scale study may inform our understanding of regional and global-scale patterns in community structure where dispersal limitation, phylogeographic constraints and covariance between biotic and abiotic variables can make causal inference weaker (Araújo and Luoto 2007). Complex community-level responses to climate change are still poorly understood, and these findings support other recent studies demonstrating that the effects of climate change on species ranges and community dynamics may be highly influenced by species interactions (Clark et al. 2011; Diamond et al. 2016). Importantly, our study also demonstrates the dynamic nature of the interplay between abiotic and biotic selective pressures on insect physiology and distributions. This is an important insight given the rapid rates of changing environmental conditions globally. As the climate changes, tropical montane regions, which often contain biodiversity hotspots with exceptionally high rates of endemism, are of particular concern (Graham et al. 2014). In all ecosystem types, however, the relative importance of abiotic and biotic effects on species distributions is likely to shift with climate change. Future research should thus focus on understanding how climate change alters the factors that mediate species distributions.

4 DROUGHT ALTERS THE TROPHIC ROLE OF AN
OPPORTUNISTIC GENERALIST IN AN AQUATIC
ECOSYSTEM³

³ Previously published as Amundrud, S. L., Clay-Smith, S. A., Flynn, B. L., Higgins, K. E., Reich, M. S., Wiens, R. H. W., and Srivastava, D. S. (2019) Drought alters the trophic role of an opportunistic generalist in an aquatic ecosystem. *Oecologia* 189: 733-744

4.1 CHAPTER SUMMARY

Abiotic change can alter species interactions by modifying species' trophic roles, but this has not been well studied. Until now, bromeliad-dwelling tipulid larvae were thought to positively affect other macroinvertebrates via a facilitative processing chain. However, under drought, we found the opposite. We performed two microcosm experiments in which we factorially manipulated water level and predation by tipulids, and measured the effects on mosquito and chironomid larvae. The experiments differed in whether high water was contrasted with low or no water, allowing us to distinguish between the effects of desiccation stress (no water) and increased encounter rates due to compression of habitat or reductions in prey mobility (low and no water). We also included a caged tipulid treatment to measure any non-consumptive effects. As well as directly reducing prey survival, reductions in water level indirectly decreased chironomid and mosquito survival by altering the trophic role of tipulids. Our results suggest that increased encounter rates with prey led to tipulids becoming predatory under simulated drought, as tipulids consumed prey under both low and no water. When water level was high, tipulids exerted negative non-consumptive effects on prey survival. Because opportunistic predators are common throughout aquatic ecosystems, the effects of drought on the trophic roles of species may be widespread. Such restructuring of food webs should be considered when attempting to predict the ecological effects of environmental change.

4.2 INTRODUCTION

Many ecosystems are characterized by fluctuating environments, and climate change threatens to affect ecosystem structure and functioning by altering patterns in environmental heterogeneity (Boyd et al. 2016; Vázquez et al. 2017). Abiotic environmental variation, such as seasonal fluctuations or spatial variation in temperature and precipitation, can structure food webs through direct physiological effects on species, as well as indirectly by altering species interactions (McMeans et al. 2015; Humphries et al. 2017). Species interactions can respond to environmental variation when abiotic conditions determine the co-occurrence or the functional responses of species (Humphries et al. 2017). The relative importance of trophic control, for instance, is often governed by environmental heterogeneity, as environmental conditions can affect consumer impacts within a food web (Power 1992). By affecting species interactions, global climate change has the potential to alter food web composition and ecological processes (McMeans et al. 2015). However, we still know little about how the effects of climate change on environmental heterogeneity alter biotic processes, particularly by affecting trophic interactions (Suttle et al. 2007; Tylianakis et al. 2008; Traill et al. 2010; Blois et al. 2013).

Environmental heterogeneity can influence trophic control when consumers exploit different trophic levels in different habitats (Tunney et al. 2012) or during different seasons (Carnicer et al. 2008). Variable environments can affect trophic interactions by altering the relative abundances (Ancona et al. 2012; Amundrud and Srivastava 2016) or the spatiotemporal overlap (Winder and Schindler 2004b; Wolkovich et al. 2012) of consumers and resources, as well as by altering the per capita interaction strengths of consumers (Kruse et al. 2008; O'Connor 2009; McCluney and Sabo 2009). For instance, flexible consumers like omnivores, who can feed

on multiple trophic levels (Pimm and Lawton 1978; Kratina et al. 2012) and shift their diets based on the availability or profitability of resources (Holt and Polis 1997), frequently shift their trophic role in accordance with changing environmental conditions (Gestoso et al. 2015; Törnroos et al. 2015; MacAvoy et al. 2016). Such diet shifts may occur if environmental variation affects consumer-resource encounter rates (e.g., Boukal 2014) or the metabolic needs of consumers (e.g., McCluney and Sabo 2009).

First, environmental heterogeneity can determine the trophic structure of an ecosystem if environmental conditions affect consumer-resource encounter rates (McMeans et al. 2015). For example, habitat compression in drying water bodies can lead to increased predator-prey encounter rates through increased prey densities (Dudgeon 1993; Magoulick and Kobza 2003; McHugh et al. 2015). Consumer-resource encounter rates can also be altered when environmental change alters predator foraging traits and/or prey vulnerability traits. Warming, for instance, can lead to altered predator-prey interactions through asymmetric effects on their respective body velocities (Dell et al. 2014). For example, increases in predatory damselfly activity levels due to warmer temperatures interact with changes in their body sizes to increase cannibalism and thus shift trophic interactions (Start et al. 2017). Prey vulnerability traits can also depend on environmental conditions. For instance, elevated CO₂ has been shown to decrease caterpillar body size and increase their vulnerability to predation (Coll and Hughes 2008). Abiotic conditions can also affect the ability of prey to detect predators (van Uitregt et al. 2013; Marino et al. 2017) or alter their propensity to flee from predators (de Barros et al. 2010).

Second, environmental heterogeneity can regulate the trophic role of consumers when new metabolic demands necessitate a shift in diet (Rall et al. 2010; Vucic-Pestic et al. 2011; McCluney 2017). For example, in a controlled laboratory experiment, warming resulted in a shift

in dietary preference of grasshoppers from mainly carbohydrates to increased protein (Schmitz et al. 2016). Similarly, predatory spiders consume crickets when stressed by desiccation, but not when water is available (McCluney and Sabo 2009). Although temperature has been shown to alter the functional and/or trophic roles of consumers (Petchey et al. 2010; Rall et al. 2010; Sentis et al. 2014; Lemoine 2017), far less studies have considered the possibility of altered precipitation regimes affecting trophic links in food webs through changes in physiological demands.

Here, we studied the effects of drought, an important stressor that is predicted to increase in both frequency and severity with climate change in some areas of the world (Prudhomme et al. 2014), on the trophic role of tipulid (Tipulidae: Diptera) larvae found in a Neotropical aquatic food web. Tank bromeliads (*Vriesea gladioliflora* H. Wendl, *Vriesea sanguinolenta* Cogn. and Marchal, and *Guzmania scherzeriana* Mez) are small detrital-based ecosystems that contain aquatic food webs consisting of macroinvertebrates and microorganisms (Srivastava and Bell 2009). In this ecosystem, drought is an important stressor that determines both species occurrences (Amundrud and Srivastava 2015) and species interactions (Amundrud and Srivastava 2016; Pires et al. 2016; Marino et al. 2017). Until now, bromeliad-dwelling tipulid larvae were considered facultative detritivores (Merritt and Cummins 1995) and thought to facilitate other bromeliad macroinvertebrates through conditioning litter (Starzomski et al. 2010). However, occasional opportunistic predatory behaviour under drought conditions has been observed (Srivastava, Amundrud pers. obs.; Amundrud & Srivastava, 2016), leading us to hypothesize that drought may alter the trophic role of bromeliad tipulids.

We performed two microcosm experiments in which we examined individual and combined effects of tipulid predation and water level on two dominant groups of bromeliad

insects, the larvae of mosquitoes and chironomids. Experiment 1 contrasted tipulid predation in ambient water level conditions and in the complete absence of water. Experiment 2 contrasted tipulid predation in ambient water level conditions and at reduced water levels. If tipulids become predatory because reductions in the water level increase encounter rates with prey (for instance by concentrating prey in space or reducing prey mobility), we hypothesize that the absence of water (Experiment 1) and a low water level (Experiment 2) should both lead to predation by tipulids. However, if tipulids become predatory because desiccation stress alters their metabolic needs, we hypothesize that only the complete absence of water (Experiment 1) should lead to predation by tipulids, as the low water level in Experiment 2 was designed to avoid any desiccation stress. In addition, we considered whether effects of tipulids on the insect community were purely consumptive, or also non-consumptive, by contrasting the effect of caged, uncaged, and no tipulids (Experiment 1).

4.3 METHODS

4.3.1 Study Site and System

To test for any interactive effects of tipulid predation and water level, we performed two microcosm experiments in which we factorially manipulated drought and tipulid predation, and measured the effects on artificially assembled communities consisting of mosquito and chironomid larvae. Experiment 1 was carried out in the fall of 2015 in a laboratory in Monteverde (10°18'N 84°48'W), Costa Rica. Experiment 2 was carried out in the fall of 2016 on

a shaded outdoor veranda at the nearby University of Georgia Costa Rica (UGA-CR) campus (10°16'N 84°47'W). In this part of Costa Rica, climate change is predicted to significantly reduce cloud cover and rainfall by up to 30% (Karmalkar et al. 2008), thereby increasing the frequency and severity of drought. The macroinvertebrate food web contained in tank bromeliads consists predominantly of the aquatic larvae of dipterans such as detritivorous crane flies (*Trentepohlia* spp., in Tipulidae) and chironomids (e.g., *Polypedilum* spp. and Orthoclaadiinae), and filter-feeding mosquitoes (e.g., *Anopheles* spp., *Culex* spp., and *Wyeomyia* spp.), as well as detritivorous aquatic beetle larvae (*Scirtes* spp., Starzomski et al. 2010).

4.3.2 *Experimental manipulation of tipulid predation and water level*

Microcosms, which mimic a typical bromeliad leaf well (Amundrud and Srivastava 2015, 2016), were necessary to precisely manipulate drought and community composition. Microcosms consisted of 50 mL centrifuge tubes rendered semi-permeable by cutting off the tapered bottoms and part of the side and covering these openings with 80 µm mesh. The tubes were placed mesh-bottom down in plastic cups so that, by altering the water level in the cups, we could manipulate the water level in the tubes without disturbing the contained communities. To each microcosm tube, we added oven-dried detritus that had been rehydrated for 24 hours in the form of a single leaf of *Conostegia xalapensis* Bonpl. (Melastomataceae) and particulate organic matter (80–850 µm diameter) obtained from bromeliads. To re-establish microbial communities on detritus that may have been lost through drying, we also added 2 mL of filtered (through 80 µm mesh) water obtained from natural bromeliads as a microbial inoculant. We monitored insect emergences with emergence traps attached to the tops of each microcosm.

4.3.2.1 Experiment 1: Effects of tipulids in the presence and absence of water

We factorially manipulated water (2 levels: presence and absence of water) and tipulids (3 levels: no tipulid, caged tipulid, and uncaged tipulid). Bromeliad insects in Costa Rica are able to survive in the complete absence of water for at least 18 days (Amundrud and Srivastava 2015), and species interactions in this system have been shown to be affected by drought lengths of up to 22 days (Amundrud and Srivastava 2016). As any negative effects of tipulids on the prey community could result from either consumptive or non-consumptive effects, we controlled for any non-consumptive effects (such as inducing a fear response in potential prey or by affecting water quality and microbial densities) by also including a caged tipulid treatment.

We acquired tipulid larvae, as well as the most common species of chironomid and mosquito larvae, from bromeliads at sites up to 10 km from the village of Santa Elena at Monteverde. We assembled 54 prey communities (n = 10 of each tipulid level for the water present treatment; n = 8 of each tipulid level for the water absent treatment) in separate microcosms. Each prey community consisted of 10 mosquitoes [5 *Wyeomyia* (subgenus *Hystatomyia*) sp. and 5 *Culex* (subgenus *Micraedes*, either *Culex jenningsi* or *Culex erethyzofer*)] and 10 chironomids (5 *Polypedilum* spp., and 5 *Orthocladinae* spp.). We initiated the experiment on 21-Nov-2015 (water present treatment) and 2-Dec-2015 (water absent treatment). Because we were not able to find the same species of *Culex* for the second set-up, the identity of the *Culex* species was confounded with water treatment (all water present treatments received *C. jenningsi*, all water absent treatments received *C. erethyzofer*). However, we show below that any effects of water treatment in our experiment are not driven by the confounding of *Culex* species identity with water treatment (see Results).

We randomly assigned each community to one of three tipulid treatments (no tipulid; caged tipulid; and uncaged tipulid). We constructed tipulid cages using mesh bags (dimensions: 3 cm x 1 cm; mesh size: 150 μ m), and caged tipulids received half of the leaf inside their cage as a food source, which sustained them to the end of the experiment (i.e., no leaf was completely consumed). Communities that were assigned to the no-tipulid or uncaged tipulid treatments received an empty mesh bag (containing neither a tipulid nor a leaf) to control for any cage effects.

To quantify any treatment effects on tipulid growth rate and control for differences in tipulid sizes between treatments, we measured body lengths of tipulids before and after the experiment. We used ImageJ (Schneider et al. 2012) to measure body lengths from digital photographs taken through a dissecting microscope. Again, we were careful to choose tipulids that were as similar as possible in their initial size for our experiment, and then confirmed that tipulid sizes were randomly distributed among treatments (Tipulid treatment: $F_{1,21} = 0.47$, $P = 0.50$; Water treatment: $F_{1,21} = 1.32$, $P = 0.26$; interaction: $F_{1,21} = 0.03$, $P = 0.86$).

We filled microcosm cups with filtered stream water to reach a level of 15 mL (i.e., a water depth of roughly 2.1 cm) inside the microcosm tubes to represent typical water levels in a bromeliad leaf well (Amundrud and Srivastava 2015, 2016), and placed microcosms indoors to ensure that the temperature was constant between the two experimental runs. After 24 hours of insect acclimation to the microcosms, we removed all water from microcosms assigned to the water absent treatment. This drying rate is identical to that used in similar experiments studying the effects of drought on bromeliad communities (Amundrud and Srivastava 2015, 2016), and field observations show that Costa Rican bromeliads can lose as much as 1-3 cm of water depth a day (Diane Srivastava, unpublished data). The aim of the water absent treatment in our

experiment was to test for sublethal effects of drought on species interactions. Thus, we chose a drought length of nine days, a length that has previously been shown to not significantly affect bromeliad insect survival in environments with high humidity (Amundrud and Srivastava 2015, 2016), while still allowing enough time for communities to respond to the treatments. During the experiment, we changed 50% of the water in microcosms subjected to the water present treatment every three days to mimic the natural flushing of bromeliads by rain. We checked and recorded emergences daily.

Nine days after initiation we added water to the microcosm cups subjected to the water absent treatment until 15 mL inside the microcosm tubes were reached. Twenty-four hours later, we emptied microcosm contents in random order and searched for surviving larvae and pupae. Before analysis, we excluded the few replicates where tipulids died or escaped, resulting in final sample sizes of five to eight microcosms for each treatment.

4.3.2.2 Experiment 2: Tipulid predation in high vs. low water

In this experiment we shift our focus from the effects of water presence vs. absence to a partial reduction in water level, in order to isolate the effects of habitat compression (imposed by both the absence of water and low water level) from those of desiccation stress (imposed only by the absence of water). We factorially manipulated water level (2 levels: high and low) and tipulid state (2 levels: alive or dead). Note that the high water level treatment is identical to the water present treatment in Experiment 1. We had initially planned a stressed tipulid treatment, but all tipulids died as a result of the pre-experimental drought stress, likely because of faster drying rates at the warmer and dryer lower elevation site of Experiment 2. We have kept the dead tipulid

treatment in the experiment as it unexpectedly provided a predation-free control. Although dead tipulids could have influenced prey through decomposition products, we will show in the results that this did not happen over the timescale of the experiment. Again, we acquired tipulid, chironomid, and mosquito larvae from bromeliads at sites up to 5 km from Monteverde, and assembled prey communities consisting of 4 chironomids (2 *Polypedilum* spp., and 2 *Orthocladiinae* spp.) and 4 mosquitoes [2 *Wyeomyia* (subgenus *Hystatomyia*) sp. and 2 *Culex jenningsi*].

Because of the difficulty of acquiring enough insect larvae at the same time, we divided the experiment into 3 temporal blocks which were initiated on 20-Oct-2016 (9 microcosms), 2-Nov-2016 (26 microcosms), and 17-Nov-2016 (18 microcosms). We placed microcosms outdoors under cover to provide shade and prevent natural inputs of precipitation. After assembling communities in microcosms, we reduced the water in the low water level treatments to 3 mL (i.e., 20% of the high water level) inside the microcosm tubes by removing water from the cups. 24 hours after set-up, we searched for surviving larvae. We then returned the microcosm contents to the tubes, and repeated this procedure for up to five days. Before analysis, we excluded the few “live tipulid” replicates in which tipulids subsequently died, disappeared or escaped, resulting in final sample sizes from 12 to 16.

4.3.3 Statistical analysis

4.3.3.1 Experiment 1: Effects of tipulids in the presence and absence of water

We quantified the effects of water, tipulids, and their interaction on total remaining prey abundance (i.e., the surviving larvae, pupae, and emerged adults of mosquitoes and chironomids together), as well as separated by taxonomic family (i.e., the surviving larvae, pupae, and emerged adults of mosquitoes and chironomids separately), using linear models. To disentangle the effects of predation from any non-consumptive effects of tipulids, we employed t-tests to explore non-consumptive (no vs. caged tipulid) and consumptive (caged vs. free tipulid) effects on prey as *post hoc* analyses when tipulid treatment, or its interaction with water treatment, was significant. Because the identity of the *Culex* species (*Culex jenningsi* vs. *Culex erethyzonfer*) was confounded with water treatment, we repeated the above analysis on the data from which all *Culex* spp. were removed from the total prey count. Although this second analysis does not rule out the possibility that *Culex* spp. had differential effects on other species, it enabled us to show that any effects of water treatment were not driven by the confounding of *Culex* species identity and water level. We used a linear model to determine the individual and interactive effects of water treatment and cage treatment on tipulid growth rates (as relative changes in body length for surviving tipulids).

For all models, our data met model assumptions (as determined by Quantile-Quantile, residual and outlier plots) without requiring transformation of the response or predictor variables. We carried out all analyses in the programming language R (version 3.2.1: R Core Team, 2015). The data to Experiment 1 are available on KNB Digital Repository (Amundrud et al. 2019).

4.3.3.2 Experiment 2: Tipulid predation in high vs. low water

We quantified the effects of water level, tipulids, and their interaction on total prey survival, as well as on chironomid and mosquito survival separately, by employing a mixed effects Cox proportional hazards survival analysis using the R package *coxme* (Terry M. Therneau 2015). Fixed effects were tipulid treatment, water level, and their interaction. Random effects were microcosm effects nested within temporal block. We obtained *P*-values by employing an analysis of deviance on the Cox models. The data met model assumptions of proportional hazards, as determined by visual inspection and tests based on the Schoenfeld residuals (Schoenfeld 1980). The data to Experiment 2 are available on KNB Digital Repository (Amundrud et al. 2019).

4.4 RESULTS

4.4.1 Experiment 1: Effects of tipulids in the presence and absence of water

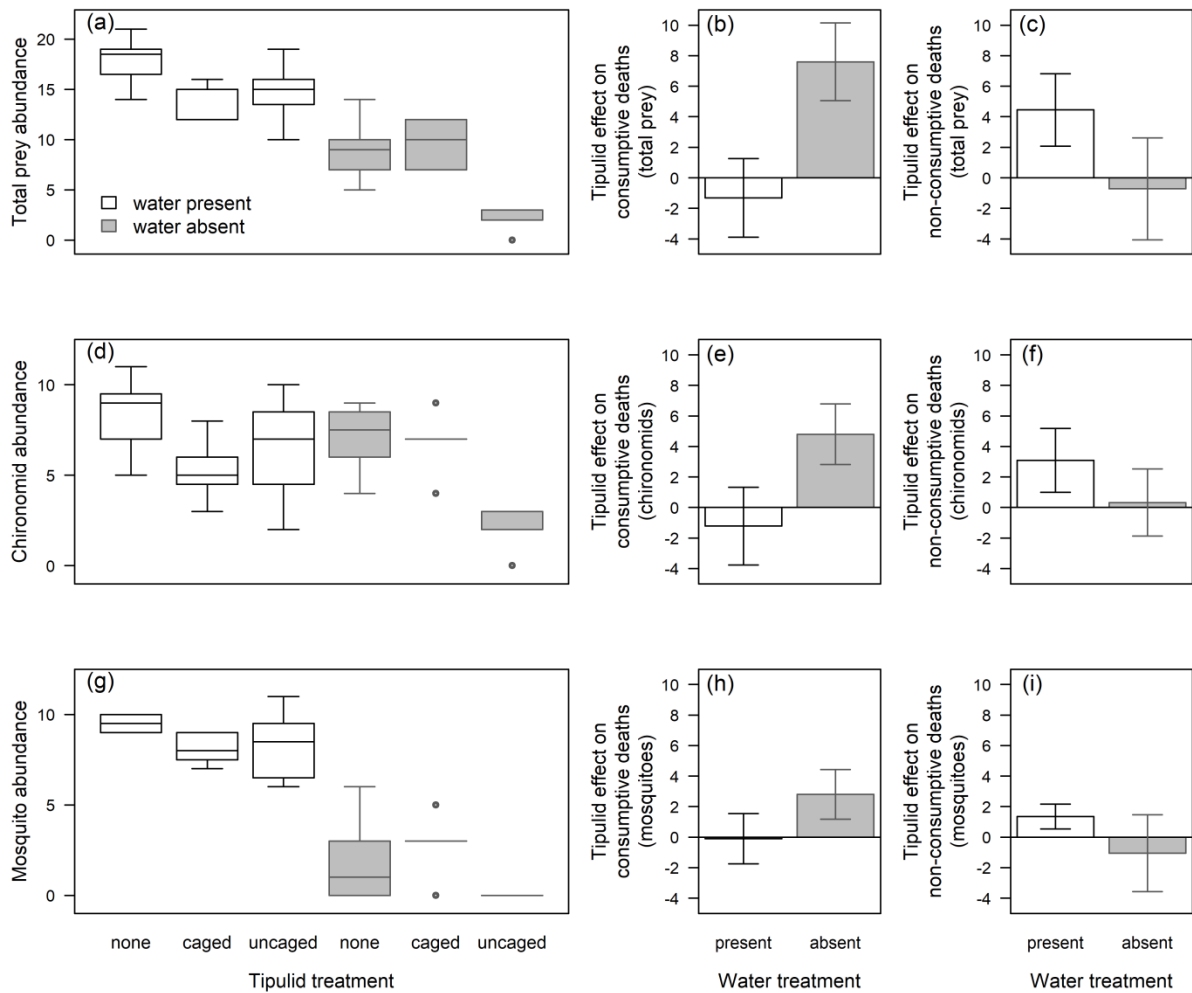
The effects of tipulids on total prey survival depended on water treatment (Table 4.1a, Figure 4.1a). As predicted, there was no prey consumption by tipulids when water was present, but tipulids consumed prey when water was absent, as uncaged tipulids decreased prey abundance by 79 % compared to caged tipulids (Table 4.1b, Figure 4.1b). In contrast, non-consumptive effects of tipulids were only important in the presence of water, where caged tipulids decreased prey abundance by 25 % relative to treatments with no tipulids (Table 4.1b, Figure 4.1c).

Table 4. 1: Effects of tipulids and water on mosquitoes and chironomids in Experiment 1. (a) Effect tests based on 2-way ANOVA, as summarized by F ratios and *P*-values. “Tipulid” represents three levels of tipulid treatments (no tipulid, caged tipulid, and uncaged tipulid), “Water” represents two water treatments (present and absent), and “Tipulid x Water” represents their interaction. Significant *P*-values after sequential Bonferroni corrections ($\alpha_1 = 0.05$, $\alpha_2 = 0.025$, and $\alpha_3 = 0.017$, α ’s are sequentially compared from largest to smallest *P* -value in each column) are indicated in bold. (b) Partitioning of tipulid effects into consumptive and non-consumptive effects. “Consumptive” effects compare caged vs. uncaged tipulid treatments for “Water present” and “Water absent” treatments, respectively. “Non-consumptive” effects compare no vs. caged tipulid treatments for “Water present” and “Water absent” treatments, respectively. Significant *P*-values after sequential Bonferroni corrections ($\alpha_1 = 0.025$, $\alpha_2 = 0.013$, and $\alpha_3 = 0.008$; α ’s are sequentially compared from largest to smallest *P* -value in each column) are indicated in bold. Because of non-orthogonality, α ’s are halved.

(a) 2-way ANOVA	Tipulid		Water		Tipulid x Water	
Response	$F_{2,36}$	<i>P</i>	$F_{1,36}$	<i>P</i>	$F_{2,36}$	<i>P</i>
Total prey abundance	12	< 0.001	151	< 0.001	12	< 0.001
Chironomid abundance	10	< 0.001	6.6	0.014	7.7	0.002
Mosquito abundance	2.6	0.092	261	< 0.001	3.6	0.037

(b) Tipulid effects	Consumptive				Non-consumptive			
	Water present		Water absent		Water present		Water absent	
Response	t_{13}	<i>P</i>	t_9	<i>P</i>	t_{13}	<i>P</i>	t_{11}	<i>P</i>
Total prey abundance	-1.1	0.289	6.7	< 0.001	4.0	0.001	-0.47	0.64
Chironomid abundance	-1.0	0.322	5.5	< 0.001	3.2	0.007	0.33	0.75
Mosquito abundance	-0.14	0.891	3.9	0.004	3.6	0.003	-0.92	0.38

Figure 4. 1: **Left Panel:** Effects of water and tipulids on (a) total prey abundance (chironomids and mosquitoes combined), (d) chironomid abundance, and (g) mosquito abundance in Experiment 1. **Middle Panel:** Impact of tipulid predation in the presence and absence of water. (b) Number of total prey consumed (chironomids and mosquitoes combined), (e) number of chironomids consumed, and (h) number of mosquitoes consumed. Number of consumptive deaths is calculated as the difference of prey abundance in communities with caged vs. uncaged tipulids. Error bars represent 95% confidence intervals. **Right Panel:** Impact of non-consumptive effects of tipulids in the presence and absence of water. (c) Number of total prey deaths (chironomids and mosquitoes combined), (f) number of chironomid deaths, and (i) number of mosquito deaths. Number of non-consumptive deaths is calculated as the difference of prey abundance in communities with no vs. caged tipulids. Error bars represent 95% confidence intervals. Chironomids are *Polypedilum* spp. and *Orthocladiinae* spp., mosquitoes are *Wyeomyia* spp. and *Culex* spp.



To further understand the responses of prey, we examined chironomid and mosquito survival separately (prey emergence rates during the experiment were low, averaging less than 4 % per microcosm). For both taxa, the effects of tipulids on the total number of surviving prey again depended on water treatment (Table 4.1a). Consistent with the results for total prey, consumptive effects of tipulids significantly decreased the survival of both chironomids and mosquitoes (by 71 % and 100 %, respectively) when water was absent, while consumption by tipulids was not important when water was present (Table 4.1b, Figure 4.1e,h). Non-consumptive effects, on the other hand, arose only in the presence of water, where they decreased chironomid and mosquito abundance by 37 % and 14 %, respectively (Table 4.1b, Figure 4.1f,i). While the removal of water by itself had a weak direct effect on chironomids, whose abundances decreased by only 20 % (Figure 4.1d), it decreased mosquito abundance by 83% (Figure 4.1g).

When we repeated the analyses on the subset of the data excluding *Culex* spp., the results for total prey abundance were qualitatively similar, signifying that the above results were not driven by the confounding of *Culex* spp. identity with water level (Appendix C.1). Although tipulids were able to consume prey in the absence of water, this cage x water level interaction did not affect the growth rates of tipulids ($F_{1,17} = 0.09$, $P = 0.77$; Appendix C.2).

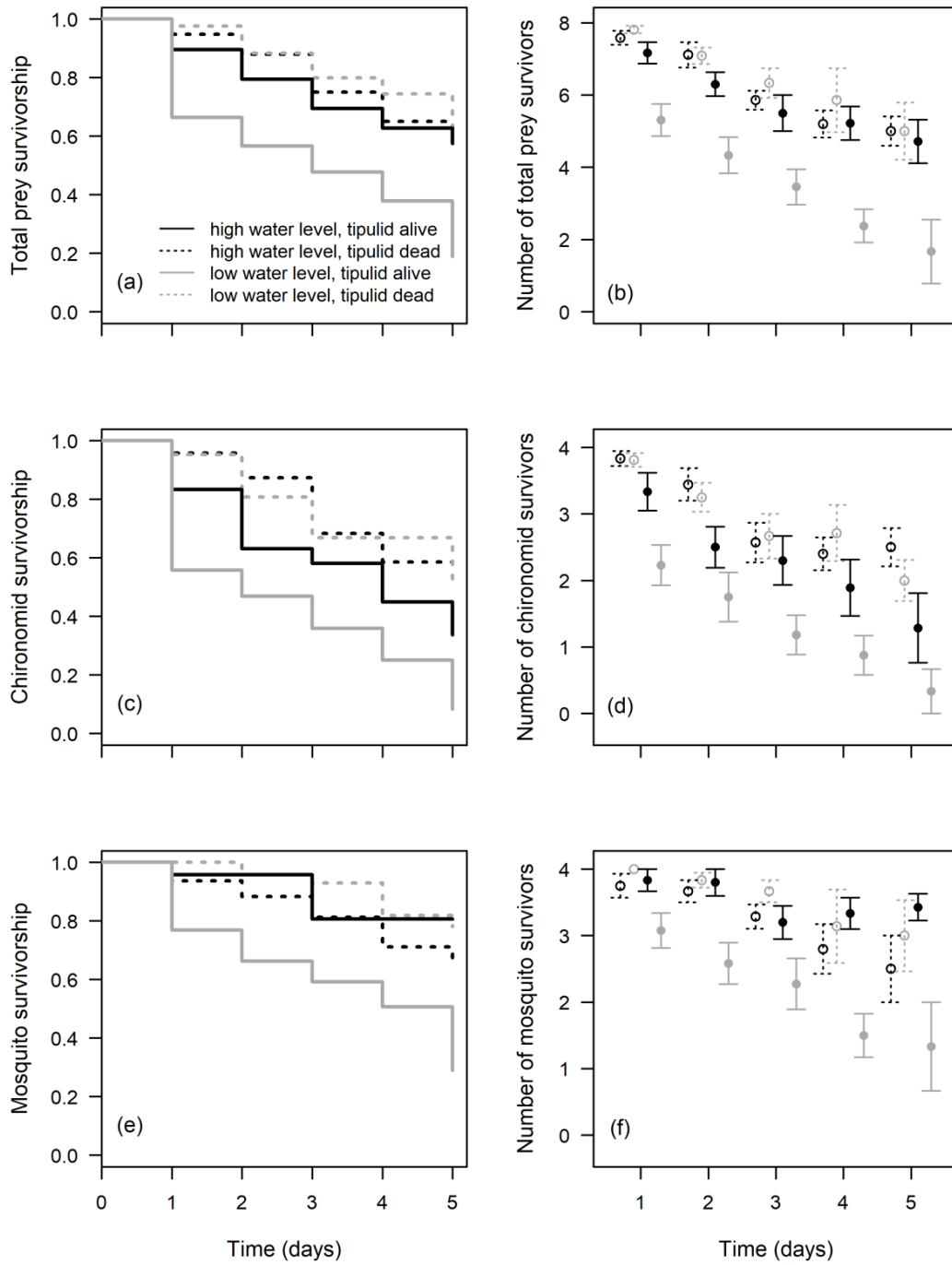
4.4.2 Experiment 2: Tipulid predation in high vs. low water

As expected, the effects of tipulids on total prey survival depended on water level (Table 4.2). When tipulids were alive, prey experienced high mortality (59 %) only at low water level, compared to a mortality of 30 % at high water level (Figure 4.2a). The latter is comparable to prey mortality when tipulids were dead (23 % for high and 21 % for low water level).

Table 4. 2: Effects of water level and tipulids on chironomid and mosquito survival in Experiment 2. “Tipulid” represents two levels of tipulid treatments (alive and dead), “Water Level” represents two levels of water level treatment (high and low), and “Tipulid x Water Level” represents their interaction. Significant *P* -values after sequential Bonferroni corrections ($\alpha_1 = 0.05$, $\alpha_2 = 0.025$, and $\alpha_3 = 0.017$; α 's are sequentially compared from largest to smallest *P* -value in each column) are indicated in bold.

Experiment 2 Response	Tipulid		Water Level		Tipulid x Water Level	
	X^2	<i>P</i>	X^2	<i>P</i>	X^2	<i>P</i>
Total prey survival	38	< 0.001	5.6	0.018	6.2	0.013
Chironomid survival	32	< 0.001	6.2	0.013	0.99	0.32
Mosquito survival	16	< 0.001	1.8	0.18	9.7	0.002

Figure 4. 2: Survivorship (left panel) and number of surviving larvae for each point in time (right panel) from Experiment 2. (a) and (b) show total prey (chironomids and mosquitoes combined), (c) and (d) show chironomids, and (e) and (f) show mosquitoes



To further understand prey responses, we then examined chironomid and mosquito survival separately. Interestingly, chironomid survival was not affected by the interaction of tipulid treatment with water level (Table 4.2). Instead, chironomid survival was significantly reduced independently by live tipulids (62 % mortality compared to 29 % mortality when tipulids were dead) and low water level (48 % mortality compared to 40 % mortality when water level was high; Figure 4.2b). For mosquito survival, on the other hand, negative effects of tipulid predation did depend on low water level (Table 4.2). When tipulids were alive, mosquitoes experienced a relatively high mortality (48 %) when the water level was low, compared to when water level was high (17 %; Figure 4.2c). The latter is comparable to mosquito mortality for treatments in which tipulids were dead (21 % for high and 11 % for low water level).

4.5 DISCUSSION

Altered environmental conditions can affect animal communities by altering species interactions. Here, we provide mechanistic insights into how drought stress affects a microecosystem through altering trophic links. In both experiments, simulated drought altered the trophic role of tipulids, who became opportunistic predators when the water column was reduced or removed. While tipulids had negative non-consumptive effects on prey at high water levels, consumptive effects of tipulids were restricted to treatments where water was absent or reduced.

There are several potential mechanisms that can explain how drought enabled tipulids to consume animal prey. First, drought could have caused mosquitoes and chironomids to become

vulnerable to predation by negatively affecting their locomotor performance or behavioural defence mechanisms. Tipulids employ crawling as the primary locomotive mode for foraging inside and outside the water, while swimming is non-directional and primarily used as evasive action (Pritchard 1985). The locomotive behaviour of chironomid larvae is similar. Chironomids primarily crawl along the substrate, although they can swim through the open water column in short non-directional bursts when disturbed and to escape predation (Brackenbury 2000). The locomotor behaviour of mosquitoes, on the other hand, is fundamentally different in that they can freely swim or glide through the water column (Christophers 1960; Brackenbury 2001). Tipulids stay mobile in the complete absence of water (Pritchard 1985; Experiment 1; Amundrud, personal observation), and although chironomids are still able to move along the substrate, they cannot escape predation from tipulids through rapidly swimming through the water column. For mosquitoes, which have no means of moving along a dry substrate, the absence of water can completely hamper their ability to escape, and indeed, no mosquito survived in treatments with both no water and uncaged tipulids (Experiment 1). In addition to affecting the ability of mosquito and chironomid prey to escape predation, drought could have also affected other behavioural defence mechanisms. *Polypedilum* chironomids build algal tubes as protection from predators (Macchiusi and Baker 1992; Baker and Ball 1995). By affecting the algal building material through drying, the absence of water could potentially prevent chironomids from building such tubes. Although adverse effects on locomotor ability and prey defence mechanisms from drought present reasonable explanations for predatory effects in the complete absence of water (Experiment 1), they do not fully explain why tipulids also became predatory when the water level was merely reduced (Experiment 2).

Second, drought could have enabled tipulids to consume animal prey by compressing the community in space, and thus increasing random encounters of tipulids with prey (Dudgeon 1993; Magoulick and Kobza 2003; McHugh et al. 2015). Inside bromeliad wells, tipulid larvae forage on a two-dimensional surface, whereas their mosquito and chironomid prey can occupy the water column. As a result, encounter rates and subsequent prey capture rates for high water levels are likely low, consistent with our finding that tipulids do not consume mosquitoes or chironomids when communities are subjected to high water levels. For organisms normally suspended in the water column, the complete absence of water (Experiment 1) effectively alters the habitat from a three-dimensional space (i.e., the water column) to a two-dimensional area (i.e., the substrate). While the reduction in water level (Experiment 2) would not change the dimensionality of the habitat, it would still result in habitat compression (Magoulick and Kobza 2003; McHugh et al. 2015). This compression of the community could effectively increase random encounter rates of tipulids with prey, potentially explaining the rise in prey consumption by this opportunistic consumer (McGill and Mittelbach 2006; Ledger et al. 2013a).

While the first two mechanisms are similar in that drought enables tipulids to consume animal prey by increasing predator-prey encounter rates, a third mechanism that could explain how tipulids became predatory under drought is that desiccation stress altered the physiological demands of tipulids, and thus their dietary protein requirements (Schmitz et al. 2016). As food selection by aquatic insect detritivores is often predominantly influenced by their nutritional requirements (Cargill et al. 1985), tipulids stressed by drought may have consumed insect prey in order to meet their altered dietary needs. We think this mechanism is unlikely, as tipulids became predatory both under the complete absence of water (Experiment 1) and under a reduction in water level (Experiment 2), but only the former should have imposed a desiccation stress. It is

important to note, however, that even a reduction in water level could have induced a stress response (for example due to increased density and cues of organisms), so we cannot fully reject this mechanism. One may also speculate that tipulids started consuming animal prey because desiccated detrital matter became unpalatable to tipulids in the absence of water, forcing them to eat other larvae. We reject this possibility as a mechanism, as tipulids consumed animal prey in both the absence of water (Experiment 1), as well as the low water level treatment (Experiment 2), but detritus could only dry in the former treatment.

Non-consumptive effects of tipulids on prey survival were also important, but only in the presence of water (Experiment 1). If predator cues are transmitted through the water column, predation risk may have resulted in reductions in the prey's foraging effort and energy income (Preisser et al. 2005), resulting in reduced prey survival. Alternatively, the observed decreases in prey survival may be a result of adverse effects of tipulids on water quality through enhancing microbial densities. Indeed, visual examination of water color showed that water quickly became cloudy when tipulids were present (live or dead), but not when they were absent (Experiment 1: no tipulid treatment). Increased turbidity with tipulid presence has also been observed in similar experiments conducted at another site in northwestern Costa Rica (e.g., Amundrud and Srivastava 2016).

Over the short duration of these experiments, we were not able to establish that there was a fitness advantage for bromeliad tipulids when they consumed animal prey, as tipulids maintained equivalent growth rates across all treatments. Bromeliad-dwelling tipulids have previously not been considered to be predatory (but see Amundrud and Srivastava 2016), although there is evidence that tipulids in other systems are predatory (e.g., streams: Martin *et al.*, 1980; Woodward & Hildrew, 2001; Panamanian tree holes: Yanoviak, 1999). On the

contrary, bromeliad-dwelling tipulids were thought to mainly have positive effects on other bromeliad macroinvertebrates via facilitation by a processing chain, as tipulid shredders have been shown to increase chironomid growth and survival by conditioning litter (Starzomski et al. 2010). The lack of studies documenting negative effects of bromeliad tipulids on other insects likely results from the fact that this species does not consume other animals when communities are submersed in water, that is, the condition under which these systems have been primarily studied.

Fresh waters are particularly vulnerable to climate change, and in several areas of the world the prevalence or duration of drought events in seasonal freshwater ecosystems is likely to increase (Prudhomme et al. 2014). Our study supports the growing amount of evidence that drought events will have major consequences to the structure and functioning of freshwater ecosystems (e.g., Chase and Knight 2003; Ledger et al. 2012, 2013b, a; Amundrud and Srivastava 2016). Drought has been shown to alter the trophic structure in various aquatic ecosystems (e.g., ponds: Chase and Knight 2003; streams: Ledger et al. 2013b; bromeliads: Amundrud and Srivastava 2016); however, in many of these studies drought generally led to a weakening of top-down control by disproportionately affecting species at the top of the food chain (e.g., Chase and Knight 2003; Ledger et al. 2011, 2013b; Amundrud and Srivastava 2016). Our study reveals that drought can also alter the trophic structure of a food web by increasing top-down control when a consumer has access to prey that were inaccessible under no-drought conditions. In a system where precipitation is expected to decrease (Karmalkar et al. 2008) and drought is expected to increase (Zotz and Thomas 1999), this has important implications for community structure and ecosystem functioning. The negative indirect effects of drought on mosquitoes and chironomids through increased top-down control will act in synergy to any direct

physiological effects of drought on these species. We thus expect a shift in species composition away from species vulnerable to drought and predation (mosquitoes and chironomids) and towards tipulids that are relatively resistant to drought, as well as a reduction in secondary production. The effects of drought on the detrital processing chain are harder to predict. Although mosquitoes and chironomids are suppressed by direct and indirect effects of drought, they are weak detrital processors compared to tipulids, which are relatively resistant to drought.

This microcosm study has several limitations. Importantly, long-term effects of drought cannot be predicted from our short-term study. Indeed, the intensification of trophic interactions resulting from drought may be short term (Ledger et al. 2013a). For longer droughts, physiological stress on species may outweigh the effect of habitat compression on biotic interactions, and we may expect a decline in mosquitoes and chironomids, as well as tipulids. Furthermore, here we just examine the larval stage of these insects, but changes in climatic variables can also affect adult stages and extrapolation of our results to population-level consequences would require modelling of all the life stages. Apart from studying the long-term effects of drought on bromeliad insect larvae and other life stages, we suggest that future work should focus on manipulating the water column height to study the effects of habitat compression on bromeliad insect communities in more detail.

In conclusion, abiotic change can alter the functional roles of species (e.g., Gormezano and Rockwell 2013; Grémillet et al. 2015), sometimes leading to trophic niche shifts (e.g., McCluney and Sabo 2009; Schmitz et al. 2016; Start et al. 2017). Species that may be particularly likely to mediate indirect effects of climate change by altering their functional role are those with flexible feeding modes or foraging behaviours, such as generalists and omnivores. As such species are ubiquitous across ecosystems (Hawlena et al. 2011; Kratina et al. 2012), this

may be a commonly overlooked mechanism by which climate change indirectly affects food webs. Given that a shift in a species' functional or trophic role will restructure food webs, we need to incorporate potential shifts in how species function under altered environmental conditions in models predicting the ecological effects of climate change.

5 DISENTANGLING HOW CLIMATE CHANGE CAN AFFECT
AN AQUATIC FOOD WEB BY COMBINING MULTIPLE
EXPERIMENTAL APPROACHES⁴

⁴ Previously published as Amundrud, S. L., and Srivastava, D. S. (2019) Disentangling how climate change can affect an aquatic food web by combining multiple experimental approaches. *Global Change Biology* 25: 3528-3538

5.1 CHAPTER SUMMARY

Predicting the biological effects of climate change presents major challenges due to the interplay of potential biotic and abiotic mechanisms. Climate change can create unexpected outcomes by altering species interactions, and uncertainty over the ability of species to develop *in situ* tolerance or track environmental change further hampers meaningful predictions. As multiple climatic variables shift in concert, their potential interactions further complicate ecosystem responses. Despite awareness of these complexities, we still lack controlled experiments that manipulate multiple climatic stressors, species interactions, and prior exposure of species to future climatic conditions. Particularly studies that address how changes in water availability interact with other climatic stressors to affect aquatic ecosystems are still rare. Using aquatic insect communities of Neotropical tank bromeliads, we combined controlled manipulations of drought length and species interactions with a space-for-time transplant (lower elevations represent future climate) and a common garden approach. Manipulating drought length and experiment elevation revealed that adverse effects of drought were amplified at the warmer location, highlighting the potential of climatic stressors to synergistically affect communities. Manipulating the presence of omnivorous tipulid larvae showed that negative interactions from tipulids, presumably from predation, arose under drought, and were stronger at the warmer location, stressing the importance of species interactions in mediating community responses to climate change. The common garden treatments revealed that prior community exposure to potential future climatic conditions did not affect the outcome. In this powerful experiment, we demonstrated how complexities arise from the interplay of biotic and abiotic mechanisms of climate change. We stress that single species can steer ecological outcomes, and

suggest that focusing on such disproportionately influential species may improve attempts at making meaningful predictions of climate change impacts on food webs.

5.2 INTRODUCTION

Climate change will alter communities and ecosystems by affecting both ecological and evolutionary processes (Parmesan 2006), but predicting the biological effects of climate change still presents a major challenge. Most studies have concentrated on the effects of a single climatic variable on one species, ignoring the complexities that arise from the interplay of biotic and abiotic components of climate change. However, climate change affects species not only directly through altering their physiology, behaviour, or life history, but also indirectly by modifying species interactions (Tylianakis et al. 2008; Blois et al. 2013). Such indirect effects of climate change in particular often lead to unexpected or counterintuitive outcomes (Suttle et al. 2007; Ockendon et al. 2014). For instance, altered species interactions resulting from sustained manipulations of precipitation regimes in grassland ecosystems reverse species responses and community trajectories by overriding physiological responses of species to water availability (Suttle et al. 2007). In addition, uncertainty over the ability of species to track environmental change (Tingley et al. 2009) or develop in situ tolerance (Gienapp et al. 2008) makes meaningful predictions ever more difficult. Given the many complexities that arise from climate change, we need controlled experiments that manipulate multiple climatic stressors, species interactions, and prior exposure of species to future climatic conditions.

Environmental conditions play major roles in shaping species interactions (Finstad et al. 2011; Hein et al. 2013), and indirect effects of climate change can arise when altered climatic conditions alter species interactions. Asymmetric responses of trophic levels to climate change, for instance, result in trophic mismatches that can disrupt ecosystem functioning by altering top-down or bottom-up processes (Winder and Schindler 2004a; Parain et al. 2016). Alternatively, interaction strengths of predators can be modified by climate change if abiotic conditions alter their functional responses (Hassell 1978; Ewald et al. 2013). Identifying and focusing research efforts on species that are particularly likely to mediate indirect effects of climate change, that is, those that both respond strongly to climate change and have large community level effects, may improve our ability to predict the indirect effects of climate change. Predators in particular have been identified as “biotic multipliers” of climate change (Urban et al. 2017), as they are both responsive to changing climatic conditions and disproportionately affect communities (Amundrud and Srivastava 2016; Urban et al. 2017).

Two important aspects of climate change are warming and altered precipitation regimes (IPCC 2014), and both can alter predator-prey interactions. Temperature can affect the functional response of predators, such as by altering their metabolic rates (Rall et al. 2010; Vucic-Pestic et al. 2011), and warming has been shown to alter predation rates in both aquatic (e.g., damselflies: Thompson 1978; fish: Meerhoff et al. 2007) and terrestrial (e.g., spiders: Barton and Schmitz 2009; beetles: Vucic-Pestic et al. 2011) systems. Interestingly, experimental warming has led to both increases and decreases in consumer-resource interactions (Marino et al. 2018). Altered rainfall patterns and increased evaporation rates shorten hydroperiods in aquatic systems (Schindler 2001; Moss 2012), and resulting increases in drought lengths and/or frequencies can affect predator-prey interactions by imposing metabolic and biomechanical constraints on

species (Woodward et al. 2016), particularly if different trophic levels are affected asymmetrically (Chase and Knight 2003; Ledger et al. 2013b; Amundrud and Srivastava 2016). As warming and altered precipitation regimes often occur in concert, any interactive effects on communities will further complicate ecosystem responses to climate change.

The ecological effects of climate change can further depend on whether species remain vulnerable to altered climatic conditions, or whether they adapt (Skelly et al. 2007), acclimatize (Gienapp et al. 2008), or track (Tingley et al. 2009) the changing climate. Climate change can drive rapid evolution (Harmon et al. 2009a), and phenotypic plasticity can also contribute to phenotypic changes (Gienapp et al. 2008). In addition, species can keep pace with changing climatic conditions by physically tracking their optimal climate (Tingley et al. 2009), such as via range shifts towards higher latitudes (Pinsky et al. 2013) or elevations (Hill et al. 2002). Whether or not species remain naïve to new environmental conditions will likely affect the outcome of climate change, but few studies have incorporated historical exposure to climate into experiments that also manipulate multiple climatic variables and species interactions. What is more, it is improbable that all species in a community respond to climate change in the same way, and asymmetric responses among community members may result in the disruption of food webs (Winder and Schindler 2004a). Any asymmetries in whether or not species remain naïve to new environmental conditions will undoubtedly add further complexities to the effects of climate change.

Studying communities along environmental gradients can aid predictions of how they will respond to climate change (Holzapfel et al. 2006; Ariza and Tielbörger 2011), assuming that existing climatic conditions in space mimic predicted climate change in time (Dunne et al. 2004). Altitudinal gradients provide suitable arenas for such space-for-time substitution studies, as

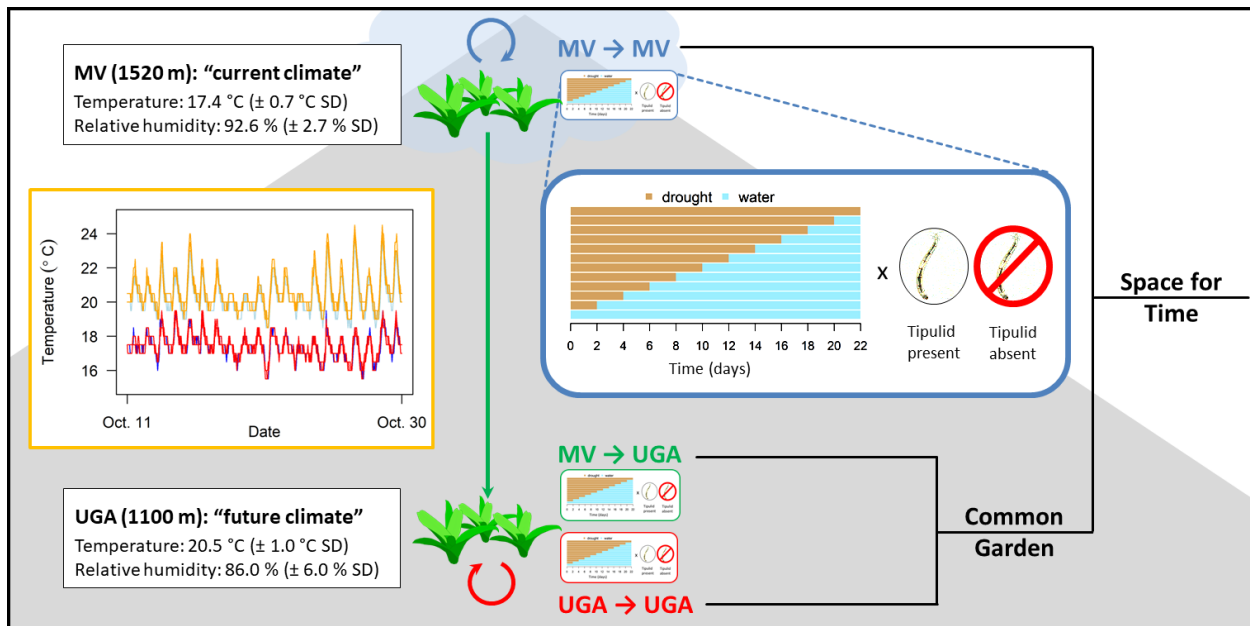
considerable climatic gradients occur over short distances. By minimizing the confounding effects of dispersal limitation, which can govern species distributions along latitudinal gradients (Qian and Ricklefs 2007; Amundrud et al. 2018), any turnover in community composition along altitudinal gradients can be attributed to changing abiotic conditions and biotic constraints (Carpenter 2005). However, simply observing community turnover along altitudinal gradients does not permit mechanistic insights, and simultaneous experimental manipulations of abiotic and biotic components are necessary to disentangle the various mechanisms by which climate affects composition and phenotype (Dunne et al. 2004; Liancourt et al. 2013). Community transplant experiments in combination with manipulations of species interactions (Ariza and Tielbörger 2011; Parain et al. 2016) and common garden experiments (De Block et al. 2013; Alexander et al. 2015) are required to unravel the effects of altered environmental conditions, species interactions, and the potential of species to adjust to the altered climate. However, we are not aware of any studies of animal communities that manipulated in a single experiment more than one climatic stressor, species interactions, and prior exposure of species to future climatic conditions. What is more, experimental manipulations of rainfall, an aspect of climate change that is still understudied, in ecosystems whose existence and dynamics depend almost entirely on precipitation, are still exceedingly rare.

Here, in one powerful experiment, we combined controlled manipulations of drought length and species interactions with a space-for-time transplant and a common garden approach (Figure 5.1). As a model system, we chose aquatic insect communities (consisting of the larvae of mosquitoes, chironomids and tipulids) found within Costa Rican phytohelm bromeliads, as it is logistically feasible to replicate, transplant, and experimentally manipulate these simple communities in microcosms (Amundrud and Srivastava 2015, 2016). Bromeliad food webs are

strongly shaped by predator-prey interactions (Srivastava 2006) and, like other small water bodies and temporary waters (Collinson et al. 1995; Wellborn et al. 1996), they are particularly vulnerable to climate change (Zotz and Thomas 1999). The high elevation laboratory at the Monteverde Cloud Forest Reserve (MV, elevation: 1520 m) represented the “current climate”, while the low elevation University of Georgia Costa Rica Campus (UGA, elevation: 1100 m) represented the “future climate” for our focal communities (Figure 5.1). The hotter, more variable conditions at UGA reflect future temperature predictions for MV under the A2 (doubled CO₂, 2071–2100) scenario (Karmalkar et al. 2008), while the lower humidity at UGA reflects warming in combination with expected declines in mist frequency due to a rise in the cloud base at MV (Pounds et al. 2006; Karmalkar et al. 2008). Our experiment had three different combinations of community origins and experimental locations (expressed in the form Origin→Location, including MV→MV, UGA→UGA, and MV→UGA; Figure 5.1). As such, the space-for-time transplant (MV→UGA) mimicked future climatic conditions, while transplanting high elevation species back into high elevation sites (MV→MV) controlled for current conditions. By accounting for any potential within-species variation arising under different climate histories, the common garden (i.e., communities originating from high [MV→UGA] vs. low [UGA→UGA] elevations) explored whether or not the outcome of simulated climate change depends on prior exposure of species to “future climatic conditions” (i.e., representing situations in which species acclimate to, adapt to, or track climate change). At MV, reductions in precipitation of up to 30 % are predicted under the A2 scenario (Karmalkar et al. 2008), and manipulating drought length allowed us to decouple the effects of resulting increased droughts from the effects of warming. Finally, manipulating the presence of tipulid larvae, which are disproportionately important consumers in terms of litter decomposition

(LeCraw 2014) and have recently been discovered to prey on other insects under drought conditions (Amundrud and Srivastava 2016; Amundrud et al. 2019), investigated the role of trophic interactions in mediating any community responses to simulated climate change.

Figure 5. 1: Experimental setup. 24 of the 48 bromeliad-dwelling detritivore communities collected at MV were placed at MV (MV→MV, blue arrow and box), and the other 24 communities were placed at UGA (MV→UGA, green arrow and box). The 24 communities collected at UGA were placed at UGA (UGA→UGA, red arrow and box). For each of these three Origin→Location treatments, we manipulated drought length (12 levels: 0 to 22 days) and tipulid presence (present and absent), resulting in 24 distinct treatment combinations (see magnified blue box for example). Comparing the communities at the two experimental locations thus represents a space-for-time design, while comparing the two communities at UGA with different origins represents a common garden design. Orange box: Temperature at the two locations inside microcosms subjected to drought and water obtained from iButtons. Dark blue: MV-water, red: MV-drought, light blue: UGA-water, orange: UGA-drought.



We demonstrate that climatic stressors can interact to affect communities, as the adverse effects of drought on the insect community were amplified at the warmer location. Moreover, we show that indirect effects of climate change mediated by species interactions can outweigh any direct effects, as adverse effect of tipulids on the community arose under drought and were stronger at the warmer location. Finally, we found no evidence that prior exposure of communities to “future climatic conditions” affects the outcome of simulated climate change. Importantly, we demonstrate that a single species can drastically affect how food webs respond to climate change, and support the proposition that predators can be important mediators of climate change (Urban et al. 2017).

5.3 METHODS

5.3.1 *Study Sites and System*

The Monteverde Cloud Forest Reserve entrance (MV: 10°18'N 84°47'W) and the University of Georgia (UGA: 10°16'N 84°47'W) Costa Rica Campus are located on the Pacific slope of the Tilaran mountain range, northwestern Costa Rica. The two sites are ~ 2.5 km apart and differ in altitude by ~ 420 m (Figure 5.1). Tank bromeliads (*Vriesea gladioliflora* H. Wendl, *Guzmania scherzeriana* Mez, and *Vriesea sanguinolenta* Cogn. and Marchal) in this area contain food webs consisting of macroinvertebrates and microorganisms that are largely sustained by detritus from the surrounding trees. The dominant macroinvertebrates in the system are the larvae of dipterans (Tipulidae: undescribed *Trentepohlia* spp., Chironomidae: especially

Polypedilum spp. and Orthoclaadiinae; and Culicidae: mainly *Culex* spp., *Wyeomyia* spp., and *Anopheles* spp.), as well as coleopteran Scirtidae (*Scirtes* spp.).

5.3.2 Manipulative Experiment

On Oct. 9, 2016, we assembled 48 insect communities collected at MV and 24 identical communities (except for the identity of the *Culex* spp., see below) collected at UGA in microcosms mimicking single bromeliad leaf wells, the scale at which individual insects spend most time foraging and interacting with each other. We constructed microcosms, which allowed us to precisely manipulate community structure and drought length, using semi-permeable 50 mL centrifuge tubes placed in plastic cups, identical to those used in Amundrud and Srivastava (2015, 2016) and Amundrud et al. (2019). Insect communities were contained in the tubes, which were permeable to water. By adding or removing water in the outer cup, we could manipulate the water level inside the microcosm tubes without disturbing the microcosm contents. To each microcosm, we added 3 mL microbial inoculant in the form of filtered (through 80 μm mesh) water obtained from bromeliads. We added detritus in the form of a pinch of oven-dried detrital particles (80–850 μm diameter) obtained from bromeliads, as well as leaf fragments ($\sim 1 \text{ cm}^2$) of *Conostegia xalapensis* Bonpl. (Melastomataceae; net dry mass of $54.7 \pm 1.2 \text{ mg}$; mean \pm SE), which, after drying to obtain initial mass, we rehydrated for three days prior to the experiment. We placed emergence traps on the microcosms, and filled microcosm cups with filtered stream water to a volume of 15 mL inside the tubes (i.e., a water depth of roughly 2.1 cm), which is within the typical range of volume for one bromeliad leaf well (Amundrud and Srivastava 2015). Using filtered stream water ensured that water quality, which varies widely among bromeliads

and even leaf wells within the same bromeliad, was standardized among microcosms. Filtered stream water has also commonly been used in other bromeliad food web studies (Srivastava 2006; Starzomski et al. 2010; Amundrud and Srivastava 2015, 2016; Amundrud et al. 2019) and to store live bromeliad insects for many weeks. We added prey communities in the form of 5 mosquito (3 *Wyeomyia pertinans* and 2 *Culex* spp.) and 6 chironomid (2 *Polypedium* spp. and 4 *Orthocladinae* spp.) larvae, and placed tipulid (*Trentepohlia* spp.) larvae to half of the microcosms (12 at UGA and 24 at MV). The identity of the *Culex* spp. differed between the two locations (*Culex erethyzonfer* at MV and *Culex jenningsi* at UGA), because neither species was abundant enough at both locations, suggesting a degree of prior habitat filtering (Appendix D.1). Although natural bromeliads contain species-rich communities (we recorded an average of 11.9 and 9.5 taxa inside bromeliads at UGA and MV, respectively), the average number of species at the scale of the leaf well is 3-7 (Trzcinski et al. 2016; LeCraw and Srivastava 2019; D. Srivastava, unpubl. data). The number of species per microcosm in our experiment is thus consistent with natural bromeliad systems, and communities in our study represent “typical” bromeliad communities (Appendix D.1).

We manipulated climate in a space-for-time design, by placing half of the communities collected at MV (n = 24) at MV (MV→MV), representing the current climate, and the other half (n = 24) at UGA (MV→UGA), representing the future climate (Figure 5.1). At each location, we added one tipulid larva to half of the microcosms (n = 12), and manipulated drought (12 drought lengths ranging from 0 to 22 days, at 2 day intervals; Figure 5.1). Our manipulation of drought was identical to methods employed in previous experiments studying effects of drought on bromeliad microcosm communities (Amundrud and Srivastava 2015, 2016; Amundrud et al. 2019), but to summarize: We initiated drought (i.e., absence of water) in all communities except

of those subjected to a drought length of zero days by pouring all water from the microcosm cups (field observations from Costa Rica show that bromeliads lose as much as 1-3 cm of water depth daily; Diane Srivastava, unpubl. data). Although this procedure removed the entire water column from the microcosm tubes, moisture was retained within the leaves and added fine detritus. Manipulating experimental location and drought length allowed us to test for any main and/or interactive effects of simulated future climate and drought on the community, as well as any indirect effects of these aspects of climate change mediated by predation by tipulids.

We employed a common garden approach to examine if the outcome of simulated climate change depended on whether or not communities are naïve to altered climatic conditions. To achieve this, we placed the 24 communities collected near UGA at the UGA location (UGA→UGA), subjecting them to the same experimental treatments (Figure 5.1). These communities represented communities already accustomed to a warmer, dryer climate, while the communities originating from MV (MV→UGA) represented communities naïve to future climatic conditions.

Microcosms were placed under a cover outside where temperature variation and evaporation levels were comparable to the adjacent forest, but without water input from precipitation. To monitor temperature within microcosms at the two experimental locations, we prepared six additional microcosms per location (3 with water and 3 without water) that did not include insect communities, but instead held iButtonsTM (DS1921G-F5# ThermoChron, 4K) that logged the temperature hourly (Figure 5.1). We obtained relative humidity values from weather stations at the sites from Aug. 25, 2010 to Feb. 7, 2011, the only timeframe that was available for MV.

Every two days, we ended the appropriate drought treatments by adding filtered stream water to the respective microcosms to a level of 15 mL inside the tubes. We also replaced 50 % of the water in no-drought microcosms to mimic the natural flushing of bromeliads by rain, and recorded any emergences. On Oct. 31, we emptied microcosms in random order to quantify surviving insects. We oven-dried the detritus and determined decomposition rates over the time of the experiment as the difference in dry mass before and after the experiment.

5.3.3 *Statistical Analyses*

We used logistic regression models with binomial errors to quantify the effects of community type (categorical, 3 levels: MV→MV, MV→UGA, and UGA→UGA), drought length (continuous, 12 levels: 0 to 22 days at 2 day intervals), and tipulid presence (categorical, 2 levels: present and absent), as well as their pairwise interaction (testing for a three-way interaction was not possible due to low statistical power), on prey survival (and chironomid and mosquito survival separately), and linear models to examine treatment effects on prey emergences and decomposition. We calculated prey survival as the fraction of surviving larvae and pupae but excluded the few insects that emerged (Amundrud and Srivastava 2016), as most emergences occurred during the drought treatment and so the intended drought length was not achieved.

To tease apart any effects of the Origin→Location treatment on our responses, we employed the same logistic regression models in combination with orthogonal contrasts in cases in which the Origin→Location treatment was significant. We defined orthogonal contrasts as (1)

MV→MV vs. MV→UGA and UGA→UGA (space-for-time contrast) and (2) MV→UGA vs. UGA→UGA (common garden contrast; Figure 5.1).

We examined model suitability by checking for overdispersion in binomial models, as well as by using quantile-quantile, residual, and outlier plots. We log-transformed drought length for prey survival, and squared drought length for decomposition as the relationship of these responses with drought length were non-linear and transformation improved model fit. Tipulid survival and prey emergences required no transformations of the explanatory variables. We performed all analyses using R statistical software (R Core Team 2017).

5.4 RESULTS

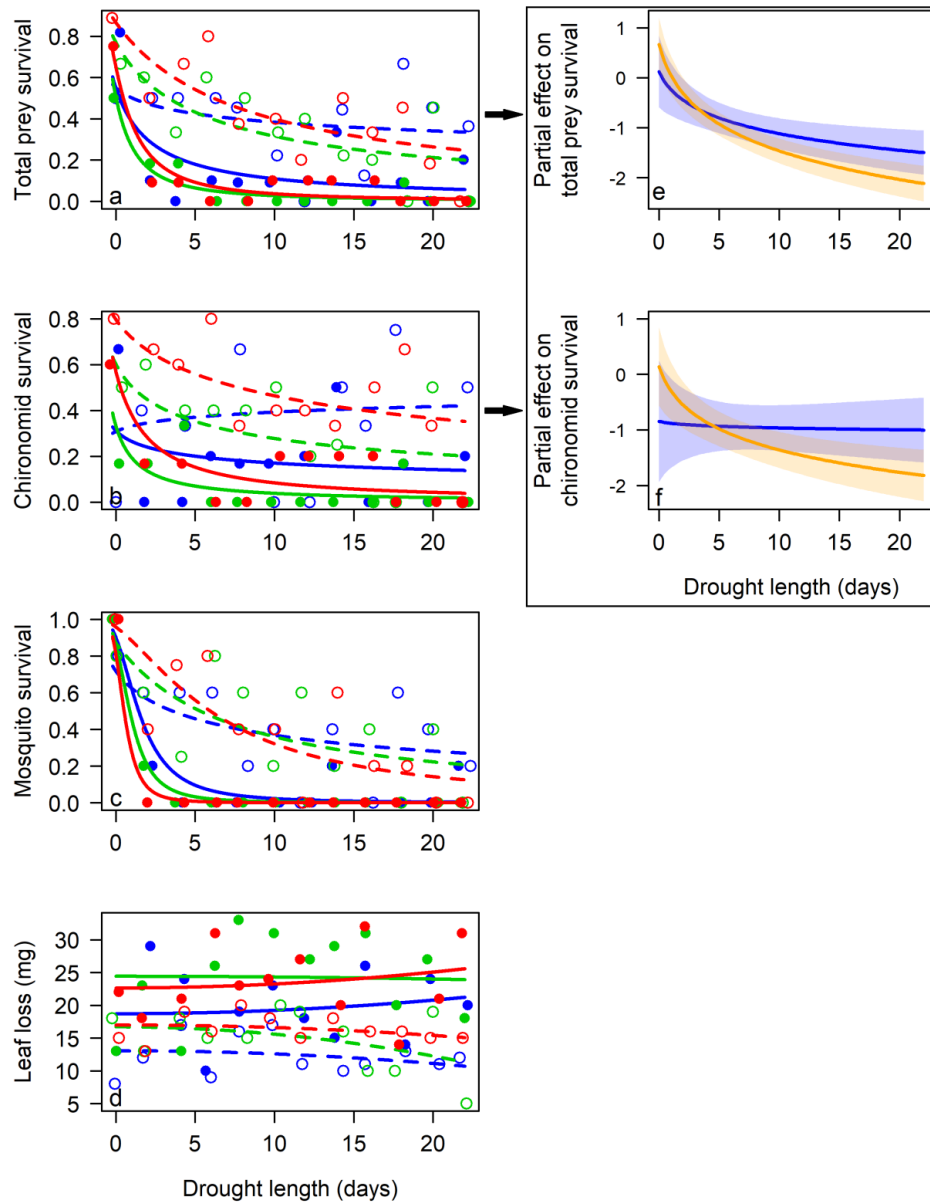
Drought reduced the survival of prey, but the magnitude depended on the Origin→Location treatment (Table 5.1: O→L x D). This interaction was driven more by experimental location than community origin, as when we partitioned the Origin→Location treatment into its two component contrasts, we found that drought interacted with the space-for-time contrast, but not the common garden contrast (Figure 5.2a, Table 5.1: SfT x D). Specifically, the negative effects of drought on total prey survival were stronger at the site representing the future climate (UGA), regardless of community origin (Figure 5.2e). Chironomids drove this response of the total prey community to the drought x space-for-time interaction (Table 5.1: O→L x D and SfT x D, Figure 5.2b). While chironomid survival was unaffected by drought at MV (i.e., the current climate), survival decreased with drought at UGA

(Figure 5.2f). In contrast, the negative effects of drought on mosquitoes (Table 5.1: D) were independent of experimental location or whether mosquitoes had been filtered locally by climate (Table 5.1: O→L x D, Figure 5.2c).

Table 5. 1: ANOVA results for insect survival (total prey, chironomids, and mosquitoes) and decomposition (as loss of dry mass of detritus). Generalized linear models with X^2 tests were used for insect survival, and linear models with F tests were used for decomposition. Model predictors are O→L = Origin→Location treatment (MV→MV, MV→UGA, or UGA→UGA), T = Tipulid treatment (present or absent), and D = ln(Drought length + 1). When O→L or its interaction with T or D was significant, orthogonal contrasts decomposed O→L into SfT = Space-for-Time contrast (MV→MV vs. MV→UGA and UGA→UGA) and CG = Common Garden contrast (MV→UGA vs. UGA→UGA).

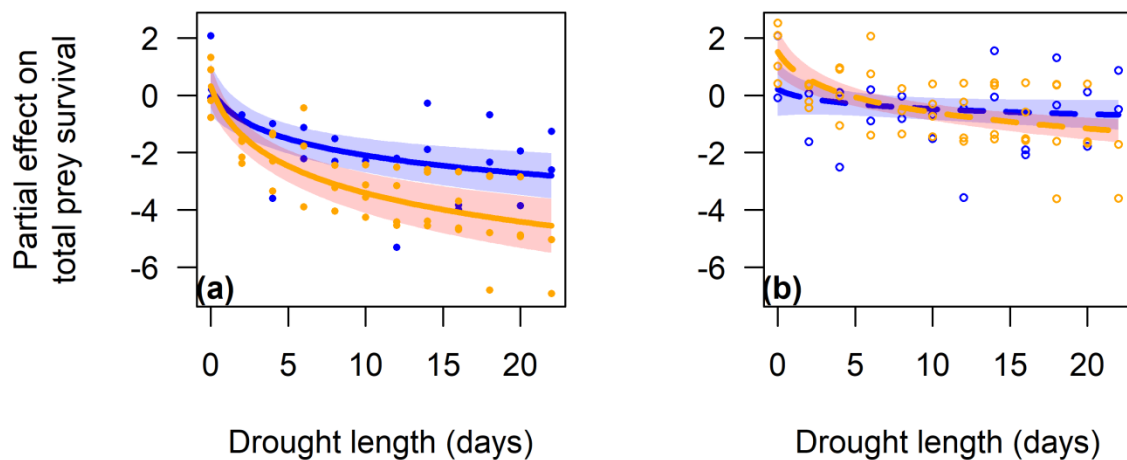
Predictor \ Response	O→L						T		D		O→L x T				O→L x D				T x D					
	SfT		CG								SfT x T		CG x T		SfT x D		CG x D							
	X^2_2	P	Z	P	Z	P	X^2_1	P	X^2_1	P	X^2_2	P	Z	P	Z	P	X^2_2	P	Z	P	Z	P	X^2_1	P
Survival																								
Total prey	3.62	0.164	--	--	--	--	92.95	<0.001	75.89	<0.001	6.48	0.039	2.51	0.012	0.09	0.932	7.35	0.025	2.69	0.007	0.41	0.679	8.69	0.003
Chironomids	6.81	0.033	-2.18	0.029	-1.03	0.301	37.71	<0.001	14.63	<0.001	3.53	0.171	--	--	--	--	6.46	0.040	2.48	0.013	0.16	0.875	2.70	0.100
Mosquitoes	0.55	0.762	--	--	--	--	60.16	<0.001	77.10	<0.001	4.92	0.085	--	--	--	--	3.70	0.157	--	--	--	--	14.40	<0.001
	F_2	P	t	P	t	P	F_1	P	F_1	P	F_2	P	t	P	t	P	F_2	P	t	P	t	P	F_1	P
Decomposition	4.83	0.011	-1.71	0.092	-0.12	0.907	46.69	<0.001	0.19	0.664	0.35	0.707	--	--	--	--	0.36	0.698	--	--	--	--	1.82	0.182

Figure 5. 2: Effects of drought length, Origin→Location (O→L) treatment, and tipulid presence on (a) total prey survival, (b) chironomid survival, (c) mosquito survival, and (d) leaf loss. Experimental location represents current (MV) and future (UGA) climate. O→L treatments are indicated by color. Blue: MV→MV, green: MV→UGA, red: UGA→UGA. Tipulid treatment is indicated by solid circles and lines (tipulid present) versus empty circles and dashed lines (tipulid absent). **Right box:** Partial residuals showing the effect of drought length and experimental location on (e) total prey survival and (f) chironomid survival to illustrate significant drought x space-for-time interaction. Only regression lines of model pooled over the tipulid treatment are shown. Color indicates experimental location. Blue: Monteverde, orange: UGA. Shaded areas represent 95 % confidence intervals.



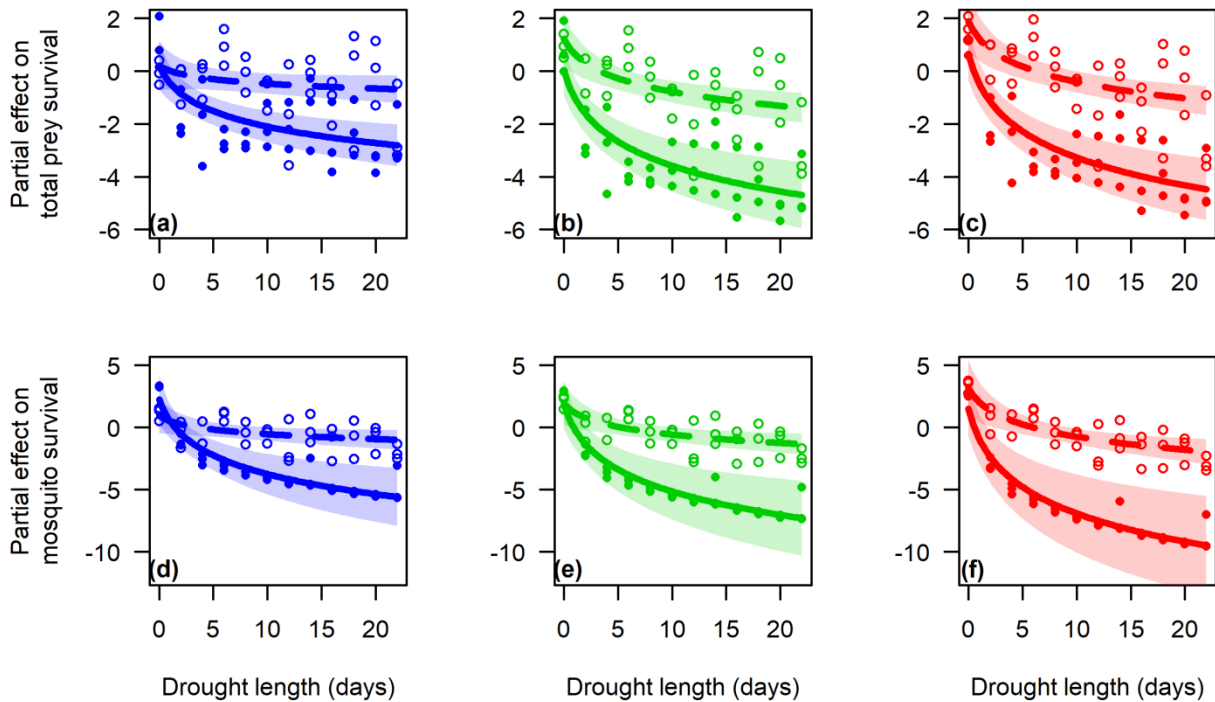
Tipulids also reduced prey survival, and the magnitude depended on the Origin→Location treatment (Table 5.1: O→L x T). This interaction was again driven by experimental location rather than community origin, as tipulids interacted with the space-for-time contrast, but not the common garden contrast (Figure 5.2a, Table 5.1: SfT x T). Specifically, when tipulids were present, prey survival at UGA (i.e., the “future climate”) was 40.6 % lower than at MV (Figure 5.3a), while prey survival did not differ between experimental locations when tipulids were absent (Figure 5.3b).

Figure 5. 3: Partial residuals showing the effect of the space-for-time treatment on total prey survival for communities in which (a) tipulids were present and (b) tipulids were absent. Experimental location is indicated by color. Blue: MV, orange: UGA. Shaded areas represent 95 % confidence intervals.



In addition, the adverse effects of tipulids on total prey survival intensified with increasing drought length (Table 5.1: T x D, Figure 5.2a). This tipulid x drought interaction was primarily driven by mosquitoes (Table 5.1, Figure 5.2c). While tipulids had negligible effects when there was no drought (i.e., drought length = 0 days), tipulids significantly decreased total prey and mosquito survival by an average of 83 % and 91 %, respectively, when drought length was two or more days (Figure 5.4). The negative effects of tipulids on chironomid survival, on the other hand, were independent of drought length (Table 5.1, Figure 5.2b).

Figure 5. 4: Partial residuals showing the effect of tipulid treatment on (a-c) total prey survival and (d-f) mosquito survival for each community treatment. Blue: MV→MV, green: MV→UGA, red: UGA→UGA. Tipulid treatment is indicated by solid circles and lines (tipulid present) versus empty circles and dashed lines (tipulid absent). Shaded areas represent 95 % confidence intervals.



Decomposition rates increased when tipulids were present, and were affected by the Origin→Location treatment, but not by drought or any treatment interaction (Table 5.1). Decomposition rates were 55.5 % higher when tipulids were present than when they were absent, consistent with tipulids being important shredders of detritus (Figure 5.2d). Moreover, experimental location was more important in affecting decomposition than community origin, as decomposition rates were 24.2 % higher at UGA (i.e., the “future climate”) than at MV (Figure 5.2d). However, this space-for-time effect is only marginally significant (Table 5.1: SfT). Tipulid presence also determined the relationship of prey mortality and litter decomposition rates. While decomposition rates increased with increasing prey mortality in the presence of tipulids, their relationship was negative when tipulids were absent (Appendix D.2).

Prey emergence rates were low (only 8.5 %) and not affected by the space-for-time treatment or the common garden treatment, but the adverse effects of drought on prey emergence rates were stronger when tipulids were present (Appendix D.3). Tipulid survival was not affected by the drought treatment, the space-for-time treatment, the common garden treatment, or any of their potential interactions.

5.5 DISCUSSION

Simulated climate change altered community structure and ecosystem processes in our experiment. The effects on the insect community were primarily mediated by the presence of

tipulids, which are known to become predatory under drought (Amundrud et al. 2019). These negative effects of tipulids were accentuated at the warmer location. In addition, direct adverse effects of drought on the community depended on temperature and were stronger at the warmer location. Although decomposition tended to be higher at the warmer location, tipulid presence was more important in affecting decomposition than simulated climate change. Thus, tipulids were disproportionately important in affecting both biotic and abiotic aspects of the bromeliad food web. Through their role as decomposers, tipulids were the main predictor of decomposition rates, and through their potential role as predators, tipulids mediated indirect effects of simulated climate change on the insect community.

For chironomids, but not for mosquitoes, the adverse effects of drought depended on temperature, underlining not only that different climatic stressors can interact to affect communities, but also that specific responses to climatic stressors often depend on species identity. Whereas drought reduced chironomid survival only at the warm location, it adversely affected mosquito survival at both locations. These species-specific responses to drought may stem from their different microhabitat use; while mosquitoes depend on vertical movement through the water column to carry out vital functions such as feeding, chironomids can carry out these functions as long as there is moisture. In our experiment, the effect of drought on the state of the water column was independent of location and thus temperature (i.e., the water column was removed at both study sites), explaining why mosquitoes experienced negative effects of drought at both locations. On the other hand, drying rates of the substrate after removal of water were likely location-dependent. The removal of the water column was unlikely to lead to complete drying of the substrate and/or insect bodies at MV, which is submersed in clouds for much of the time. In contrast, low humidity combined with high temperatures at UGA lead to

higher evaporation and thus desiccation rates with drought, explaining why chironomids experienced negative effects of drought only at UGA. By disentangling the effects of drought and temperature on the prey community, these results emphasise that different climatic variables often interact to affect organisms on a species-specific basis. As communities consist of diverse species assemblages, the complexities that arise from the multifaceted effects of climate change have to be accounted for when attempting to predict its ecological effects.

Altered species interactions further complicated community responses to climate change in our experiment, as both drought and warmer temperatures enhanced the negative effects of tipulids on the prey community. Drought enhanced adverse effects of tipulids on mosquitoes, but not on chironomids, again stressing that climate change responses are often species specific. By removing the water column, drought likely hampered the ability of mosquitoes to escape predation by tipulids, supporting previous conclusions that climate change can inhibit the capability of prey to flee from predators (de Barros et al. 2010; Amundrud et al. 2019). On the other hand, drought is unlikely to significantly alter the mobility of chironomids, which can still avoid predation by moving along the substrate, likely explaining why drought did not enhance negative effects of tipulids on chironomids (Amundrud et al. 2019). Indeed, many chironomids survived in the presence of tipulids even at long drought lengths. Although we were not able to specifically measure prey consumption rates by tipulids in this study due to logistical constraints, we know from previous experiments that drought (through both the removal and the reduction of the water column) enables tipulids to consume insect prey (Amundrud and Srivastava 2016; Amundrud et al. 2019). In one of these previous studies (Amundrud et al. 2019), we used manipulations of caged and non-caged tipulids to differentiate between consumptive and non-consumptive effects of tipulids on other insects, and showed that only consumption was

important under drought conditions. Importantly, these consumptive effects of tipulids under drought conditions were particularly severe for mosquitoes, while chironomids were able to avoid predation to some extent, likely by still being mobile in the absence of water. This difference between mosquitoes and chironomids is echoed in our current study.

The negative effects of tipulids on the prey community were also enhanced by the warmer temperatures at UGA. Tipulids may have exhibited higher predation rates at the warmer location due to behavioural or metabolic changes caused by higher temperatures (Gilman 2017). Warming has been shown to increase predation rates in a diverse suite of predators such as fish (Meerhoff et al. 2007), terrestrial (Harmon et al. 2009a) and aquatic (De Block et al. 2013) insects. However, a recent meta-analysis found that warming generally weakens top-down control at warm locations such as the tropics (Marino et al. 2018), which is inconsistent with the increase of adverse effects of tipulids with warming in our experiment. Here, warming may have increased predation rates by affecting the predator's foraging behaviour (Barton 2011) and/or activity levels (Dell et al. 2014). Regardless of the mechanism, our findings suggests that the warmer and dryer climate predicted with climate change will likely affect bromeliad communities through increased predation rates from tipulids, which may translate into increased extinction risk for prey (De Block et al. 2013), and demonstrate that altered abiotic conditions can affect communities by altering the functional role of one of its members.

Decomposition rates were primarily affected by tipulid presence, and tended to be higher at the warmer location. Despite the general consensus that climate and litter quality are the best predictors of decomposition rates (Harmon et al. 2009b; Currie et al. 2010), the disproportionate effect of tipulids on litter decomposition in our experiment is consistent with previous findings in

this system (Amundrud and Srivastava 2016). Tipulids are known to have the highest per capita litter decomposition rates of all detritivores in tank bromeliads (LeCraw 2014), even after accounting for their relatively large body size (Srivastava and Bell 2009). Interestingly, increased prey consumption by tipulids facilitated by drought and higher temperatures at UGA did not affect their role as decomposers, suggesting that tipulids supplement their diet with prey, rather than switching their diet. A supplementary rather than complementary role of tipulid predation with litter processing is also supported by the positive relationship of decomposition rates with prey mortality in communities where tipulids were present (Appendix D.2), suggesting that those tipulids that exhibit high litter processing rates are also consuming a lot of prey. As decomposition rates were largely independent of temperature and drought, our results support other studies showing that detritivore composition can be more important in influencing litter decomposition than climate (Schimel and Schaeffer 2012; Bradford et al. 2016).

The common garden manipulation represented a strong test of the ability of the insect community to adapt (in the broad sense) to climatic differences. Yet, the origin of communities, whether UGA (i.e., “future” climatic conditions) or MV (i.e., “current” climatic conditions), had no effect on how they responded to simulated climate change. However, tipulids do display a ~ 3 °C higher heat tolerance (i.e., CT_{max}) at UGA than at MV (Appendix D.4), which corresponds to the actual temperature difference between the locations. Despite this apparent climatic filtering of tipulids, tipulid origin was not important in driving any responses to experimental treatments, nor did tipulids from different origins differentially affect the prey community or decomposition rates. Although the origin of insect larvae in our experiment had no effect on the outcome of simulated climate change, it is possible that filtering by local climate is more important for other life stages (such as adults or eggs).

Here, in one powerful experiment, we combined controlled manipulations of drought length and species interactions with a space-for-time transplant and a common garden approach. This design enabled us to decouple the effects of two climatic stressors, warming and drought, as well as account for the role of species interactions in mediating any community responses to these stressors. In addition, the common garden approach allowed us to explore if the outcome of simulated climate change depended on whether communities were locally filtered by climate (representing situations in which communities acclimate to, adapt to, or track climate change). We found that the adverse effects of drought on the bromeliad community were enhanced at the warmer location, adding to the growing amount of evidence that different climatic stressors interactively affect communities (Vinebrooke et al. 2004; Darling et al. 2013). Moreover, adverse effects of simulated climate change on the prey community were amplified by negative effects of tipulids, supporting the view that predators can act as biotic multipliers of climate change (Urban et al. 2017). Importantly, the presence of just one community member, tipulids, drastically affected how the food web responded to climate change, stressing that a single species can steer ecological outcomes to climate change. Focusing predominantly on such “leverage species” (Harley et al. 2006) may improve our ability to predict the ecological outcomes of climate change.

6 CONCLUSION

This dissertation demonstrates first that spatial scale can influence the relative importance of abiotic and biotic processes in shaping species distributions and ecological communities, and second that the interplay of abiotic and biotic processes can depend on environmental context. I reached these conclusions by combining local experiments with regional surveys and modeling techniques in a natural model system spanning a large geographic range. Through this combination of methods, I was able to disentangle the factors that operate across a range of spatial scales, from the local habitat, to the landscape, to the geographic region. While species interactions were crucial in shaping community composition and ecosystem functions at the local scale, biotic interactions were not important predictors of species distributions at the geographic scale. Interestingly, at the intermediate scale of the landscape, the relative importance of abiotic and biotic processes depended on environmental context, an important insight given that abiotic conditions are already shifting as a result of climate change.

At the **geographic scale**, physical barriers to dispersal (i.e., ocean barriers and the Andes mountain range) and climatic constraints (i.e., low temperatures and low precipitation) were the main predictors of the distribution of the damselfly *M. modesta*, while biotic interactions from other bromeliad-dwelling odonates were not important (Chapter 2; Amundrud et al. 2018). The finding that *M. modesta* is limited by cold and dry conditions is consistent with several other studies. For example, I demonstrated in my Masters' research that *M. modesta* exhibits a disproportionately high vulnerability to drought compared to other bromeliad invertebrates, and as a result does not occupy small bromeliads that have a high likelihood of experiencing drought (Amundrud and Srivastava 2015; Srivastava et al. 2020). Second, the observational survey of bromeliad communities at Monteverde Mountain (Chapter 3; Amundrud and Srivastava 2020)

demonstrates that this predator is absent from areas that are relatively cold (i.e., high elevations) and dry (i.e., the Pacific slope). Because *M. modesta* is limited by cold conditions, it is likely that this predator will track climate change to higher elevations, with potentially strong effects on naïve high-elevation bromeliad food webs.

At the **landscape scale**, the relative importance of abiotic and biotic processes in determining invertebrate elevational distributions and community structure depended on environmental context (Chapter 3; Amundrud and Srivastava 2020). On the wet Atlantic slope, insect physiological tolerances to high temperatures explained their elevational distributions better than trophic interactions from damselflies or crane flies. On the dry Pacific slope, by contrast, negative effects of crane flies on other insects were more important in explaining their elevational distributions than physiological tolerance limits to high temperatures. The finding that damselflies did not exert any significant biotic effects on the community was surprising, given that these predators can exert large-scale community and ecosystem-level effects (e.g., Amundrud and Srivastava 2016), and was likely due to damselflies being rare in areas where they were present (i.e., on the low elevation Atlantic slope). Instead, crane flies, which were disproportionately abundant on the warm and dry low elevation Pacific slope, exerted negative effects on other bromeliad invertebrates and thus mediated the effect of elevation on their distributions. It is likely that access to a more lucrative food source under drought conditions (Chapter 4; Amundrud et al. 2019), together with a relatively high heat tolerance (Chapter 3; Amundrud and Srivastava 2020) and drought tolerance (Amundrud and Srivastava 2015, 2016, 2019) caused crane flies to thrive under dry and warm conditions. These results are also consistent with the findings of an observational study by Melissa Guzman, a former member of

the Srivastava lab, who showed that the trophic interaction strength of bromeliad-dwelling crane flies in Brazil increases as bromeliad water level decreases (Guzman et al. 2018). Because crane flies responded strongly to abiotic conditions in terms of their abundance and their functional response (i.e., a drought-induced trophic niche shift), they will likely act as “biotic multiplier” of climate change (Zarnetske et al. 2012; Urban et al. 2017) when conditions become warmer and dryer (Karmalkar et al. 2008). These findings shed new light on complex community-level responses to climate change, which are still poorly understood. Not only do they support the idea that the effects of climate change on species ranges and community dynamics at the landscape scale may be highly influenced by species interactions (Clark et al. 2011; Diamond et al. 2016), but they also demonstrate that the interplay of abiotic and biotic selective pressures on species physiology and distributions can be highly dynamic and depend on environmental context. This is an important insight given the rapid rates of changing environmental conditions as a result of global change.

At the **local scale**, the effects of simulated climate change on the invertebrate community were strongly mediated by biotic interactions from crane flies, whose presence altered both community structure and ecosystem processes far beyond any direct community-level effects of warming or drought. At this scale, negative interactions from crane flies on other insects arose under drought conditions (Chapters 4 and 5; Amundrud and Srivastava 2019; Amundrud et al. 2019), and were accentuated at the warmer location (Chapter 5; Amundrud and Srivastava 2019). As such, the presence of just one community member drastically affected how the food web responded to simulated climate change. Moreover, this work uncovered the mechanism of how simulated climate change resulted in crane flies exerting such strong effects on the community.

Using controlled experiments, I demonstrated that crane flies became predatory under drought conditions, and that this drought-induced predatory behavior arose because of increased encounter rates of crane flies with potential prey species as a result of habitat compression. As such, climate change can alter the trophic structure of a food web affecting the functional role of an opportunistic consumer. Because opportunistic foragers are relatively common across ecosystems (Hawlena et al. 2011; Kratina et al. 2012), this may be a commonly overlooked mechanism by which climate change indirectly affects food webs.

I took advantage of a broad-ranging natural ecosystem that can be easily manipulated and replicated to learn about the processes that govern communities and species distributions across a range of spatial scales. By combining modeling techniques with observational surveys along environmental gradients and controlled experiments, I demonstrated that the relative importance of abiotic and biotic processes that affect species distributions and the structure of ecological communities can be scale-dependent. While biotic interactions were key drivers of community responses at small and intermediate spatial scales, they were not detectable at the large geographical scale, lending support to the Eltonian Noise Hypothesis (Soberón and Nakamura 2009). Interestingly, at the intermediate scale of the landscape, the importance of biotic interactions in driving species elevational distributions and thus community structure depended on environmental context, suggesting that, at the landscape scale, the relative importance of physiological and biological drivers of species distributions may shift with changing abiotic conditions such as climate change. These results were driven by the response of a single species to abiotic conditions, and caused by the trophic niche shift of the crane fly larvae in response to drought. Altered top-down effects from climate change will likely affect food webs across many

ecosystem types (Marino et al. 2018), but studies on how potential shift in species' functional or trophic roles under altered environmental conditions will restructure food webs are still scarce. Fresh waters are particularly vulnerable to climate change, and in several areas of the world the prevalence or duration of drought events is likely to increase (Prudhomme et al. 2014). It is thus possible that habitat compression in ponds or streams due to drought will lead to similar effects on increased top down control in food webs (Dudgeon 1993). Future studies that investigate the dynamic nature of the relative importance of abiotic and biotic effects in other systems would be informative.

As ecologists hasten to predict how communities and ecosystems will respond to global change, many efforts still focus on direct responses of species to altered environmental conditions, ignoring complexities that arise from altered species interactions. However, the evidence that species interactions can be of paramount importance in mediating the effects of global change on ecological communities (Suttle et al. 2007) and ecosystem processes (Schmitz et al. 2003) is growing. However, due to the sheer number of complex interactions among species and their environment, such indirect effects are inherently difficult to predict, and little progress has been made in incorporating species interactions into ecological forecast models. Harley et al. (2006) proposed that impacts on “leverage species” can result in large-scale ecosystem level changes (Harley et al. 2006). However, the challenge remains to correctly identify such leverage species. Based on the findings of my PhD and MSc theses, potential leverage species might be species that exhibit a strong *response* to environmental change (e.g., through demographic and/or per capita responses), as well as having disproportionately large ecosystem-level *impacts* (e.g., through exerting strong interactions on other species). For

example, in my MSc work I showed that disproportionately adverse effects of drought on the survival of a keystone predator damselfly larva can reshape communities and alter ecosystem functions far beyond any changes resulting from direct effects of drought on individual species (Amundrud and Srivastava 2016). In this dissertation, I found that crane flies responded to drought by shifting their trophic role, causing them to exert strong consumptive effects on other insects with subsequent community-level effects that exceeded any direct effects of drought. Future research could synthesize the literature to explore whether species that mediate effects of global change display certain traits that make them likely to respond strongly to environmental change and/or have large community level effects. By focusing on characteristics that determine *why* certain species might be particularly likely to mediate global change effects, such a mechanistic framework could be used to help (1) identify (and direct conservation efforts towards) species that are particularly likely to mediate the effects of global change, (2) predict which communities are most likely to experience indirect effects, and (3) improve predictions of how ecosystems respond to global change.

Climate change is rapidly altering food webs globally, but we still lack an adequate understanding of how global change affects food webs and their associated ecosystem functions. Apart from the challenge to incorporate species interactions into forecast models, there are additional aspects of multifaceted global change that hamper our ability to make accurate predictions, such as multiple climatic variables shifting in concert with other drivers of global change such as land use, and uncertainty over the ability of species to develop in situ tolerance or track environmental change. I demonstrated how we can unravel some of these complexities, by performing the first controlled experiment that manipulated multiple climatic stressors, species

interactions, and prior exposure of species to future climatic conditions, and thus showed how uncertainties arise from the interplay of multiple biotic and abiotic mechanisms of climate change (Amundrud and Srivastava 2019). However, we still only have a limited understanding of how climate change and other aspects of global change interact to affect food webs and their associated ecosystem functions. Future studies that combine observational surveys along land use and climate gradients with controlled experiments that manipulate climate and land use (e.g., space-for-time transplants, warming experiments in the field, etc.) and species interactions (presence or absence of potential leverage species) could be a good first step in uncovering the combined effects of climate change and land use change on ecological systems.

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APPENDICES

A SUPPLEMENTARY INFORMATION TO CHAPTER 2⁵

⁵ Previously published as Supporting Information of Amundrud S.A., Videla M., & Srivastava D.S. (2017) Dispersal barriers and climate determine the geographic distribution of the helicopter damselfly *Mecistogaster modesta*. *Freshwater Biology* 63: 214-223.

A.1 DETAILED METHODS AND RESULTS OF THE MAXENT MODELS OF THREE POTENTIAL COMPETITORS OF *M. MODESTA*

To examine whether competition determines the geographic distribution of *Mecistogaster modesta*, we used the modeled distributions of three of its potential competitors. We searched for occurrence records of these species using the same resources as for *M. modesta* (see main article). We focused on bromeliad-dwelling odonate species with known occurrence records in the north of South America, as their ranges may overlap with that of *M. modesta*. The possible competitor species of *M. modesta* belong to the *Bromeliagrion* genus and have been recorded in Guyana, Venezuela, Ecuador, Peru, and Brazil. As occurrence records for *Bromeliagrion bebeanum*, *B. fernandezianum* and *B. rehni* were sparse (6, 6, and 11, respectively), we used Maxent, a widely used algorithm for presence only data that performs better than others when sample sizes are small (Hernandez et al. 2006; Wisz et al. 2008), to model their distributions.

For each potential competitor species, we ran a Maxent model using 19 bioclimatic variables at 2.5 arc-minutes resolution from the WorldClim database (Hijmans et al. 2005). Based on variable importance and low correlation ($r < 0.8$), we chose three to four bioclimatic variables to model the distributions of the three odonate species (Table A.1).

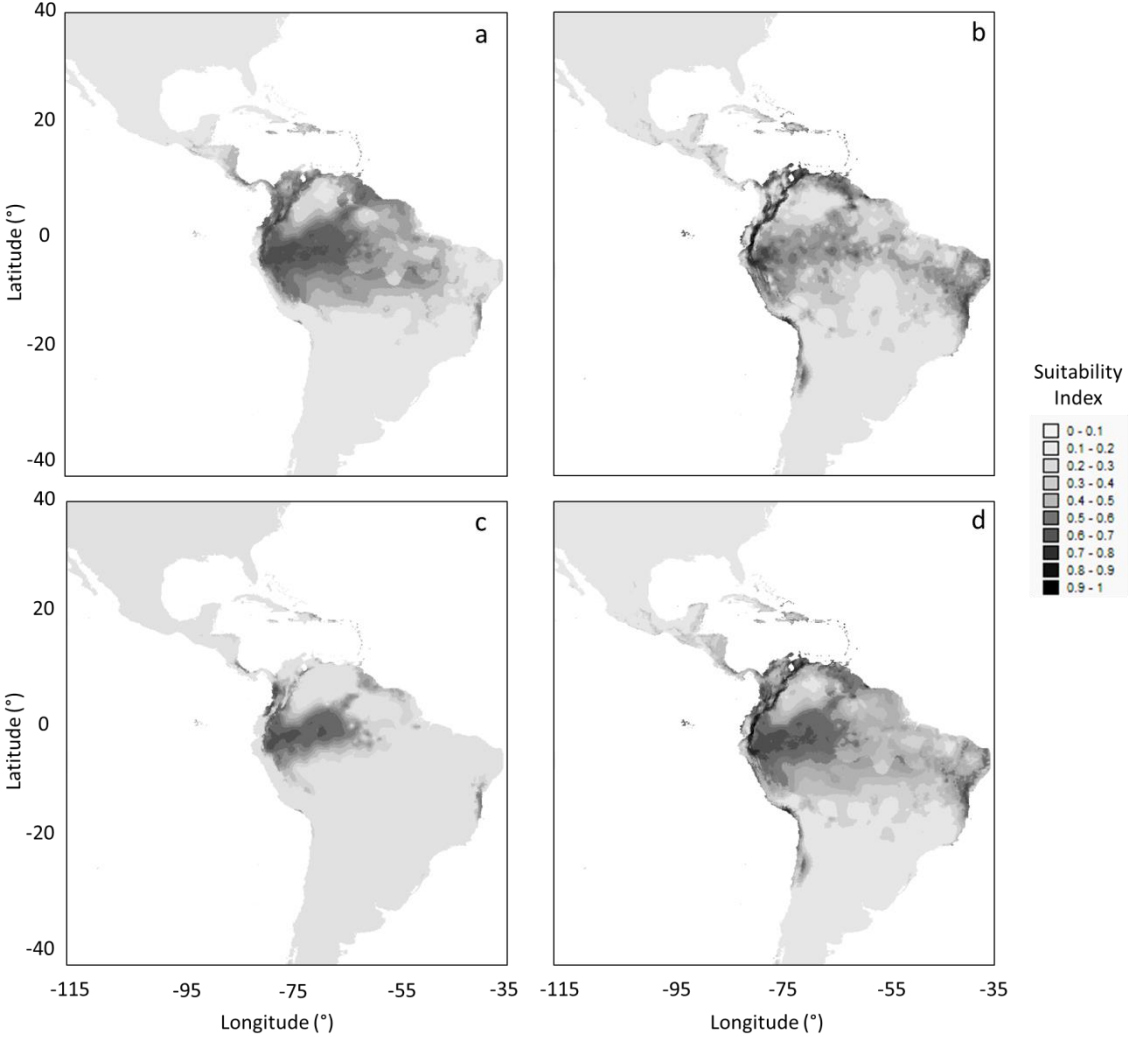
We validated models using the jackknife (or “leave one out”) approach proposed by Pearson *et al.* (2007). This approach is especially suitable when records are sparse and partitioning the data randomly into ‘training’ and ‘test’ sets is not recommended (Pearson et al. 2007). This procedure requires the transformation of continuous scores (suitability index) into binary (presence/absence) data, which is achieved by setting a threshold above which the model output is considered a prediction of presence. Selection of a threshold is controversial given that

the choice of threshold could influence the results. Therefore, we performed the analysis using three different threshold selection criteria (minimum training presence, 10% training presence, and equal sensitivity and specificity) following De Araújo et al. (2014). The results did not vary with the threshold selection criteria used, so we present the results obtained from using the equal sensitivity and specificity criteria (Table A.1 and Figure A.1).

Table A. 1: Environmental variables and their importance used in Maxent models of Bromeliagrion species distributions. Success rates and p-values result from model validation using the leave one out approach (Pearson et al. 2007).

Species	BioClim Variable	Contribution (%)	Success Rate	p-value
<i>Bromeliagrion bebeanum</i>	Temperature Seasonality (bio4)	74.6	0.833	0.000061
	Precipitation Seasonality (bio15)	23.0		
	Precipitation of Coldest Quarter (bio19)	2.4		
<i>Bromeliagrion fernandezianum</i>	Temperature Seasonality (bio4)	51.9	0.666	0.00185
	Temperature Annual Range (bio7)	28.2		
	Precipitation of Wettest Month (bio13)	16.5		
	Precipitation Seasonality (bio15)	3.3		
<i>Bromeliagrion rehni</i>	Temperature Seasonality (bio4)	37.6	0.909	0.000001
	Minimal Temperature of Coldest Month (bio6)	35.8		
	Precipitation of Driest Month (bio14)	24.8		
	Precipitation Seasonality (bio15)	1.7		

Figure A. 1: Habitat suitability maps for (a) *Bromeliagrion bebeanum*, (b) *B. fernandezianum*, (c) *B. rehni* and (d) all species combined.



A.2 REFERENCES

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B SUPPLEMENTARY INFORMATION TO CHAPTER 3⁶

⁶ Previously published as Supporting Information of Amundrud, S. L., and Srivastava, D. S. (2020) Thermal tolerances and species interactions determine the elevational distributions of insects. *Global Ecology and Biogeography* 29: 1315-1327

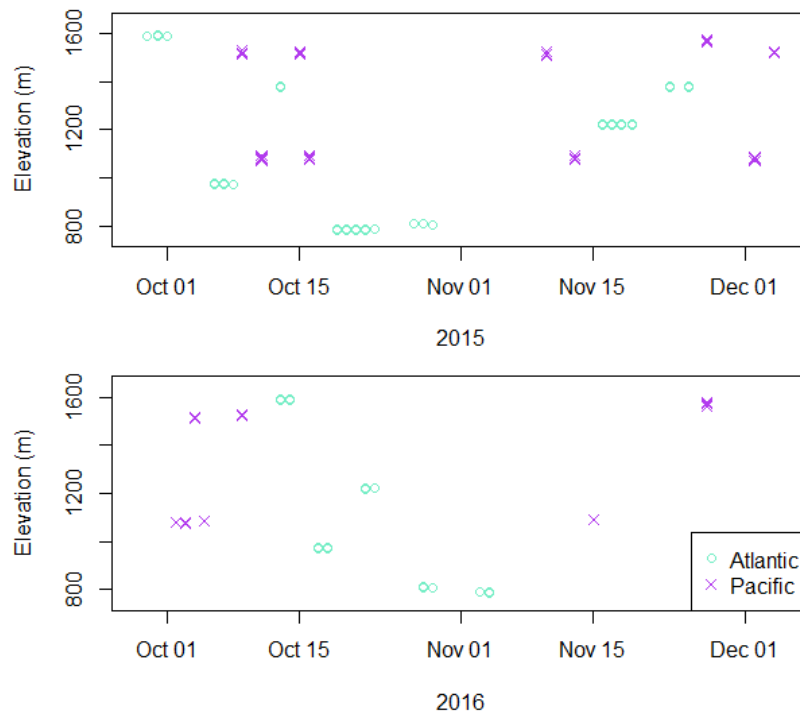
B.1 INFORMATION OF THE STUDY SITES ON THE PACIFIC AND ATLANTIC SLOPES OF MONTEVERDE MOUNTAIN

We surveyed bromeliad food webs at nine sites along two elevational gradients (i.e., on the Pacific and Atlantic slope of Monteverde Mountain) from late September to early December in 2015 and 2016, that is, during the rainy season when bromeliads contain most insect larvae (Table B.1). Because sampling time can affect abundance patterns of insects due to seasonal effects, we ensured that sampling occurred in the shortest timeframe that was logistically possible, and was performed non-systematically with respect to mountainside and elevation (Figure B.1). Only two sites (San Luis and Research Trail) were relatively easily accessible, and were thus sampled several times throughout the seasons. The other sites were either only accessible by day hikes (Brillantes and Dos Ases) or multiday field trips (El Valle, San Gerardo, Aleman, Eladios, Poco Sol), and could not be sampled repeatedly in the same year because of logistical constraints.

Table B. 1: Mountainside, elevation (in meters), geographic coordinates, and sampling dates of the nine study sites on Monteverde Mountain. The number of bromeliads sampled at each date is indicated in brackets.

site	side	elevation	coordinates	sampling dates
San Luis	Pacific	1082	N10° 16.9' W84° 47.6'	11/10/2015 (n=4); 16/10/2015 (n=4); 13/11/2015 (n=4); 02/12/2015 (n=4); 02/10/2016 (n=1); 03/10/2016 (n=2); 05/10/2016 (n=1); 15/11/2016 (n=1)
Research Trail	Pacific	1517	N10° 17.8' W84° 47.6'	09/10/2015 (n=3); 15/10/2015 (n=4); 10/11/2015 (n=4); 04/12/2015 (n=3); 04/10/2016 (n=3); 09/10/2016 (n=2)
Brillantes	Pacific	1573	N10° 17.5' W84° 47.0'	27/11/2015 (n=5); 31/11/2015 (n=5); 27/11/2016 (n=4)
El Valle	Atlantic	1590	N10° 19.4' W84° 45.9'	29/09/2015 (n=2); 30/09/2015 (n=6); 01/10/2015 (n=2); 13/10/2016 (n=2); 14/10/2016 (n=3)
Dos Ases	Atlantic	1379	N10° 17.9' W84° 46.8'	13/10/2015 (n=6); 23/11/2015 (n=6); 25/11/2015 (n=6)
San Gerardo	Atlantic	1221	N10° 21.8' W84° 47.4'	16/11/2015 (n=4); 17/11/2015 (n=4); 18/11/2015 (n=8); 19/11/2015 (n=3); 22/10/2016 (n=2); 23/10/2016 (n=1)
Aleman	Atlantic	974	N10° 18.0' W84° 44.9'	06/10/2015 (n=4); 07/10/2015 (n=7); 08/10/2015 (n=2); 17/10/2016 (n=2); 18/10/2016 (n=3)
Eladios	Atlantic	809	N10° 18.5' W84° 43.0'	27/10/2015 (n=1); 28/10/2015 (n=5); 29/10/2015 (n=3); 28/10/2016 (n=4); 29/10/2016 (n=1)
Poco Sol	Atlantic	787	N10° 21.0' W84° 40.1'	19/10/2015 (n=4); 20/10/2015 (n=5); 21/10/2015 (n=5); 22/10/2015 (n=6); 23/10/2015 (n=1); 03/11/2016 (n=2); 04/11/2016 (n=2)

Figure B. 1: Sampling dates of bromeliad communities along elevational gradients on the Pacific (purple crosses) and Atlantic (green circles) slopes of Monteverde Mountain in 2015 and 2016. In both years, sampling was conducted non-systematically with respect to elevation and mountainside.



B.2 ELEVATION PREFERENCE AND MEAN ELEVATION OF OCCURRENCE FOR BROMELIAD INSECT SPECIES FOR EACH MOUNTAINSIDE

Because elevation differentially affected insect abundances, elevation preferences (i.e., the slope of the elevation term in the Poisson model; Figure 3.2 in Chapter 3) of bromeliad macroinvertebrates were species-specific. On both mountainsides, marsh beetles (*Scirtid* spp.) exhibited a preference for high elevations, while chironomids (*Polypedilum* spp.) showed no significant elevation preference. Damselflies (*M. modesta*) preferred low elevations at the Atlantic slope, and were absent from the Pacific slope. Interestingly, the elevation preferences of mosquitoes (*Culex erethyzonefer*) and crane flies (*Trentepohlia* spp.) depended on mountainside: while mosquitoes preferred high elevations on both slopes, the preference was much stronger on the Atlantic slope (Figure B.2a) than on the Pacific slope (Figure B.2b; elevation preference is marginally non-significant). Crane flies exhibited no elevation preference on the Atlantic slope (Figure B.2a), but they preferred low elevations on the Pacific slope (Figure B.2b).

The mean elevation of occurrence (MEO) of all individuals within each species follows a similar pattern to the elevation preferences of bromeliad insects (Figure B.3). On the Atlantic slope, mosquitoes (*C. erethyzonefer*) occurred at the highest elevations, damselflies (*M. modesta*) occurred at the lowest elevations, and the other species occurred at intermediate elevations (Figure B.3a). On the Pacific slope, crane flies (*Trentepohlia* spp.) occurred at the lowest elevations, while the other three species occurred at similar elevations (Figure B.3b).

Figure B. 2: Elevation preferences of bromeliad insects on (a) the Atlantic slope and (b) the Pacific slope of Monteverde Mountain. Elevation preference (EP) is the slope of the elevation term from the Poisson model in Figure 3.2 in Chapter 3. Error bars represent 95% confidence intervals (approximated by $1.96 * SE$). When mountainside did not interact with elevation (*Polypedilum* spp. and *Scirtid* spp.), the EPs from the model without side is shown. Otherwise, the EPs from separate models for the Atlantic slope and Pacific slope are shown.

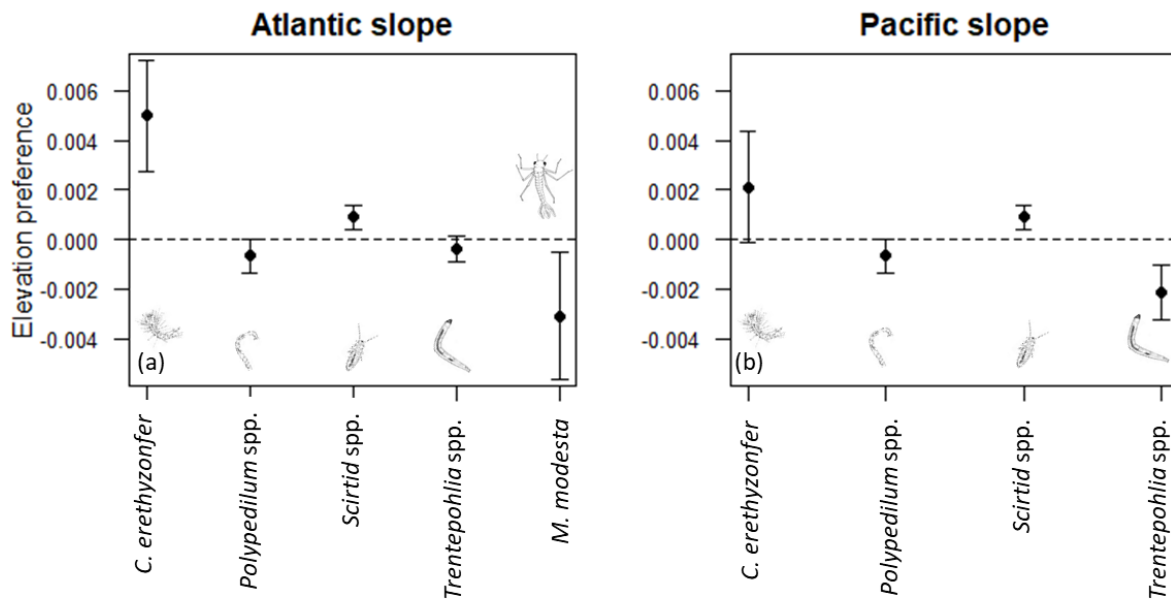
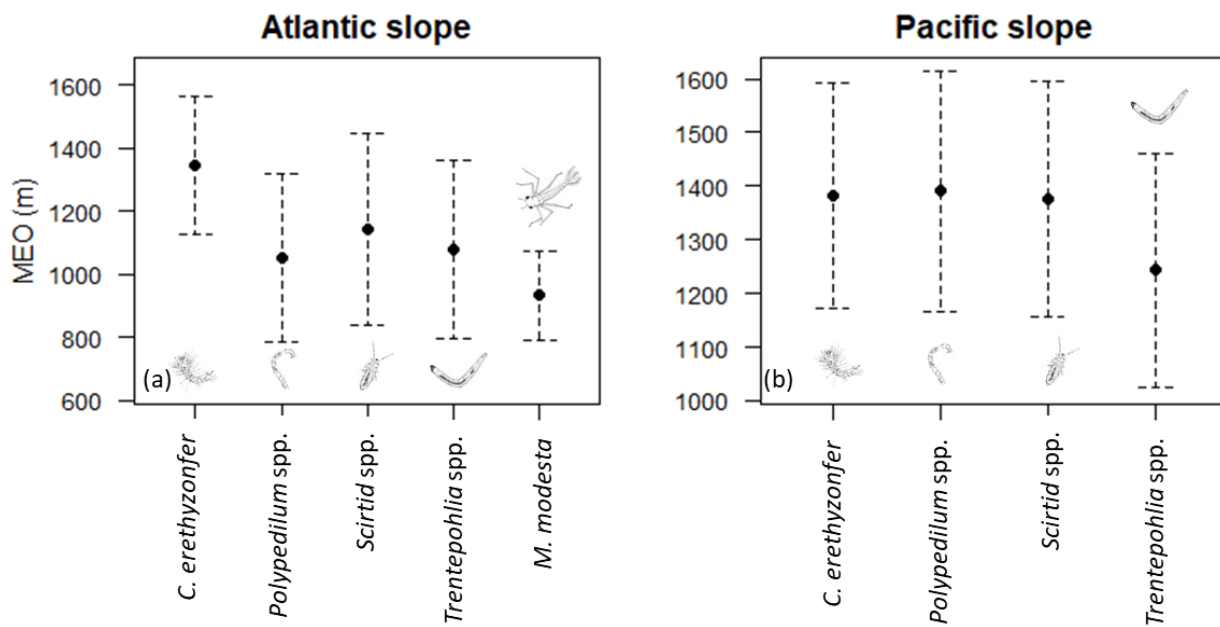


Figure B. 3: Mean elevation of occurrence (MEO) of each species for insects from (a) the Atlantic slope and (b) the Pacific slope of Monteverde Mountain. Error bars represent standard deviation. Species with large error bars thus occurred widely across elevations, while species with narrow error bars occurred over narrow elevational distributions within our study area.



B.3 STRUCTURAL EQUATION MODELS USING AN OBLIGATE PREDATOR VARIABLE INSTEAD OF THE *M. MODESTA* VARIABLE AS POTENTIAL MEDIATOR TO EXPLAIN EFFECTS OF ELEVATION ON FOCAL SPECIES

When replacing *M. modesta* with an obligate predator variable [i.e., by using the combined abundances of diving beetles (*Copelatus* sp.) and damselflies (*M. modesta*)], the results are qualitatively similar to using only damselflies as in Chapter 3 (Table B.2).

Table B. 2: The relative abundance of each of three focal species (columns) is modelled with structural equation models (SEMs), with each SEM being composed of multiple paths (rows, with letters corresponding to Figure 3.4). The significance (p values) of individual paths is assessed with Z-scores. Instead of damselflies, an obligate predator variable was used which represents the combined relative abundance of damselflies (*M. modesta*) and diving beetles (*Copelatus* sp.).

Atlantic slope path	<i>C. erethydonfer</i>		<i>Polypedilum</i> spp.		<i>Scirtid</i> spp.	
	Z	p	Z	p	Z	p
a: obligate predator ~ elevation	-4.656	< 0.001	-4.656	< 0.001	-4.656	< 0.001
b: focal species ~ obligate predator	-0.282	0.778	-1.599	0.110	0.238	0.812
c: <i>Trentepohlia</i> spp.~ obligate predator	0.144	0.886	0.144	0.886	0.144	0.886
d: focal species ~ <i>Trentepohlia</i> spp.	-2.205	0.027	-3.609	< 0.001	-0.405	0.685
e: <i>Trentepohlia</i> spp.~ elevation	0.196	0.845	0.196	0.845	0.196	0.845
f: focal species ~ elevation	2.844	0.004	-4.710	< 0.001	3.476	0.001
ab: indirect effect mediated by obligate predator	0.281	0.778	1.512	0.130	-0.237	0.812
ed: indirect effect mediated by <i>Trentepohlia</i> spp.	-0.195	0.845	-0.196	0.845	-0.177	0.860
acd: indirect effect mediated by obligate predator + <i>Trentepohlia</i> spp.	0.143	0.886	0.143	0.886	0.135	0.892

C SUPPLEMENTARY INFORMATION TO CHAPTER 4⁷

⁷ Previously published as Online Resource 1 of Amundrud, S. L., Clay-Smith, S. A., Flynn, B. L., Higgins, K. E., Reich, M. S., Wiens, R. H. W., and Srivastava, D. S. (2019) Drought alters the trophic role of an opportunistic generalist in an aquatic ecosystem. *Oecologia* 189: 733-744

C.1 ANALYSES ON THE DATA FROM WHICH ALL CULEX SPP. WERE REMOVED FROM THE TOTAL PREY COUNT

Because the identity of the *Culex* species (*Culex jenningsi* vs. *Culex erethyzonfer*) was confounded with water treatment, we repeated the analyses on a subset of the data from which all *Culex* spp. were removed (i.e., mosquitoes are represented by *Wyeomyia* spp. only). The results for total prey abundance were qualitatively similar, suggesting that the confounding of *Culex* spp. identity with water treatment did not bias the results (Table C.1).

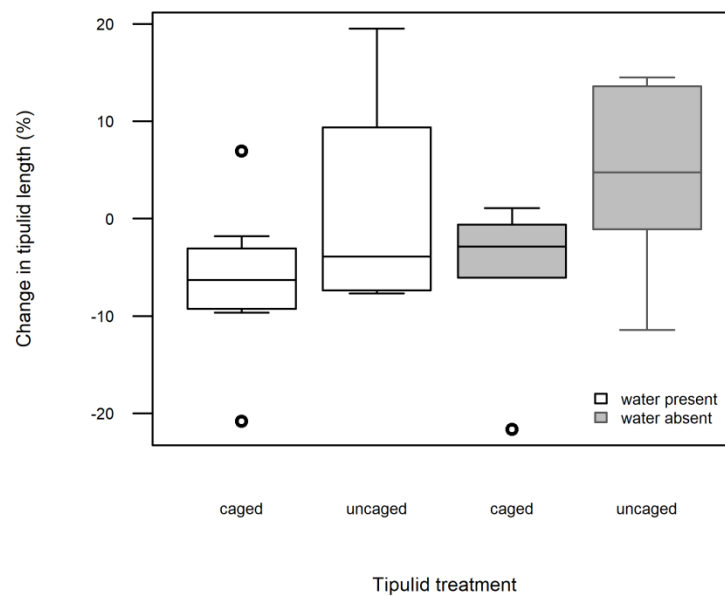
Table C. 1: Effects of tipulids and water on mosquitoes and chironomids in Experiment 1. Analyses were performed on a subset of the data from which all *Culex* spp. were removed, thus mosquitoes are represented by *Wyeomyia* spp. only. (a) Effect tests based on 2-way ANOVA, as summarized by F ratios and *P*-values. “Tipulid” represents three levels of tipulid treatments (no tipulid, caged tipulid, and uncaged tipulid), “Water” represents two water treatments (water present and absent), and “Tipulid x Water” represents their interaction. Significant *P*-values after sequential Bonferroni corrections ($\alpha_1 = 0.05$, $\alpha_2 = 0.025$, and $\alpha_3 = 0.017$, α ’s are sequentially compared from largest to smallest *P* -value in each column) are indicated in bold. (b) Partitioning of tipulid effects into consumptive and non-consumptive effects. “Consumptive” effects compare caged vs. uncaged tipulid treatments for “Water present” and “Water absent” treatments, respectively. “Non-consumptive” effects compare no vs. caged tipulid treatments for “Water present” and “Water absent” treatments, respectively. Significant *P*-values after sequential Bonferroni corrections ($\alpha_1 = 0.025$, $\alpha_2 = 0.013$, and $\alpha_3 = 0.008$; α ’s are sequentially compared from largest to smallest *P* -value in each column) are indicated in bold. Because of non-orthogonality, α ’s are halved.

(a) 2-way ANOVA	Tipulid		Water		Tipulid x Water	
Response	$F_{2,36}$	p	$F_{1,36}$	p	$F_{2,36}$	p
Total prey abundance	14	< 0.001	58	< 0.001	9.2	< 0.001
Wyeomyia abundance	3.8	0.031	106	< 0.001	1.2	0.32

(b) Tipulid effects	Consumptive				Non-consumptive			
	Water present		Water absent		Water present		Water absent	
Response	t_{13}	P	t_9	P	t_{13}	P	t_{11}	P
Total prey abundance	-0.65	0.52	6.3	< 0.001	3.4	0.005	0.02	0.99
Wyeomyia abundance	0.88	0.40	3.0	0.015	2.4	0.032	-0.31	0.76

C.2 EFFECTS OF WATER AND CAGE TREATMENT ON TIPULID GROWTH IN EXPERIMENT 1

Figure C. 1: Effects of water and cage treatment on tipulid growth. Tipulid growth was not affected by cage treatment ($F_{1,17} = 4.10$, $p = 0.059$), water treatment ($F_{1,17} = 0.12$, $p = 0.73$), or their interaction ($F_{1,17} = 0.09$, $p = 0.77$).



D SUPPLEMENTARY INFORMATION TO CHAPTER 5⁸

⁸ Previously published as Supporting Information of Amundrud, S. L., and Srivastava, D. S. (2019) Disentangling how climate change can affect an aquatic food web by combining multiple experimental approaches. *Global Change Biology* 25: 3528-3538

D.1 COMMUNITY COMPOSITION IN MICROCOSMS AND NATURAL BROMELIADS

Bromeliad-dwelling communities vary widely in species composition and relative abundances, and our goal was to replicate “typical” bromeliad communities in microcosms. We assembled communities consisting of the most common taxa in order to allow for replication, and show here that these artificially assembled communities resemble natural bromeliad communities occurring in a typical bromeliad leaf well.

D.1.1 Quantification of natural bromeliad communities

We surveyed the food web inside bromeliads across the two study sites by quantifying the entire contents of 51 bromeliads (24 at MV, 27 at UGA) prior to the Experiment in 2016. The purpose of this survey was to (1) describe the bromeliad food web in the area, and (2) obtain insects to use in our experiment. A total of 42 bromeliads (21 at each site) were collected and hose rinsed in order to quantify their entire food web, while the contents of the remaining 9 bromeliads (3 at MV and 6 at UGA) were collected with a turkey baster. Both methods allow for a thorough quantification of the aquatic macroinvertebrate food web, but we were able to obtain the maximum water holding capacity, an index commonly used as bromeliad size, only for the rinsed bromeliads. For the basted bromeliads, the maximum capacity was estimated from a known correlation of bromeliad size and total aquatic invertebrate abundance at the two study sites (bromeliad capacity = $101.0567 + 1.1235 \cdot \text{abundance}$, $R^2 = 0.28$).

To quantify a “typical” community in a natural leaf well of maximum water holding capacity of 30 mL, we calculated the mean densities of all aquatic invertebrates at the two sites per 30 mL bromeliad capacity, and compare this to the artificially assembled communities inside our microcosms (Figure D.1). Although we found a total of 25 morphospecies between the two study sites, most were very rare and represented occasional occurrences. Of the 25 taxa, only nine occurred at densities higher than one individual per leaf well. Of these nine, only four occurred at densities of at least one individual at both sites (Figure D.1).

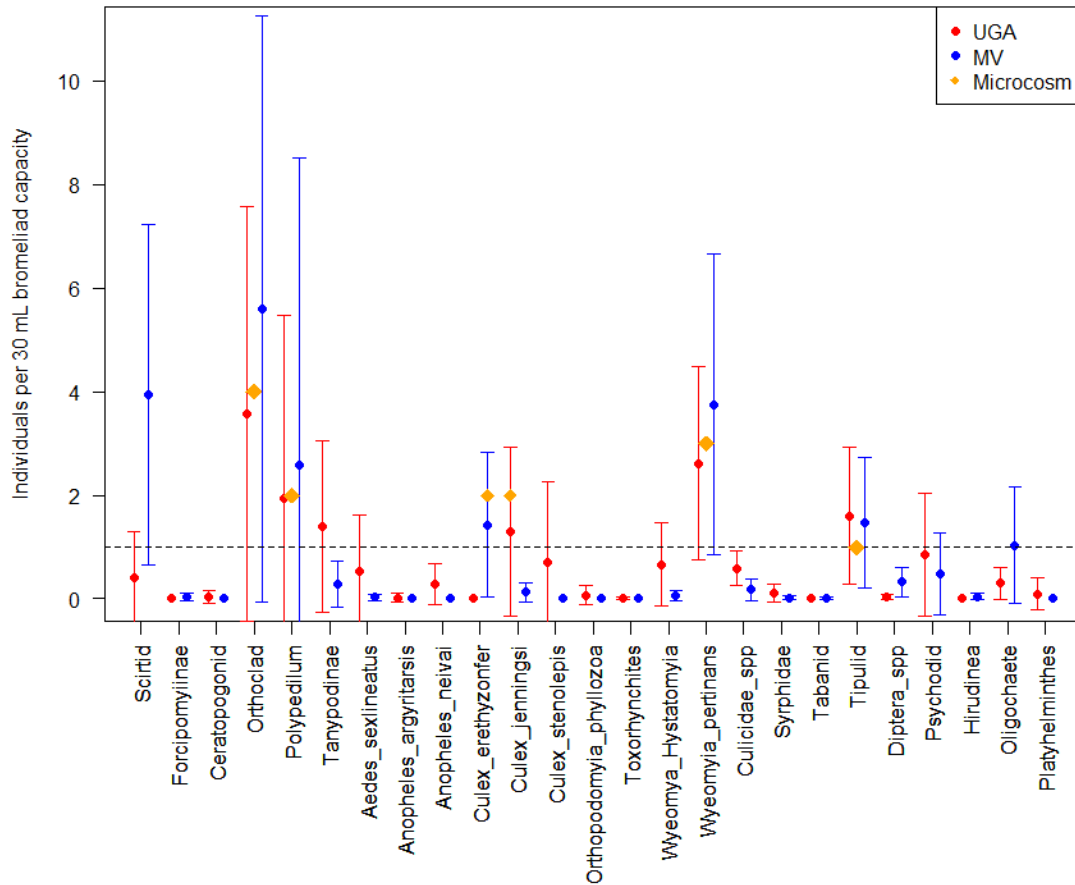
D.1.2 Microcosm communities represent natural bromeliad communities

Microcosms were designed to mimic a bromeliad leaf well with a maximum capacity of 30 mL. The ambient (no drought) conditions in our microcosms thus mimicked a leaf well at a water level at 50% of the maximum capacity (i.e., 15 mL inside microcosms, or a water depth of about 2.1 cm), which is within the typical range of volume for one bromeliad leaf well (Amundrud and Srivastava 2015). Our goal was to replicate identical communities at the two sites, while keeping microcosm communities as close to natural communities as possible in both species composition and relative abundances. By assembling communities based on insects available to use from the bromeliad survey, we obtained communities that reflected those occurring naturally (Figure D.1: yellow diamonds).

The artificially assembled communities represent communities for which the mean natural abundance of each species per 30 mL leaf well is at least one (Figure D.1, dashed line). Since we had to replicate communities exactly between the two sites, we only added species

whose abundance was greater than one at both sites (i.e., Scirtids and Oligochaetes were not included as they were rare at UGA, while Tanypodinae was not included as it was rare at MV).

Figure D. 1: Natural and experimental densities of taxa in our study. Red and blue points represent the mean abundances per 30 mL bromeliad maximum capacity from the survey (UGA: red, MV: blue). Error bars are standard deviations. Yellow diamonds represent abundances of taxa in our microcosms. The dashed line represents a mean abundance of one individual per leaf well, the threshold to include a given taxa in our microcosms. Note that the identity of the *Culex* species in the microcosms differs for the two sites, as *C. erethyazonfer* was common at MV and *C. jenningsi* was common at UGA.

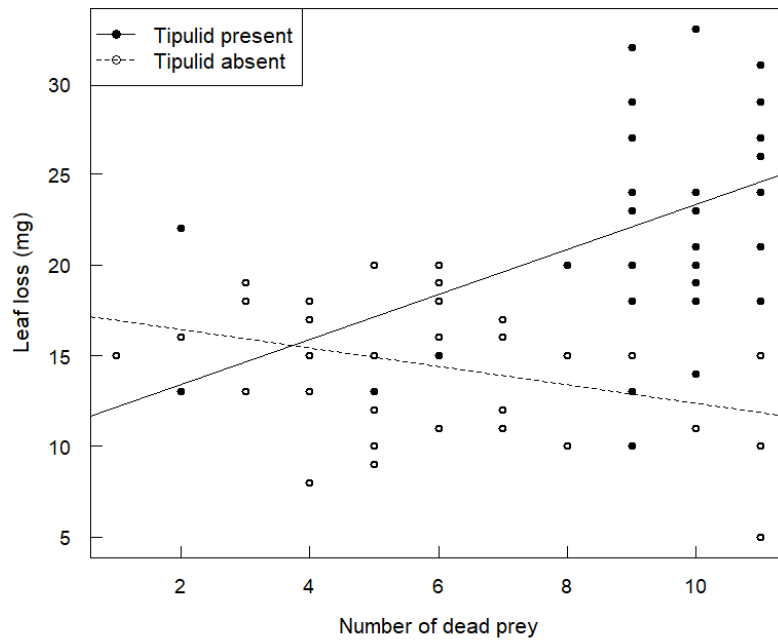


D.2 EVIDENCE OF SUPPLEMENTARY PREY CONSUMPTION BY TIPULIDS

To test whether tipulid predation in our experiment was supplementary or compensatory to leaf processing, we examined the relationship of leaf loss to prey deaths. Unfortunately, we do not know what number of prey died from tipulid consumption vs. other causes like drought, so we performed a multiple linear regression where we predicted decomposition rates (as leaf loss) from prey mortality (as number of dead prey), tipulid presence or absence, and their interaction. To account for prey deaths from the drought treatment, we included drought length as a covariate in the model.

Both tipulid presence and the interaction of prey mortality with tipulid presence significantly affected decomposition rates (Tipulid treatment: $F_1 = 18.8$, $p < 0.001$; interaction of prey mortality with Tipulid treatment: $F_1 = 12.5$, $p = 0.001$), while prey mortality and drought length had no significant effects on decomposition rates ($R^2 = 0.49$). When tipulids were absent, prey mortality had negative effects on decomposition rates (Figure D.2), presumably because there were less detritivores (i.e., chironomids) left to consume detritus. When tipulids were present, decomposition rates increased with increasing prey mortality, suggesting that those tipulids that exhibit high predation rates are also consuming a lot of detritus. These results support a supplementary rather than a compensatory role of predation with decomposition by tipulids.

Figure D. 2: Leaf loss increases with prey mortality in communities with tipulids, but not in communities without tipulids.



D.3 TREATMENT EFFECTS ON PREY EMERGENCES

Prey emergence rates were not affected by the Origin→Location treatment or its interaction with tipulids or drought (Table D.1, Figure D.3), indicating that neither the space-for-time nor the common garden treatment affected prey emergence rates. However, the effects of drought on prey emergence rates depended on tipulid presence (Table D.1: T x D, Figure D.4). While prey emergence rates decreased as drought length increased in the absence of tipulids, emergence rates were generally low and independent of drought length in the presence of tipulids, likely because the adverse effects of tipulids on prey survival (see main document) resulted in fewer individuals available to emerge. Chironomids drove this result, as mosquito emergence rates during the experiment were insignificant (1.7 % of the mosquitoes and 14.1 % of the chironomids emerged over the timeframe of the experiment).

Table D. 1: ANOVA results for insect emergence rates (total prey and chironomids) from linear models. Model predictors are O→L = Origin→Location treatment (MV→MV, MV→UGA, or UGA→UGA), T = Tipulid treatment (present or absent), and D = Drought length. Because of few mosquito emergences, an analysis on mosquitoes was not possible.

Emergences	O→L		T		D		O→L x T		O→L x D		T x D	
	F ₂	P	F ₁	P	F ₁	P	F ₂	P	F ₂	P	F ₁	P
Total Prey	2.71	0.074	21.03	<0.001	11.32	0.001	0.09	0.916	1.18	0.314	5.86	0.018
Chironomids	2.88	0.064	22.30	<0.001	4.77	0.033	0.09	0.911	0.16	0.854	7.13	0.010
Mosquitoes	--	--	--	--	--	--	--	--	--	--	--	--

Figure D. 3: Effects of drought length, Origin→Location (O→L) treatment, and tipulid presence on the emergence rates of (a) total prey, (b) chironimids, and (c) mosquitoes. Experimental location represents current (MV) and future (UGA) climate. O→L treatments are indicated by color. Blue: MV→MV, green: MV→UGA, red: UGA→UGA. Tipulid treatment is indicated by solid circles and lines (tipulid present) versus empty circles and dashed lines (tipulid absent).

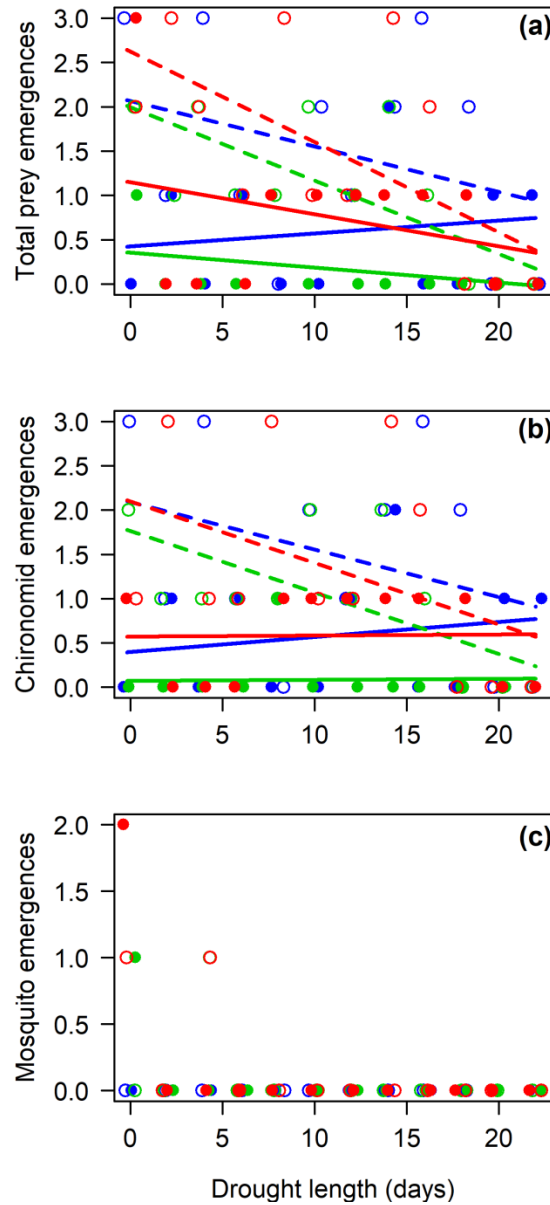
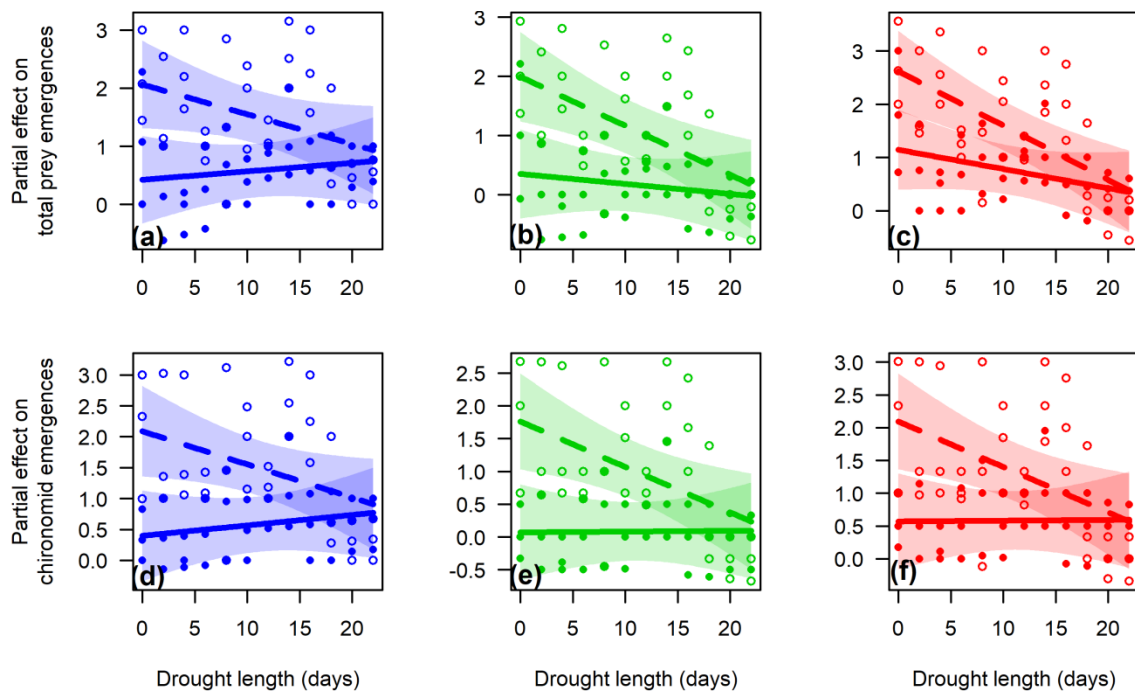


Figure D. 4: Partial residuals showing effect of tipulid treatment on (a-c) total prey emergences and (d-f) chironomid emergences for each community treatment. Blue: MV→MV, green: MV→UGA, red: UGA→UGA. Tipulid treatment is indicated by solid circles and lines (tipulid present) versus empty circles and dashed lines (tipulid absent).



D.4 HEAT TOLERANCE (CT_{MAX}) OF TIPULIDS ORIGINATING FROM MV AND UGA

We experimentally determined the heat tolerance of tipulids originating from MV ($n = 10$) and UGA ($n = 10$) as their critical thermal maximum (CT_{max}). Tipulids were collected from bromeliads near MV and UGA between September and November 2015, and individually placed in a temperature controlled water bath that was heated at a rate of ~ 0.27 °C per minute. When tipulids ceased to move in response to a tactile stimulus, the temperature was recorded as CT_{max} .

The mean CT_{max} of tipulids originating from MV (40.75 °C \pm 0.50 °C SE) was ~ 3 °C lower than the mean CT_{max} of tipulids originating from UGA (43.50 °C \pm 0.60 °C SE; $F = 12.46$, $p = 0.002$; Figure D.5), which corresponds to the actual temperature difference between the two sites.

Figure D. 5: Heat tolerance (CT_{max}) of tipulids originating from MV (n = 10) and UGA (n = 10).

