

**THE INFLUENCE OF SPATIAL PROCESSES AT MULTIPLE SCALES ON LOCAL  
COMMUNITY STRUCTURE AND FUNCTION**

by

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## **ABSTRACT**

Spatial patterns, at multiple scales, can influence the functioning of local communities, but studies of community interactions are often conducted at a local scale. To investigate how spatial complexity at local, regional, and geographic scales influences a local aquatic macroinvertebrate community, I designed experiments using the natural mesocosm of bromeliad phytotelmata, quantifying community structure (functional diversity and trophic structure) and function (decomposition) of an entire food web in Puerto Rico, Costa Rica, and Brazil. At the local scale I studied the effects of habitat patch size on trophic structure and decomposition rates at all three sites. The relationship between decomposition and bromeliad size varied by site. In Costa Rica, size-sensitive top predators drove strong top-down control of leaf decomposition in larger bromeliads causing a negative relationship between decomposition and bromeliad size. In Puerto Rico this relationship was positive, as the lack of a large top predator allowed reduced top-down control in larger bromeliads. In Brazil, climatic conditions potentially shifted decomposition processes to microbial control, and no relationship between bromeliad size and decomposition rate existed. At the regional scale, by enclosing varying numbers of bromeliads I determined how functional traits of species determined extinctions within the metacommunity. Small metacommunities became less diverse and local extinctions were more stochastic than in large ones. Large-bodied predators and invertebrates requiring resources in the terrestrial matrix were most sensitive to metacommunity size. At the geographic scale, I combined experimental replicates in each site and community-analogues in common sites to identify mechanisms of context-dependency of community structure and function relationships among study sites. Top-down control of detritivore communities by predators was influenced by geographic differences in species traits, whereas cascading effects of predators on decomposition were influenced by

geographic variation in environmental conditions. With these studies I was able to identify relationships between community functions and spatial processes operating at a hierarchy of spatial scales. I identified how biogeographical shifts in climate and large-scale connectivity among study sites can influence traits in the species pool which can affect both metacommunity dynamics and sensitivity of species to local extinctions due to habitat patch size.

## **PREFACE**

All chapters of this work are original works by R.M. LeCraw. Chapter 2 is a literature review with co-author P. Kratina currently submitted for publication and in review. The original idea and structure of the paper was developed and written by R.M.L with subsequent suggestions and additions to the manuscript on theoretical stability by P. Kratina. Chapter 3 is currently submitted for publication and in review co-authored with D.S. Srivastava. Chapter 4 is currently submitted for publication and in review with co-authors D.S. Srivastava and G.Q. Romero. The experimental design of all data chapters (3, 4 & 5) was developed by R.M.L in conjunction with supervisor D.S. Srivastava. All data were collected by R.M.L except for invertebrate surveys in chapter 3 – Puerto Rico surveys were conducted by M.J. Richardson and B.A. Richardson, Costa Rica surveys were conducted by D.S. Srivastava and J. Petermann, and Brazil surveys were conducted by D.S. Srivastava and G.Q. Romero. Data analysis for all chapters was performed by R.M.L.

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## 1. GENERAL INTRODUCTION

In the field of community ecology, questions regarding the assemblage and interactions among populations of species in a given area are fundamental to understanding of how ecosystems function. It is becoming clear, however, that we cannot understand the mechanisms and predict the interactions occurring in a community without understanding its spatial context. Historically, a strong focus has been on how aspects of local and landscape scales, from fragment size and isolation to the arrangement of habitats in a large-scale matrix, affect community structure in terms of biodiversity (MacArthur and Wilson 1967, Addicott et al. 1987, Stendera et al. 2012, Chase and Knight 2013). More recently, however, attention has shifted to theoretical studies of how spatial aspects of habitat affect more ecologically relevant aspects of community such as trophic interactions (Amarasekare 2008, Holt 2009, Ljungberg et al. 2013), ecological functions (Massol et al. 2011) and functional diversity (Tschamntke et al. 2012). Empirical studies have also uncovered patterns of how ecological functions in natural communities are influenced by their spatial arrangement at several spatial scales (e.g. Starzomski and Srivastava 2007, Jamoneau et al. 2012, McCall and Pennings 2012).

However, despite evidence that communities are influenced by patterns and processes operating at multiple spatial scales (Ricklefs and Schluter 1993), experiments spanning these scales are rare. Hierarchical studies on commonly studied systems and communities are still needed to understand the results of local community experiments, and how they may vary in the context of their local, regional, and geographic habitat arrangement.

Experimental studies of community interactions, especially in common model systems such as freshwater ponds and phytotelmata, are often conducted at a local scale, however

communities are affected by processes operating at many spatial scales from local to regional (Ibanez et al. 2013). Spatial aspects of the local habitat can include characteristics of a given patch (a contiguous area of a single type of environment with defined edges) such as its size and shape (Krawchuk and Taylor 2003) which influence processes such as colonization, competition, and local extinction. At the regional scale, habitats can be arranged in metacommunities: groups of habitat patches connected by dispersal of interacting species. Spatial aspects of the metacommunity can include the number of habitat patches (Bonsall et al. 2002), connections among patches (Chisholm et al. 2011), and surrounding types of habitat (Watling et al. 2011). All of these can influence species persistence within metacommunities and species turnover within patches. At a large geographic scale, the same type of community can be affected differently by regional characteristics such as climate (Pennings and Silliman 2005, McCall and Pennings 2012), and historical colonization and migration (Kitching 2001). By determining the processes operating on particular types of communities at different spatial scales, synthesis across studies can be made and general patterns identified across a wider geographic scale.

Studying community interactions in a system that can be manipulated at the local and regional scale, and occurs over a large geographic range, will demonstrate which spatial scales affect the community structure and function, and how these scales may interact. The aquatic community in water filled bromeliads is an ideal system for this investigation. Bromeliads form a natural aquatic mesocosm in which leaf axils collect rainwater and fallen leaf litter that forms the basal resource for a food web of bacteria, fungi, and macroinvertebrates. The macroinvertebrate species include those with simple life cycles completed within the bromeliad, and complex life cycles – insects that emerge as terrestrial adults and disperse to other

bromeliads. Insect larvae include many functional groups including different types of detritivores, filter feeders of the water column, and predators. This food web allows for studies of many types of interactions within the community including resource use, competition, predation, and the consequences of dispersal. A common theme in my experiments is the role of top-down control, defined as the impact of an upper trophic level on the behaviour or biomass of lower trophic levels. In the case of the bromeliad system, top-down control is expressed as variation in leaf litter decomposition resulting from the presence of macroinvertebrate detritivore species and predators.

There have been criticisms of using mesocosms as model systems, which need to be addressed at this point. The generally smaller size of these model systems may make them more susceptible to the disturbances that tend to be tested on them. Likewise, the short generation times of species inhabiting these systems and the inability of most species to move away from the disturbance (for instance, in an isolated mesocosm patch) may also amplify the effects of disturbances. However, while used as model systems, bromeliads are in fact natural ecosystems and any general principles being tested should, by definition, be applicable to them as well (Srivastava et al. 2004). These very properties of being small, isolated, and with species of short generation time, may in fact allow us to identify community responses not observable in larger ecosystems (Srivastava et al. 2004).

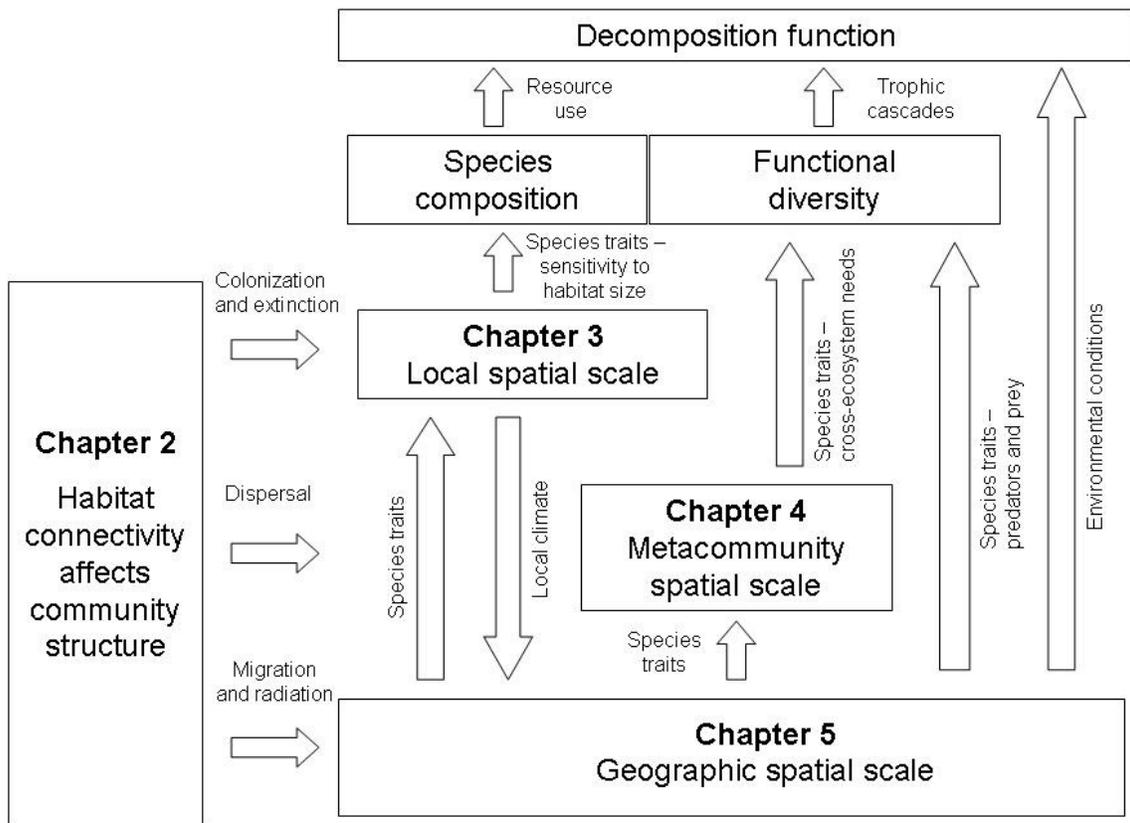
Bromeliads themselves vary in several spatial characteristics. Individual plants display a wide range of sizes from a water-holding capacity of a few millilitres up to more than three litres. They also vary in their connections to surrounding habitat patches; in some environments they grow as solitary epiphytes or in small clumps, whereas in others they grow in a dense ground cover of thousands of plants per patch. Bromeliads also have a large geographic range

covering all of the neotropics from Florida to Argentina, and a variety of ecosystems from dry coastal sand dunes to montane rainforest. Across this range, there are differences in the bromeliad-dwelling species pool, which has been attributed to differences in island size and isolation (Richardson 1999), and proximity to the geographic centre of bromeliad radiation (Givnish et al. 2011). Among the sites I studied, the species pool is highest in Brazil and includes novel functional groups such as a species of case-building caddisfly. Costa Rica, which is separated from the centre of bromeliad radiation and the Brazilian species pool by the barrier of the Andes, has a smaller species pool, lacking caddisflies. Puerto Rico, being an island, is the most isolated site and has the smallest species pool lacking not only the caddisflies, but also top predator taxa present in the other sites. These spatial patterns in the bromeliad system allow us to identify how patterns in community interactions vary with spatial context across a range of spatial scales.

I used the bromeliad system in the El Yunque National Forest in Puerto Rico, the Area de Conservación Guanacaste in Costa Rica, and Parque Estadual Ilha do Cardoso in Brazil, to answer questions of community ecology in three spatial contexts. As the bromeliad system forms natural metacommunities in which connectivity between patches is one of the main influences of community dynamics, I begin with a review of theoretical and empirical patterns of how connectivity affects the complexity (link density and connectance) and stability (persistence of trophic levels) of food webs. Following this are three studies using local experiments and replication across geographic sites to address the following questions:

- 1) How are macroinvertebrate community structure and leaf litter decomposition affected by individual patch size?
- 2) How are the richness of functional groups and community trophic structure at the patch level affected by the size (number of patches) of the surrounding metacommunity?
- 3) How are the effects of predation on prey communities and litter decomposition affected by the geographic location of the experiment?

A concept map in Figure 1.1 illustrates how the literature review and three experimental studies relate to each other. Mechanisms linking habitat connectivity with community structure can operate at all three spatial scales (Chapter 2), including long distance migration determining geographic species pools, dispersal among patches determining metacommunity diversity, and extinctions within a patch determining local trophic structure. The three experimental chapters (Chapters 3,4,5) each show how these community structuring processes influence species composition and trophic structure, and in turn, decomposition function. In turn, processes at different spatial scales interact to shape community structure; the species pool and environmental processes at the geographic scale (Chapter 5) determines the sensitivity of the community to local habitat size (Chapter 3), and metacommunity and cross-ecosystem dynamics (Chapter 4) based on species traits. The relationships among the results of these chapters are discussed in the general conclusions (Chapter 6).



**Figure 1.1.** Concept map of relationships among thesis chapters. Habitat connectivity (left box) is related to community composition at each spatial scale (lower three boxes), determining overall community composition and decomposition (upper boxes). Arrows indicate mechanisms relating community structure and decomposition function.

## Study Sites

**Parque Estadual Ilha do Cardoso, São Paulo, Brazil.** Ilha do Cardoso is located at 25°00'S, 47°55'W in southern São Paulo state, Brazil. The field site is located on the coast at an elevation of 8 m asl in restinga forest (coastal sand dune) with closed canopy approximately 10 m high. Temperature ranges from 10-39°C, averaging 29°C in the warmest quarter (December to February), and rain fall averages 2000 mm per year falling mostly between December and April. The primary ground-dwelling bromeliad species in the restinga is *Quesnelia arvensis* (Vellozo Mez.), which was used for all experiments. This site has the highest diversity of bromeliad-dwelling invertebrate species of the three field sites, containing at least 53 detritivore species and 40 predatory species (D.S. Srivastava and G.Q. Romero, unpubl. data).



**Figure 1.2.** Restinga forest in Parque Estadual Ilha do Cardoso, São Paulo, Brazil

**Area de Conservación Guanacaste (Pitilla sector), Costa Rica.** The field station is located in northwestern Costa Rica at 10°59'N, 85°26'W, at an elevation of 700 m asl in secondary montane rainforest. Temperature ranges from 13-35°C with an average of 23°C and rainfall is approximately 4000 mm per year, falling mostly between May and February. The most common bromeliad species growing in this area that were used for experiments include *Vriesea sanguinolenta* (Linden ex Cogn. & Marchal), *V. gladifolia* (H. Wendl.), *Guzmania sherzeriana* (Mez.), *G. desautelsii* (L.B. Smith & R.W. Read), and *G. donnell-smithii* (Mez ex Donnell Smith). This site is intermediate in invertebrate diversity with a species pool of at least 32 detritivore species and 8 predatory species (D.S. Srivastava, unpubl. data).



**Figure 1.3** Montane rainforest in Area de Conservación Guanacaste, Costa Rica

**El Yunque National Forest, Puerto Rico.** El Yunque National forest is located within the Caribbean National Forest at 18.3°N, 65.5°W. The forest is classified as montane rainforest, and experimental sites were in the tabonuco forest type at 365 m asl under closed canopy. Temperature in the tabonuco forest ranges from 16-33°C, averaging 28°C in the warmest quarter, and rainfall averages 3000 mm per year. There are several species of bromeliads in the forest in the genera *Guzmania*, *Vriesea*, and *Tillandsia*. *Guzmania lingulata* (L. Mez.) and *Guzmania berteriona* (Schultes f. Mez.) were used for all experiments. This site has the lowest diversity of the three field sites with a species pool of at least 20 detritivore species and 8 predatory species (M.J. Richardson and B.A. Richardson, unpubl. data).



**Figure 1.4.** Bromeliads in montane rainforest in El Yunque Forest, Puerto Rico



**Figure 1.5** Map of study sites (red circles denote site)

## **2. FOOD WEB COMPLEXITY AND STABILITY ACROSS GRADIENTS OF HABITAT CONNECTIVITY**

### **INTRODUCTION**

Connectivity within ecosystems determines the movement and dispersal of species, which are key processes contributing to community structure and maintaining ecological function. Ongoing and accelerating environmental changes such as deforestation, urbanization, drought, and climate warming all fragment natural habitats, and limit the ability of species to move among patches (Prugh et al. 2008). Recent research has begun to unravel how reduced habitat connectivity alters not only the species richness, but also the structure of entire food webs (Watling and Donnelly 2006, Pillai et al. 2011, Perdomo et al. 2012). This connection between spatial and trophic ecology, in terms of how individuals move among habitat patches and interact within patches, can advance our understanding of community responses to habitat fragmentation.

The earliest theory regarding how the spatial arrangement of habitat influences ecological communities was the theory of island biogeography, in which the size and isolation of an island affects the processes of colonization and extinction (MacArthur and Wilson 1967). Following that, another significant spatial theory was the development of a metacommunity framework which places more emphasis on species interactions within patches (Leibold et al. 2004). Recent models create a more complete picture of between- and within-patch dynamics (Holt and Hoopes 2005) by integrating more details about habitat patch arrangement and types of species interactions to uncover general rules for shaping food web structure and dynamics in metacommunities (Gravel et al. 2011, Pillai et al. 2011). While many attributes of food webs

can potentially be affected by habitat connectivity (e.g., keystone species effects, predator:prey ratios), this synthesis focuses on two related and intensively studied aspects of community structure: food web complexity, referring to the number and saturation of trophic links (link density and connectance, respectively), and stability, referring primarily to persistence time of populations. These properties were chosen because they have been most commonly related to habitat connectivity in the literature.

Two rigorous reviews (Amarasekare 2008, Holt 2009) have identified the mechanisms by which movements among patches can affect community complexity and persistence. Amarasekare reviews how the persistence (determined by extinctions) and diversity (determined by coexistence) of food webs can be affected by food web complexity, and the type of movement displayed (Amarasekare 2008). Holt begins with the Theory of Island Biogeography and explores how spatial and trophic processes were implicitly related in that monograph. The historical discussion is followed by exploring how those relationships have been explored more contemporarily in theory, including the development of a model of top-down and bottom-up processes on an island in the context of island biogeography (Holt 2009). Our synthesis expands on those reviews to draw general predictions from the theoretical literature and examines the links between theory and empirical evidence.

Although empirical work is lagging behind the theory, it is now beginning to test the new predictions of how food web complexity and stability respond to habitat fragmentation. While a great deal of empirical research has explored the relationship between habitat connectivity and species richness (Fahrig 2003), relatively few studies have incorporated the effects of connectivity on trophic interactions and their consequences. Trophic interactions characterise the food web structure that may result from trait-mediated differences in species

responses to habitat fragmentation (Ewers and Didham 2006). For example, a bias toward smaller body size resulting from greater extinction risk of apex predators may skew the community structure in isolated patches (Shulman and Chase 2007) and thus reduce the complexity of trophic links, affecting the food web stability. Thus, predicting the effects of habitat fragmentation on community structure and dynamics requires a synthesis of island biogeography, metacommunity theory, and food web ecology.

Here, I present the emerging patterns of spatial-food web ecology by bringing together the theory and empirical findings of the relationship between habitat connectivity, food web complexity, and food web stability. Food web complexity can include omnivory, branching links between a resource and multiple consumers, link density, and connectance. Similarly, food web stability is a broadly defined term that refers to both the outcome of internal community dynamics as well as the responses of food webs to perturbations (Grimm and Wissel 1997, McCann 2000, Ives and Carpenter 2007). I specifically focus on persistence, a commonly used concept often defined by the time to extinction. Because of the emerging nature of the connectivity literature assessing the effects of habitat connectivity on food web structure and function, there are still limited studies explicitly examining these relationships. To examine a broad foundation of papers, I have included studies directly testing the relationships among connectivity, complexity, and stability as well as those that can imply these relationships indirectly from their results. I conclude the synthesis by identifying the future steps for advancing the field of spatial food web ecology and conservation of fragmented ecosystems.

## **Habitat connectivity**

The ecological concept of connectivity has two main components: habitat connectivity, or connectedness, and functional connectivity. Habitat connectivity refers to the spatial connections among habitat patches, while functional connectivity describes processes through which sub-populations are combined into a single demographic unit by dispersal success (Tischendorf and Fahrig 2000, Opermanis et al. 2012). Alternatively, connectivity can be defined as the ability of species to move among patches (Moilanen and Nieminen 2002), mediated through different aspects of the landscape: the size and distance among habitat patches (MacArthur and Wilson 1967, Moilanen and Nieminen 2002, Chase et al. 2010), or the presence of a corridor between patches (Paillex et al. 2007, Matter et al. 2009, Staddon et al. 2010). In fragmented landscapes, the structure of patch edges can also influence the movement of species into the patch (Cadenasso and Pickett 2001). The different edge structure may modify resource availability among patches with repercussions for the entire food web (Weathers et al. 2001, Wimp et al. 2011).

Movement of individuals and species can occur over different temporal and spatial scales. Large biogeographic regions can be connected through infrequent long-distance dispersal over many generations, while local habitats can be connected over shorter time periods through frequent colonization and migration events (MacArthur and Wilson 1967, Lookingbill et al. 2010). Because of the difficulties created by synthesizing studies with different methods of quantifying habitat connectivity, here I understand ‘connectivity’ as a qualitative concept incorporating the number of patches available for dispersal, the connectedness of those patches, and the functional connectivity determined by dispersal success of species (Table 2.1).

While the reduction of connectivity has been shown to have negative impacts on several aspects of biotic communities, species' ability to disperse to other patches may attenuate those effects (Fischer and Lindenmayer 2007). The rate at which dispersal or colonization occurs relative to demographic processes within a patch impacts local food web structure, and different frameworks have been used to describe this gradient. When patches are highly connected so that dispersal occurs on a timescale faster than local demographics, community structure may be strongly influenced by immigration/emigration from outside the patch. For example, dispersal on a timescale of foraging behaviour allows apex consumers to link the dynamics of patches through "spatial coupling" (McCann et al. 2005). When dispersal is sufficient within a generation, "sink" populations can be stabilized through "mass effects", or the colonization of individuals from stable populations in connected patches (Leibold et al. 2004). As dispersal becomes less frequent, local demographics become more important than colonization resulting in a "patch dynamics" paradigm in which community structure is determined by local birth and death rates, supplemented by infrequent immigration and emigration (Leibold et al. 2004). To relate connectivity and dispersal for the purpose of this synthesis, in cases where the degree of connectivity is not explicitly stated, we assume that the rate of dispersal is positively correlated to the connectivity among habitat patches.

As patches become more connected, dispersal rates of species can vary among trophic levels. Most of the studies in this synthesis assumed predators to be larger and more mobile than prey species. Thus as patches become more connected, dispersal of predators at a foraging or demographic timescale is predicted to increase first, followed by increased dispersal of prey (e.g. Rooney et al. 2008). This assumption is violated in several cases however, such as when parasitoids are the top trophic level.

Connectivity at a landscape level is important among patches of a similar habitat type, as well as among disparate habitats. For example, the movement of organisms and energy between aquatic and terrestrial habitats can have profound effects on food web structure (Polis et al. 2004, Greig et al. 2012). Likewise, organisms have different abilities to move through different environments in the ‘matrix’ between habitat patches, and this can determine the effective connectivity of patches (Ricketts 2001). Furthermore, the movement rates of nutrients, sediments, or organic detritus can also vary as a function of connectivity. Although I focus mostly on the dispersal of organisms among similar patches, this additional aspect of connectivity is discussed in the final sections of the synthesis.

**Table 2.1** Definitions of terms commonly used in synthesis

	<b>Term</b>	<b>Definition</b>	<b>References</b>
<b>CONNECTIVITY</b>	Connectivity	The degree to which organisms move among patches as mediated by the number of available patches, patch connectedness, and dispersal success.	Moilanen & Neiminen, 2002 Opermanis et al., 2012 Tischendorf & Fahrig, 2000
	Movement	Migration of individuals in and out of patches at a short time scale, such as foraging behaviour. Movement can result in spatial habitat coupling and mass effects (see previous section).	Leibold et al., 2004 McCann et al., 2005
	Dispersal	One-way migration of individuals from one breeding site to another. Dispersal results in mass effects and patch dynamics (see previous section).	Lincoln et al., 1998 Leibold et al., 2004
<b>COMPLEXITY</b>	Connectance	The proportion of all possible trophic links that actually occur in a food web.	May, 1973 Pimm et al., 1991
	Linkage Density	The mean number of trophic links per species.	Pimm et al. 1991
	Branching Links	The number of “forks” in a food web diagram for which a single resource supports multiple consumers.	Pillai et al., 2011
<b>STABILITY</b>	Equilibrium Resilience	The return time of population or community biomass to a stable equilibrium following a small perturbation.	May, 1973
	Persistence	Long-term survival of all species in a food web, characterized by minimum population densities or biomass bounds greater than zero; i.e. time before any interacting focal species goes locally extinct.	Bonsall et al., 2002
	Variability	The degree of variance of population size or biomass, or community biomass over time or space, often measured as coefficient of variation (CV).	Howeth & Leibold, 2010

## **FOOD WEB COMPLEXITY**

Food web complexity encompasses several concepts such as connectance (DeAngelis 1975), linkage density (Pimm et al. 1991), degree of omnivory (Pimm and Lawton 1978), and number of branching links (Pillai et al. 2011). Its usefulness for characterising food web structure and its debated relationship with stability has made food web complexity the focus of much recent work (e.g. Calcagno et al. 2011, Gonzalez et al. 2011, Pillai et al. 2011).

Predictions about complexity, including connectance and link density in relation to habitat connectivity are becoming more common in an effort to model more diverse natural food webs (Pillai et al. 2011).

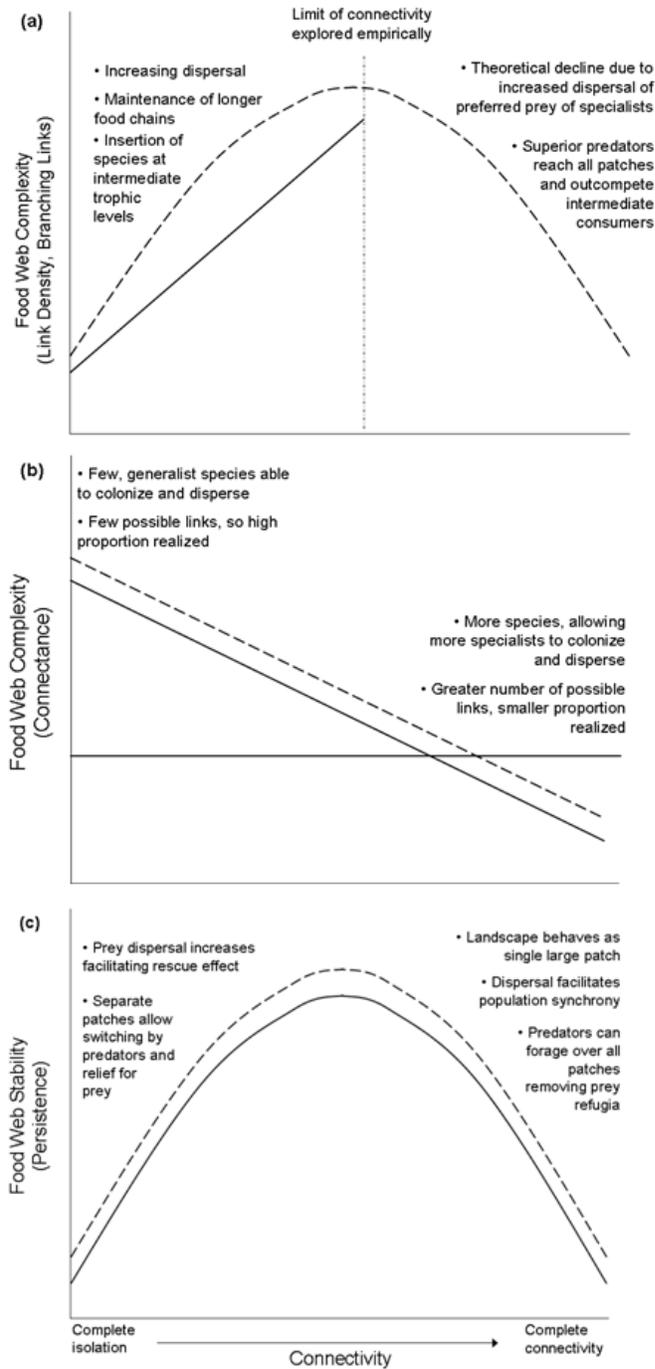
While many metrics fall into the broad category of “complexity”, they may measure different properties of food webs (Dunne et al. 2002). For example, link density meaning the average number of links per species; and connectance meaning the proportion of all possible links realized in a food web (May 1973). These two metrics have historically been predicted to show different relationships with food web size. Link density has been predicted to increase with number of species but connectance has been predicted to be constant regardless of food web size (Warren 1994). These relationships have been further discussed since then, resulting in predictions of decreasing connectance with increased food web size (Banasek-Richter et al. 2009) and elongated food chains (Vermaat et al. 2009). Connectance can also be influenced by foraging behaviour of individuals and overall diet breadth in the food web (Beckerman et al. 2006). Another recently developed metric of complexity is the number of branching links (i.e., “forks” in a food chain diagram), that quantifies how many consumers can be supported by a common resource (Pillai et al. 2011). With this variation in definitions of complexity, it is

challenging to draw general conclusions about complexity and connectivity, and each metric should be considered individually.

These metrics are useful to describe the stability and structure of natural food webs. While there is a considerable body of literature focusing on the relationship between complexity and stability, theoretical studies are just beginning to generate first testable predictions about the underlying consequences of habitat connectivity via species colonization and dispersal.

### **Theoretical relationships between connectivity and food web complexity**

Few theoretical studies have modeled trophic link complexity along a gradient of habitat connectivity. A recent search for a unifying theory of food web complexity in a metacommunity context analyzed the number of branching links, omnivory, and generalism of consumers in response to species colonization and dispersal (Pillai et al. 2011). The model outcomes showed that the complexity of the regional food web is maximized at intermediate dispersal rates (Table 2.2, Fig. 2.1a). Food chain length and branching links, generated by omnivory within patches and generalists feeding across patches, initially increased with species dispersal rates. However, at very high dispersal the number of branching links declined because a consumer's preferred prey would colonize all patches and thus feeding specialization of the consumer increased. In addition, at high levels of dispersal superior predators can exploit prey in all patches, but at intermediate levels of dispersal, inferior predators persist in patches where superior predators have not colonized (Pillai et al. 2011).



**Figure 2.1.** Conceptual diagrams of general theoretical (dashed lines) and empirical (solid lines) patterns between patch connectivity and food web properties: (a) Link density, (b) Connectance, and (c) Stability (persistence). Mechanisms for unimodal (a,c), and declining (b) patterns are outlined. Both declining and constant patterns of connectance have been found and are represented by two solid lines.

Connectance, on the other hand, has been shown to increase monotonically with declining habitat connectivity (Table 2.2, Fig. 2.1b). In a model of realistic mutualistic networks, specialists with few linkages were the first to be lost with destruction of habitat patches and the generalists with the greatest number of linkages persisted longest (Fortuna and Bascompte 2006). The authors suggest that surviving generalists may form a dense core of interacting species that are robust to habitat loss. If this is the case, extinction of specialist species may reduce the number of possible links while maintaining a large number of realized links in the generalist core and thereby maintaining or increasing connectance (Fortuna and Bascompte 2006). The few theoretical studies that have explicitly tested the effect of patch connectivity on food web complexity leave many opportunities to derive predictions from new theoretical models.

**Table 2.2.** Theoretical studies predicting the relationship between food web properties and habitat connectivity

<b>Food Web property</b>	<b>Unimodal</b>	<b>positive</b>	<b>Negative</b>	<b>None</b>
<b>Complexity</b>	<b>Branching links</b> Pillai et al. 2011		<b>Connectance</b> Fortuna & Bascompte 2006	
<b>Stability</b>	<b>Persistence</b> Bonsall et al. 2002 McCann et al. 2005 Wilson et al. 1998 Hassell et al. 1991 Loreau et al. 2003a	<b>Persistence</b> Jansen 1995		

### **Empirical studies of connectivity and food web complexity**

Empirical studies explicitly testing the effect of habitat connectivity on food web complexity are scarce, and results vary across the individual metrics used. Metrics of

complexity that increase with the number of trophic links, such as link density, tend to have a positive relationship with habitat connectivity (Fig. 2.1a, Table 2.3). For instance, the link density was significantly higher in highly connected herbivore-parasitoid food webs in oak tree patches than in food webs with low connectivity (Murakami et al. 2008). Likewise, more feeding links were possible in river channels of intermediate connectivity to the main channel due to the higher number of intermediate predator species (Roach et al. 2009). The authors suggest this increased the food chain length in intermediate channels and likely resulted in greater linkage density than in main or isolated channels across the river system.

Connectance is a metric of complexity measured as the ratio of feeding links in the food web ( $L$ ) to the total number of possible links ( $P$ ). As such, connectance ( $L/P$ ) can increase with both an increase in actual feeding links among species, but also with an overall decrease in the number of possible links or the size of the overall food web. Empirical results show both decreasing and unchanged connectance with increasing connectivity (Fig. 2.1b, Table 2.3). Connectance was enhanced in small plant-herbivore-parasitoid food webs with fewer trophic links in forest fragments as compared with contiguous forest habitat (Valladares et al. 2012). Similarly, connectance was found to decrease with increasing colonization over time, in a reanalysis of the island colonization experiment of Simberloff and Wilson (1969, 1970) by Piechnik et al. (2008). Connectance decreased with time of colonization because specialists colonized later in the process (Piechnik et al. 2008); it has similarly been suggested that specialists will colonize more readily with greater patch connectivity (Fortuna and Bascompte 2006, Pillai et al. 2011). However, there was no correlation between connectance and distance to the nearest source of dispersal (Piechnik et al. 2008), and this supports the traditional theory of constant connectance (Warren 1994). Similarly, connectance did not change with increasing

habitat connectivity in host-parasitoid food webs in oak stands, despite an increase in link density (Murakami et al. 2008, Kaartinen and Roslin 2011).

Achieving maximum connectivity treatments (i.e. patches of the same type of habitat are contiguous with no discernable separation) has proven to be logistically challenging in the field. Only one of the studies above assessed a full connectivity treatment in the form of contiguous forest, but did not measure a gradient of connectivity beyond ‘fragmented’ or ‘unfragmented’ (Valladares et al. 2012). The other studies relied on distance among patches as a gradient of connectivity (Simberloff and Wilson 1969, Murakami et al. 2008, Kaartinen and Roslin 2011), however full connectivity could not be tested because individual trees and islands always had some level of isolation. Since the full gradient of connectivity has yet to be tested empirically, it is possible that the monotonically increasing pattern of linkage density found in natural systems to date represents only the increasing portion of the predicted unimodal relationship (Fig. 2.1a). If more empirical studies are able to test the full range of habitat connectivity, from isolated to completely connected, we may yet observe decreasing linkage densities at the highest levels of connectivity. The relationship between connectance and habitat connectivity remains to be clarified, as some studies support the theoretically predicted decrease with increasing connectivity, while others support constant connectance among food webs (Fig. 2.1b).

**Table 2.3.** Empirical studies supporting different possible relationships between food web properties and habitat connectivity

Food Web Property		Unimodal	Positive	Negative	None
Complexity	Linkage Complexity		<b>Link density</b> Murakami et al. 2008 Roach et al. 2009	<b>Connectance</b> Valladares et al. 2012	<b>Connectance</b> Murakami et al. 2008 Kaartinen & Roslin 2011 Piechnik et al. 2008
		Stability	Persistence/ Variability	<b>Persistence</b> Huffaker 1958 Holyoak 2000a; b Bonsall et al. 2002; 2005 Vogwill et al. 2009	
<b>Variability (prey)</b> Howeth & Leibold 2010*					

\*This unimodal pattern for prey was reversed from most other studies; lowest stability at intermediate connectivity

## FOOD WEB STABILITY

Stability is a multifaceted aspect of food webs that includes resistance and resilience to environmental perturbations, the occurrence of stable point equilibria, variability, alternative attractors, limit cycles and chaos (McCann 2000, Ives and Carpenter 2007). Early research used mainly the equilibrium approach that measured the rate and return time of population density to its previous state after a small perturbation (May 1973, Pimm 1982). Temporal variability is a commonly used metric often approximated by the dispersion of population or community biomass around the arithmetic mean (Howeth and Leibold 2010). More recent theory and much of the empirical research has focused on persistence, or time to extinction, characterized by the distance of the minimal population densities from zero (Bonsall et al. 2002). In this synthesis I

refer to persistence as the length of time all interacting focal species survive before local extinction.

A large body of research has investigated the relationship between stability and food web complexity. Based on limited evidence, stability was historically predicted to increase with increasing diversity of resources and number of trophic links (Elton 1927, MacArthur 1955). However, the mathematical models of randomly assembled food webs generated a negative relationship between stability and food web complexity (Gardner and Ashby 1970, May 1973). It was demonstrated later that stability of model food webs can increase with complexity when interactions among species are predominantly weak (McCann et al. 1998), as is the case in many natural systems (e.g. Wootton 1997). Connectance of food webs also has a strong influence on stability in that the removal of highly connected ‘node’ species can reduce the robustness of the food web to subsequent extinctions more than the loss of species with fewer interactions and lower connectance (Dunne et al. 2002). How this relationship between food web stability and complexity is affected by habitat connectivity and species dispersal is much less understood. In particular, empirical studies that explicitly test the links between habitat connectivity and stability are lagging behind the theory (McCann et al. 2005, Holt 2009, Vogwill et al. 2009).

### **Theoretical relationships between connectivity and food web stability**

Most theoretical models analyzed to date have predicted increased stability at an intermediate level of habitat connectivity (Fig. 2.1c, Table 2.2). The proposed landscape theory of food web architecture (Rooney et al. 2008) posits that food webs are stabilized by the opposing forces of relatively isolated low trophic levels with low dispersal ability promoting spatial asynchrony, and mobile top predators coupling patches by moving from areas of low to

high resources. Intermediate trophic levels create variation in the rates of energy transfer between patches, allowing adaptation to disturbance (Rooney et al. 2008). Models that formalized these patterns show how variation in dispersal among trophic levels at intermediate levels of connectivity stabilizes food webs.

Early models predicted that dispersal between two patches allows food web persistence where isolated food webs inevitably go extinct (Jansen 1995). Later work expanded on the simple two-patch system in more complex spatial arrangements. In lattice-type models, a network of patches is connected through dispersal ranging from local (to neighbouring patches only) to global (dispersal equally likely to all patches). The persistence time of predators and prey in the models allowing only local dispersal, was found to be greater than in the models with global dispersal (Bonsall et al. 2002). Hassell et al. (1991) also found that persistence of a model host-parasitoid system increased with increasing lattice size, but that patchiness of the parasitoid maintained by local (rather than global) dispersal was necessary for stable dynamics. This indicates that intermediate connectivity facilitates the greatest persistence of simple food webs. This pattern may result from different mechanisms including spatial coupling by predators (McCann et al. 2005), rescue effects of prey (Wilson et al. 1998), and maintaining asynchronous dynamics among patches (Gouhier et al. 2010).

The dispersal ability of predators can increase or decrease stability through spatial coupling. When habitat patches are connected by a mobile predator, the resources within patches are more likely to persist due to relief of top-down pressure caused by predator switching to another patch (McCann et al. 2005). However, when increased connectivity allows predators to forage easily among patches over a shorter time scale, variability in populations increases because the landscape behaves as a single continuous patch (McCann et al. 2005).

Apparent competition resulting from spatial coupling, where mobile predators are sustained by prey in one patch while overexploiting prey in another patch, can also reduce stability (Holt and Lawton 1994). Thus, some level of connectivity allowing predators to switch foraging patches along with some isolation preventing global dispersal and maintaining heterogeneity among patches seems to be necessary for stable food webs (Briggs and Hoopes 2004).

Dispersal of prey can also stabilize food webs through rescue effects. This effect sustains sink populations through immigration from source patches (Wilson et al. 1998, Holyoak 2000). However, a rescue effect relies on spatial variation in predation or environmental disturbance to ensure a stable population from which the immigrants originate. This asynchrony in populations is maintained by limiting dispersal among patches (Liebhold et al. 2004). Since dispersal is predicted to both stabilize food webs in a metacommunity through repeated immigration, and destabilize food webs through increased synchrony between patches (Abbott 2011), the processes require further scrutiny.

Some isolation of patches maintaining asynchrony of population dynamics is a key characteristic of stable metacommunities. The degree of asynchrony can explain variation in the connectivity-stability relationship among types of food web networks (Amarasekare 2008) and environmental perturbations (Gouhier et al. 2010). In simple exploitative or apparent competition modules (Holt 1997), it is predicted that high connectivity increases synchrony among patches and reduces stability. However, in more complex networks such as intraguild predation or tritrophic food chains, the relationship depends upon the trophic level with greater dispersal. If upper trophic levels have high dispersal, synchrony is increased through shared predation, and stability reduced with connectivity. If lower trophic levels have high dispersal, inferior competitors with greater resistance to predation may decrease synchrony between

patches and thereby increase stability (Amarasekare 2008). Population asynchrony among patches can also determine stability in response to environmental disturbance. When high dispersal facilitates population synchrony, weak environmental disturbance can be stabilizing by creating more asynchrony among patches. Conversely, when low dispersal maintains asynchrony weak disturbance can be destabilizing by inducing synchrony in population responses to the disturbance (Gouhier et al. 2010).

Theory generally predicts that stability is maximized at intermediate levels of connectivity. Some connectivity allows repeated immigration of individuals from successful populations resulting in a rescue effect that would not be possible in isolated habitats. However, at very high levels of connectivity, spatial coupling of patches by predators reduces stability and persistence through apparent competition, and increased synchrony of patch dynamics precludes the possibility of a rescue effect (Fig. 2.1c).

### **Empirical studies of connectivity and food web stability**

The predictions of greatest persistence at intermediate levels of habitat connectivity are supported by the few empirical studies conducted to date (Fig. 2.1c, Table 2.3). These studies have been restricted to laboratory microcosms testing the effects of patch connectivity and spatial arrangement on persistence of predators and prey. In the seminal work by Huffaker (1958), the interaction between a single predator and single prey species was maintained longest in a landscape of intermediate connectivity composed of many patches with some physical barriers creating prey refugia. Other experiments have shown that predators and prey are able to persist longer in metacommunities with more patches (Holyoak 2000, Bonsall et al. 2002) and with more connections among patches (Holyoak 2000). However, in highly connected patches that could be considered a single homogenous habitat, persistence of predators and prey was

reduced due to synchrony of population dynamics (Holyoak 2000, Bonsall et al. 2002, Bonsall et al. 2005, Vogwill et al. 2009).

The importance of asynchrony among patches for maintaining stability of metacommunities has been supported by several empirical studies. Connected microcosms with ciliate prey and predators have shown greater asynchrony when patches were isolated by greater distance or reduced dispersal (Holyoak 2000, Vasseur and Fox 2009) resulting in longer predator persistence (Holyoak 2000). Likewise, in microcosms with a beetle host and wasp parasitoid, persistence of both species increased with the number of available patches. However, persistence time more than doubled in the largest metacommunity with limited dispersal compared to the same size metacommunity with unlimited dispersal (Bonsall et al. 2002). It was also found that predators enhance the positive effect of dispersal on synchrony among patches (Vasseur and Fox 2009, Vogwill et al. 2009). In at least one experiment the synchronizing effect of predators reduced stability with increased dispersal, whereas in the absence of predators, dispersal increased stability by compensating for stochastic fluctuations (Vogwill et al. 2009).

Experiments in larger aquatic mesocosms showed strong effects of dispersal rates on spatial and temporal ecosystem stability, measured as low temporal variability (coefficient of variation) in community biomass (Howeth and Leibold 2010). Low dispersal increased spatial variability of producer biomass, reduced temporal variability of ecosystem productivity and had no effect on spatial variability of consumers (Howeth and Leibold 2010). These findings imply that dispersal rates may differentially affect stability across multiple trophic levels and alter temporal dynamics in ecosystem function.

In summary, persistence of food webs in experimental environments increases from single isolated patches to multiple connected patches that allow species immigration to rescue

populations. The persistence decreases as dispersal becomes global in fully connected metacommunities allowing population synchrony (Fig. 2.1c). Experiments in larger mesocosms including more trophic levels suggest potentially variable impact of dispersal across trophic levels, opening a promising venue for future research.

## **FUTURE DIRECTIONS**

### **Linking concepts**

Several areas discussed above require further investigation. In particular, empirical research lags behind theoretical work, leaving many theoretical predictions untested. For example, generalist feeding may facilitate more complex metacommunities since more patches would include suitable prey (Holt 2009, Pillai et al. 2011). This mechanism has been used to partially explain the insensitivity of some experimental food web modules to reductions in connectivity (Schneider et al. 2007). However, the role of feeding generalism in mediating the relationships between food web complexity, stability and habitat connectivity has not been explicitly tested. Furthermore, most of the empirical systems investigating food web complexity to date have not allowed either fully isolated, or fully connected patches, leaving the prediction of maximum complexity at intermediate connectivity largely untested. While large-scale natural systems are irreplaceable in the study of connectivity and complexity, this research field would benefit from complementary use of experimental mesocosms in which the levels of connectivity can be directly and easily manipulated (e.g. Howeth and Leibold 2010).

The key question also arises: how are the three concepts of connectivity, complexity, and stability interconnected? If those concepts are pictured as vertices of a triangle, studies of the relationships between each combination of two vertices are widespread. The dynamics within

the triangle as a whole, however, is a new frontier with few early studies (e.g. Gravel et al. 2011). For example, a large body of literature has explored the relationship between complexity and stability (May 1973, DeAngelis 1975, McCann 2000, Gravel et al. 2011) and our synthesis identifies how both properties are modulated by habitat connectivity. However, novel research needs to explore further how connectivity or fragmentation gradients affect the *relationship* between food web complexity and stability. These types of studies would lend themselves well to mesocosms such as aquatic patches in cattle tanks, in which the initial food web complexity and connectivity of tanks can be manipulated and stability can be observed over time in natural ‘open’ conditions.

### **Metaecosystem connectivity**

Our synthesis has focused on connectivity as the ability of organisms to move across a fragmented ecosystem. However, another important aspect of habitat connectivity is the movement of organisms and energy between different ecosystem types such as aquatic and terrestrial ecosystems. These cross-ecosystem fluxes in a connected landscape, called a metaecosystem, have been well documented in nature (Polis and Hurd 1995, Rose and Polis 1998, Willson et al. 2004), and have inspired novel theoretical work on the connectivity of metaecosystems and food web structure (Loreau, Mouquet, and Holt 2003, Massol et al. 2011).

The flow of nutrients can, most intuitively, increase the resource base in an unproductive habitat (Huxel et al. 2002, Leroux and Loreau 2008). More than that, cross-ecosystem inputs can support food webs to such an extent that it can even reverse the source-sink dynamics of an ecosystem (Gravel et al. 2010). Combining the movements of materials and organisms can also alter the predictions of traditional patch dynamic theories (Massol et al. 2011). For example,

herbivore movements among metaecosystem patches can result in counterintuitive predictions of consumers maximizing resource productivity as the movement of organisms can increase occupancy of the landscape and allow more efficient use of nutrients as they are transported across ecosystem boundaries (Massol et al. 2011). Cross ecosystem subsidies can also increase the strength of trophic cascades, exemplified in aquatic ecosystems which have been shown to receive the greatest allochthonous inputs and experience the strongest trophic cascades (Leroux and Loreau 2008). Effects of cross ecosystem subsidies, however, can vary based on the recipient habitat, and also the trophic level at which the resource enters the food web (Marczak et al. 2007), suggesting many opportunities for experiments and synthesis to identify general patterns.

Most work in this field has focused on fluxes of nutrients and organic materials. The logical extension is to explore the effects of connectivity within the metaecosystem on complexity and stability of regional food webs and how these relationships shift with multiple global perturbations (Greig et al. 2012). This can be accomplished with manipulative experiments similar to those studying species movements among cells to measure persistence, but also including nutrient or resource subsidy flows. Natural experiments in systems with variation in allochthonous inputs and organism migration may also be possible, for example along river continuums from headwaters to large rivers (Vannote et al. 1980, Fagan 2002)

## **CONCLUSIONS**

Establishing general patterns of community structure and dynamics along a connectivity gradient requires a definition of habitat connectivity in terms of both physical space and species dispersal ability. Incorporating these spatial and trait-based factors that influence connectivity is

critical to understanding the impacts of pervasive habitat fragmentation on community complexity and stability.

Theoretical explorations of both food web complexity and stability often predict a unimodal relationship with connectivity when studies that manipulate patch connectedness and those that manipulate species dispersal ability are considered in tandem (Table 2.2). These findings suggest that strong habitat fragmentation destabilizes food webs, and can result in species extinctions. However, some degree of habitat isolation is beneficial, as it relaxes strong top-down pressure through the creation of refugia for prey, and allows predators to switch among patches.

Outcomes of empirical studies focusing on food web complexity depend on the attributes measured. The number of trophic links per species shows a positive relationship with habitat connectivity while the proportion of all possible links shows a negative relationship (Fig. 2.1a,b, Table 2.3). Experimental tests have not discounted a unimodal relationship yet. Rather, they lack extreme ends of the connectivity gradient to test for the pattern. Species traits such as consumer diet breadth may also mediate the relationship between complexity and connectivity. Due to the multiple prey options and more complex network structure, generalist consumers may be more robust to extinctions following fragmentation than specialists.

There is remarkable agreement between theoretical predictions and empirical evidence in the unimodal relationship between connectivity and stability (Tables 2.2 and 2.3). Low levels of dispersal allowing predator switching among patches and prey rescue effects generate this relationship. This is balanced by sufficient habitat isolation to maintain asynchrony in population dynamics in the face of local disturbances. As recent findings suggest that dynamics at different trophic levels may respond differently to habitat fragmentation, this line of research

promises new insights into our ability to predict the responses of the dynamics of a food web as a whole.

The relationship among connectivity, complexity, and stability is fundamental to an understanding of community responses to changing environments. Ongoing and accelerating fragmentation isolates habitat patches from contiguous landscapes, and also reduces the size and connectivity within naturally patchy environments. In light of the main detected relationships, conservation efforts should focus on preserving large habitat tracts while maintaining the spatial structure necessary for asynchronous population dynamics supporting stability of the food web.

Patterns of complexity and stability in patchy environments need to be incorporated into the next generation of metaecosystem models. These models include fluxes of organisms among ecosystems and energy in an attempt to understand the global implications of habitat fragmentation. Understanding how habitat connectivity modulates the relationship between complexity and stability of food webs is a key future challenge of global change ecology.

### **3. GEOGRAPHIC SHIFTS IN HOW HABITAT SIZE AFFECTS TROPHIC STRUCTURE AND DECOMPOSITION**

#### **INTRODUCTION**

A fundamental attribute of a habitat is its size. Habitat size is known to affect several aspects of ecological communities including the number of species (Preston 1962), the size of populations (Bender et al. 1998), and the trophic structure of the food web (Post et al. 2000). These properties are often measured in aquatic systems (e.g. Post et al. 2000) because features such as lakes, ponds, and phytotelmata have defined edges making their size or volume relatively easy to calculate. The boundaries of terrestrial ecosystems may be more difficult to define, but the principles of habitat size should apply to those with distinct edges.

Such effects of habitat size on community structure may also have consequences for the ecological processes carried out by communities (Wardle et al. 1997), but this is less well established. A number of studies show impacts of fragment size on rates of ecosystem function including parasitism (Fenoglio et al. 2012), herbivory (Valladares et al. 2006), decomposition (Klein 1989), and pollination (Cunningham 2000). However, other studies have found no effect of habitat size on these functions (Donaldson et al. 2002 [pollination], Schnitzler et al. 2011 [herbivory], Coudrain et al. 2013 [parasitism], Neame et al. 2013 [pollination]). There are a number of potential explanations for these mixed results including: (1) differences in the range of habitat sizes examined between studies; (2) differences between study sites or systems in how community structure is affected by habitat size, potentially due to differences in species or species traits among sites; and (3) differences between sites in which components of the system (i.e. microbes, higher trophic levels, abiotic conditions) are the main driver of the function.

The function of leaf litter decomposition is crucial in freshwater aquatic systems for nutrient release and cycling, making it important to understand what influences the rate of this function. The rate of decomposition can be driven by the climatic and chemical characteristics of the habitat (Petersen and Cummins 1974, Sangiorgio et al. 2004, Cusack et al. 2009), the microbial community including bacteria and fungi (Hieber and Gessner 2002), macroinvertebrate detritivores (Graça 2001) and indirect trophic cascades initiated by invertebrate or vertebrate predators (Greig and McIntosh 2006, Lecerf and Richardson 2011). Litter decomposition can also be affected by physical abrasion due to the substrate environment and flow velocity (Fonseca et al. 2013).

Determining the sensitivity of leaf decomposition rates to habitat size depends on identifying the main drivers of decomposition in the system, and the response of those drivers to the size of the habitat. For example, in freshwater aquatic systems, shredder macroinvertebrate species are often the primary drivers of decomposition (Hieber and Gessner 2002), and these can be regulated by large-bodied predators (Williams et al. 2003, Winkelmann et al. 2007). As large-bodied, upper trophic species tend to be more sensitive to habitat size than their prey (Holt et al. 1999, Drakare et al. 2006, Srivastava et al. 2008), decomposition rates in systems that are strongly influenced by the top-down control of predators are expected to respond strongly to habitat size. Thus, in tri-trophic systems we predict that as habitat size increases, predators will become present and more abundant, reduce the abundance of decomposer species and reduce the rates of ecosystem function (Sangiorgio et al. 2010). In systems lacking large-bodied predators, detritivorous macroinvertebrates increase in abundance in larger habitats thereby increasing the rates of ecosystem functions.

The water-filled leaf wells of bromeliads in the neotropics provide a contained aquatic habitat ranging from a capacity of a few millilitres up to more than two litres, in which the effect of habitat size on ecosystem function can be measured. Bromeliads contain a food web based on fallen leaf litter which supports macroinvertebrate detritivores and predators. Insect larvae with a leaf shredding feeding habit, such as crane fly larvae (Diptera: Tipulidae) and caddisfly larvae (Trichoptera: Calamoceratidae) are present in the food web and are often primarily responsible for leaf litter breakdown in freshwater systems (Petersen and Cummins 1974, Merritt and Cummins 1984). The top predators in the bromeliad system are species of damselfly nymphs (Odonata: Zygoptera), which are large-bodied relative to their prey, voracious generalists, can move freely among the leaf phytotelmata in a bromeliad, and have been demonstrated to be sensitive to overall bromeliad size in at least some sites. In Costa Rica, damselfly nymphs show a distinct bromeliad size threshold, below which they will not colonize phytotelmata (Srivastava et al. 2008). Therefore we would expect that as bromeliad size increases, damselflies become more abundant, and reduce prey populations resulting in a larger ratio of predator to prey biomasses. This increase in top-down control is predicted to result in reduced litter decomposition in larger bromeliads.

The geographic range of bromeliads from Florida to Argentina allows us to determine if variation in the published effects of habitat size may be due to differences among study sites. There are many more potential differences among sites than these listed, but of the possible explanations listed above, we were able to examine potentially different responses of the community to bromeliad volume (2) and different drivers of litter decomposition (3). These differences are potential mechanisms explaining different relationships between habitat size (bromeliad volume) and ecosystem function (decomposition rate) among sites. We were able to

control for the possibility of different size ranges causing conflicting results in the literature (1) by using a similar known range of bromeliad sizes (up to 23-fold) in each country. The wide geographic range of our study system also encompasses a range of characteristics in the predator community, in which we can test the prediction of stronger top-down control by predators and reduced decomposition in larger habitats. On Ilha do Cardoso, Brazil, the diverse community supports four species of predatory damselfly, while in Guanacaste, Costa Rica there is a single species of bromeliad dwelling damselfly, and bromeliads in Puerto Rico lack any large-bodied predators.

We used survey data of food webs in each of these sites to determine how trophic structure varies with bromeliad size, and used litter bags over a range of bromeliad sizes to measure rates of decomposition. We predict that damselflies in Brazil and Costa Rica will drive increases in the ratio of predator to prey biomass and decreases in decomposition with increasing bromeliad size, but that the relationship will be less evident in Puerto Rico where the large-bodied predator is absent.

## **METHODS**

Experiments were conducted in El Yunque National Forest in Puerto Rico in February 2012, in Guanacaste, Costa Rica in October of 2002 and 2012, and on Ilha do Cardoso, Brazil in April 2011.

In each field site at least 27 bromeliads representing the natural size range, measured as the maximum water holding capacity in mL of the bromeliad were selected. Capacity of bromeliads was estimated *in situ* by measuring the maximum width and height of the plant, and

the number and basal width of leaves and converting to capacity using previously-established allometric equations:

- Brazil:  $n = 53$ ,  $R^2 = 0.87$ ,  $\text{Ln}(\text{capacity in mL}) = -3.27 + 0.74(\text{Ln}(\text{max plant width in cm})) + 0.01(\text{leaf width at base in cm}) + 1.40(\text{Ln}(\text{number of leaves}))$ , (R.M. LeCraw)
- Costa Rica:  $n = 52$ ,  $R^2 = 0.91$ ,  $\text{Ln}(\text{capacity in mL}) = -1.12 + 0.08(\text{number of leaves}) + 0.52(\text{leaf width at base in cm}) + 0.01(\text{max plant width in cm})$ , (D.S. Srivastava)
- Puerto Rico:  $n = 21$ ,  $R^2 = 0.92$ ,  $\text{Ln}(\text{capacity in mL}) = -3.07 + 2.72 (\text{Ln}(\text{number of leaves})) + 1.03 (\text{Ln}(\text{max plant width in m}))$ , (B.A. Richardson and M.J. Richardson)

Bromeliad capacity ranged from 81 to 1836 mL in Brazil (40 bromeliads), 9 to 2841 mL in Costa Rica (40 bromeliads in 2002 and 27 bromeliads in 2012), and 19 mL to 540 mL in Puerto Rico (30 bromeliads). All bromeliads were undisturbed at the time of the experiment.

Two leaf packs were submerged in leaf wells of each bromeliad for 30 days to measure the rate of decomposition, measured as mass of leaf litter lost. Leaf packs were 3 cm x 3 cm, and constructed of 2 mm diameter mesh. Leaf packs contained 200 mg (+/- 25%) dry mass of leaf fragments that had been collected as fresh leaves and oven dried to constant mass. In Costa Rica in 2002 leaf packs contained only 100 mg dry mass of leaf fragments. Leaf fragments were rehydrated for 24 hours before being placed in leaf packs. Using a common species of leaf litter in all sites was not logistically feasible, and would not have represented the natural resource base in each site, therefore leaf species were chosen to be representative litter appropriate to the site. Leaf species were selected based on three criteria: they were abundant in the study site, naturally found in bromeliads, and rapidly decomposed in bromeliads as determined by week-long trials in leaf packs before the start of the experiment. Leaf species used were Myrtaceae:

*Psidium cattleianum* Sabine in Brazil, Melastomataceae: *Conostegia xalapensis* Bonpl. in Costa Rica, and Melastomataceae: *Miconia prasina* Sw. in Puerto Rico. While the difference in leaf species was appropriate to best represent conditions at the site, it has the potential to be an environmental cause of differences in decomposition. At the end of the experiment, the remaining leaf fragments in each leaf pack were rinsed and oven dried to constant mass before taking the final mass. Initial and final leaf masses were summed for each pair of leaf packs per bromeliad.

### **Invertebrate community composition surveys**

Patterns of predator:prey biomass ratios across bromeliad size gradients were determined using previously collected data on the capacity and full invertebrate composition of bromeliads in each study site. Several species (most notably damselfly predators) are capable of moving among leaf wells, therefore we treat the complete bromeliad as the habitat patch. Capacity data were collected by rinsing all water, detritus, and invertebrates out of collected bromeliads and directly measuring the maximum volume of water that could be held in the leaf wells.

Invertebrate data were then collected by dismantling the bromeliad and rinsing all material from the leaves, and all individuals visible to the naked eye removed from the rinsed material.

Invertebrates were identified to the lowest possible taxonomic level, and assigned to functional feeding guilds (predators, and detritivores/prey). These macroinvertebrate surveys were conducted in Brazil in 2008 (D.S. Srivastava and G.Q. Romero, unpublished data), in Costa Rica in 1997, 2000, 2002, and 2010 (D.S. Srivastava, unpublished data), and in Puerto Rico in 1993, 1994, 1996, 1997, and 2010 (M.J. Richardson and B.A. Richardson, unpublished data).

## Analysis

Relationships between decomposition rate and bromeliad size were determined using linear regression of log-transformed bromeliad capacity on rate of leaf loss. Regression strengths are reported as adjusted  $R^2$  values, calculated in the `lm` routine in R using Wherry's formula, to account for the number of variables in the model. Decomposition rate is reported as percent of dry leaf mass lost per day. Predator to prey ratios were calculated using dry biomass of each trophic group, determined by converting invertebrate abundances from survey data to biomass using previously determined conversion factors (D.S. Srivastava, M.J. Richardson, and G.Q. Romero, unpublished data). Relationships between predator:prey ratios and bromeliad size were determined using linear regression of  $\ln$  predator:prey ratio on  $\ln$  bromeliad capacity. To better understand the patterns in predator:prey ratios, we also examined how predator and prey biomass individually changed with bromeliad size by using linear regression.

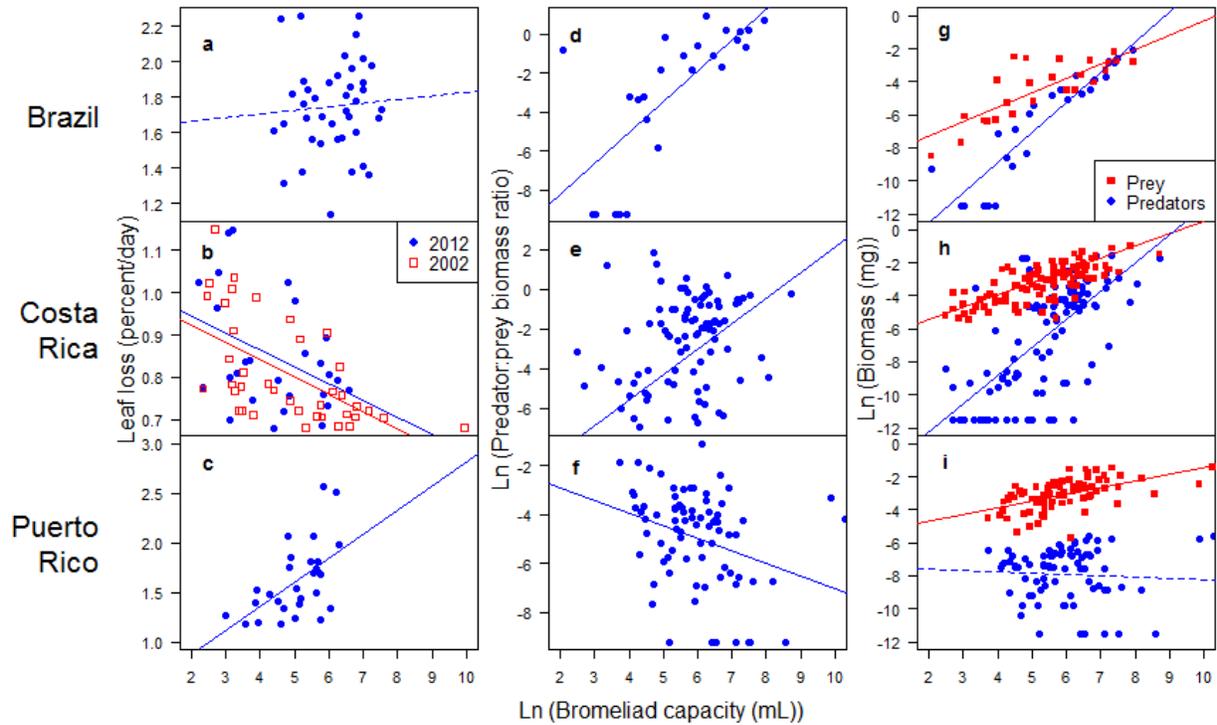
## RESULTS

The relationship between the magnitude of leaf litter loss and bromeliad size differed among the three sites (Fig. 3.1a,b,c). There was no significant relationship in Brazil ( $\text{adj.}R^2 = -0.02$ ,  $p = 0.69$ ), a significant negative relationship in Costa Rica (2002:  $\text{adj.}R^2 = 0.33$ ,  $p < 0.01$  and 2012:  $\text{adj.}R^2 = 0.13$ ,  $p = 0.04$ ), and a significant positive relationship in Puerto Rico ( $\text{adj.}R^2 = 0.28$ ,  $p < 0.01$ ).

The survey data from previous years showed that the relationship between predator:prey biomass ratios and bromeliad size also differed among sites. In Brazil the predator:prey ratio increased with bromeliad size ( $\text{adj.}R^2 = 0.53$ ,  $p < 0.01$ ; Fig. 3.1d), driven by a steep increase in predator biomass with bromeliad size ( $\text{adj.}R^2 = 0.83$ ,  $p < 0.01$ ) but a more gradual increase in

prey biomass ( $\text{adj.}R^2 = 0.64$ ,  $p < 0.01$ ; Fig. 3.1g). In Costa Rica the ratio also increased with bromeliad size ( $\text{adj.}R^2 = 0.36$ ,  $p < 0.01$ ; Fig 3.1e) again, driven by a steep increase in predator biomass ( $\text{adj.}R^2 = 0.41$ ,  $p < 0.01$ ) and more gradual increase in prey biomass ( $\text{adj.}R^2 = 0.62$ ,  $p < 0.01$ ; Fig.3.1h) with bromeliad size.

To test the dominance of the damselfly predator in driving this pattern in Costa Rica, we tested the relationship between predator:prey ratio and bromeliad size with all damselflies removed from the macroinvertebrate survey data and found no relationship ( $\text{adj.} R^2 = 0.01$ ,  $p = 0.69$ ). In Puerto Rico the predator:prey ratio decreased significantly with bromeliad size ( $\text{adj.}R^2 = 0.09$ ,  $p < 0.01$ ; Fig.3.1f), with a slight increase in prey biomass with bromeliad size ( $\text{adj.}R^2 = 0.28$ ,  $p < 0.01$ ), but there was no change in predator biomass ( $\text{adj.}R^2 = -0.01$ ,  $p = 0.46$ ; Fig.3.1i).



**Figure 3.1.** Patterns of decomposition and trophic structure over the range of bromeliad sizes. Decomposition (panels a,b,c) is shown as percent of leaf litter lost from leaf packs per day in 2012 with data from the Costa Rica site in 2002 overlaid on panel b in red points. Trophic structure shown as the natural log of the ratio of predator:prey biomass (panels d,e,f), and the natural log of total biomass of predators and prey (panels g,h,i). Trend lines show linear regressions, all of which are significantly different than zero (solid lines) except leaf loss in Brazil, and predator biomass in Puerto Rico (dashed lines).

## DISCUSSION

I found that the relationship between leaf litter decomposition and habitat size differed by study site: decomposition either increased, decreased or remained the same as bromeliad size increased. This variation between sites is unlikely to reflect year to year variation in the local effects of bromeliad size, for the pattern was robust between two experiments in Costa Rica conducted a decade apart. Instead, the bromeliad size-decomposition relationship was related to the trophic structure of the invertebrate community in Puerto Rico and Costa Rica, but not

Brazil. The trends of decomposition decreasing with bromeliad size in Costa Rica, and increasing in Puerto Rico could be explained by the change in predator:prey ratios over the size gradient, as I detail later in the discussion. However, in Brazil, despite an increase in the predator:prey ratio in larger bromeliads, no corresponding change in decomposition rate occurred. This variation in patterns among sites suggests different roles of top-down control of the system in the different communities.

In Costa Rica the rate of decomposition decreased with increasing bromeliad size in both years of the experiment, and survey data confirmed an increase in the predator:prey ratio in larger bromeliads. This is consistent with our prediction of increased top-down control by the size-sensitive damselfly predator. This conclusion is supported in another study of decomposition in springs in which decomposition decreased in larger springs, which corresponded with greater fish biomass and lower macroinvertebrate shredder density (Sangiorgio et al. 2010). From my calculations of predator biomass and bromeliad volume, it is clear that in Costa Rica predator density increased with habitat size. This increase in predator density with habitat size has been previously documented in the analogous system of seasonal forest pools (Pearman 1995, Wilcox 2001, Brooks and Colburn 2012). As the damselfly predator in Costa Rican bromeliads has been demonstrated to significantly reduce detritivore density and, indirectly, leaf decomposition (Srivastava 2006, LeCraw 2013 unpubl. data), the increased predator density resulted in increased top-down control of the ecosystem which reduced decomposition.

In Puerto Rico the opposite pattern to Costa Rica occurred: decomposition increased with bromeliad size. The high decomposition rate in large bromeliads likely reflects diminished top-down control in larger bromeliads, as evidenced by a decline in the predator:prey biomass

ratio as bromeliad size increased – again, opposite to the pattern in Costa Rica. The difference between Costa Rica and Puerto Rico in turn is primarily due to divergence in the response of predators to bromeliad size, potentially because the Puerto Rican predator community lacks damselflies. This result mirrors previously documented trophic patterns in species richness of bromeliad fauna between these two countries, which were shown to be due largely to avoidance of small bromeliads by the damselfly *Mecistogaster modesta* Selys in Costa Rica (Srivastava et al. 2008). In our study, when we omitted *M. modesta* from the Costa Rican macroinvertebrate survey data, predator:prey ratios were much less sensitive to bromeliad size, which suggests that damselfly presence was also driving differences between Costa Rica and Puerto Rico in biomass-bromeliad size relationships.

In fact, in Puerto Rico predator biomass was even less sensitive than prey biomass to bromeliad size. Body size can be a determinant of sensitivity to habitat size (Drakare et al. 2006), and many of the predatory species in Puerto Rican bromeliads (e.g. the Dipterans Chironomidae: *Monopelopia*, and Ceratopogonidae: *Bezzia*) are smaller than the key detritivores in the system (e.g. Diptera: Tipulidae, and Coleoptera: Scirtidae). This difference in body size may be driving the decrease in predator:prey ratio in larger bromeliads, thereby releasing detritivores from predation and increasing litter decomposition.

In the Brazil site, bromeliad size and decomposition rate were not related, despite an increase in the predator:prey ratio with bromeliad size. Given the presence of multiple predatory damselfly species in the community, we had expected the increase in predator:prey ratio in larger bromeliads to drive stronger top-down control of the detritivore population, thereby reducing decomposition. The lack of a size-related pattern in decomposition rate suggests that

the macroinvertebrate predator-detritivore pathway is not an important determinant of decomposition in Brazil, and that the factors that are responsible are not sensitive to habitat size.

The conclusion that macroinvertebrates are not driving leaf litter decomposition in Brazil is supported by data in chapter 5 of this thesis, showing that despite the presence of a predator-resistant shredder in Brazil (case-building caddisfly larvae) which reduced the impact of predation on detritivore survival, decomposition was unrelated to shredder biomass. Differences in leaf litter quality between the restinga forest in Brazil and the montane rainforest sites in Puerto Rico and Costa Rica may be responsible for the decoupling of patterns in the macroinvertebrate community and decomposition (Garibaldi et al. 2011). The warmer, drier conditions of the restinga result in tougher leaves with a higher lignin content than those in rainforest (Castanho and de Oliveira 2008), qualities which reduce the availability of leaf litter to macroinvertebrate detritivores (Schindler and Gessner 2009, Fernandes et al. 2012). In fact, experiments in chapter 5 show that damselflies at the Brazil site significantly reduce detritivore populations, but have no indirect effect on decomposition.

Despite the lack of macroinvertebrate influence on decomposition, the rate of leaf breakdown was still high relative to the other sites (Fig 3.1a,c. note difference in leaf loss scale), suggesting that rapid microbial decomposition processes may have had a strong influence on decomposition. The stronger influence of bacteria, relative to macroinvertebrates, on decomposition in the Brazilian restinga has recently been supported by experiments in which litter decomposition responded more strongly to the presence/absence of bacteria than of macroinvertebrates (T. Bernabe, pers. comm.). The small size of fungi and bacteria relative to the habitat size of a bromeliad may explain the lack of response in microbial decomposition rates to habitat size. Other studies have shown that microbial composition in restinga bromeliads

is largely constant between bromeliad species differing substantially in size (Haubrich et al. 2009).

In this study I have demonstrated that the rate of decomposition in aquatic bromeliad habitats can vary with habitat size, and that the nature of the relationship depends on the biotic drivers of decomposition. When decomposition is controlled by a top-down trophic cascade originating from a dominant predator, and this predator is sensitive to habitat size, then decomposition decreases in larger bromeliads. In the absence of this size-sensitive top predator, however, weaker top-down control in larger bromeliads results in increased decomposition. When the main driver of decomposition is not the macroinvertebrates but potentially microbial activity, habitat size has no effect on decomposition.

The difference in patterns among sites, while consistent with differences in the species pool, may also be apparent due to the differences in bromeliad sizes among sites. Care was taken to sample bromeliads over the natural range of water-holding bromeliads, however it is clear from the first column of Figure 3.1 that the size range in Brazil lacks the smallest capacities in Costa Rica, and the range in Puerto Rico lacks the largest. By constraining the data to include only the size range common to all sites (between 81 mL and 540 mL), there is still no relationship in Brazil ( $\text{adj.R}^2 = -0.01$ ,  $p = 0.38$ ), the relationship in Costa Rica disappears ( $\text{adj.R}^2 = -0.03$ ,  $p = 0.44$ ), and it is still significant but weaker in Puerto Rico ( $\text{adj.R}^2 = 0.13$ ,  $p = 0.05$ ). While it would be desirable to sample the same size range in all sites, this variation may indicate that the pattern in Costa Rica is most sensitive to the extreme ends of the bromeliad size distribution.

Thus, we have shown that the pattern of habitat size and decomposition – even in the same general study system - differed by study site, which may explain some of the contradictory

evidence for these relationships in the literature. Geographic variation in decomposition-bromeliad size relationships was due both to biogeographic changes in species traits (especially covariance between sensitivity to habitat size and trophic position, as exemplified by the Costa Rican damselfly species), as well as bioclimatic changes in the relative importance of microbial and macroinvertebrate decomposition (especially as these two parts of the food web likely differed in terms of sensitivity to bromeliad size). The role of differences in the chemical composition of leaf litter among sites in driving these differences in microbial activity would be interesting to investigate in future studies, potentially through the use of common leaf species across sites. Understanding these mechanisms driving context-dependence in habitat size-ecosystem function relationships will allow the synthesis of a broader range of studies in the future.

## **4. METACOMMUNITY SIZE INFLUENCES AQUATIC COMMUNITY COMPOSITION IN A NATURAL MESOCOSM LANDSCAPE**

### **INTRODUCTION**

Dynamics of ecological communities are rarely independent of surrounding communities. Dispersal of species between communities can influence local dynamics, and this group of interconnected communities has been called a metacommunity (Holyoak et al. 2005). Metacommunity theory posits that community composition is influenced by the size and composition of the surrounding metacommunity as well as the ability of organisms to disperse between patches (Holt and Hoopes 2005, Amarasekare 2008). As such, the metacommunity concept can be defined as a set of local communities linked by dispersal (Hanski and Gilpin 1991), where a community is a set of interacting species occupying a particular locality (Holyoak et al. 2005). Thus, removing a locality, or patch, reduces the number of local communities and therefore the size of the metacommunity. Viewing the metacommunity in light of this spatial definition, it is particularly pertinent for predicting how loss of habitat patches may affect the structure and functioning of ecological communities.

Such an application of metacommunity theory, however, requires that the effective size of the metacommunity be measurable (i.e. total number of patches and extent of matrix habitat), and the sensitivity of species behaviour and survival in communities to loss of habitat patches within the metacommunity be predictable. Both of these qualities have proven to be challenging to assess empirically. As experimental reductions in patch number or extent are often not feasible, it is difficult to quantify the sensitivity of local communities and their functioning to reductions in metacommunity size. In addition, since species within communities often differ in

their dispersal abilities and patch size requirements, the net effect of reducing metacommunity size on community structure and function is difficult to assess without full knowledge of the ecological roles and traits of species (De Bie et al. 2012). In this study, I use an experimental approach to assess the influence of metacommunity size and spatial extent on an ecological community, and interpret the results in terms of species traits.

The number of patches in a metacommunity could influence local community richness by providing a greater amount of total habitat in the region, and thus more species and individuals in the regional pool (Preston 1962). In general, greater regional richness can lead to higher local richness when the latter is more influenced by dispersal rates than by interspecific competition for space (Srivastava 1999, Fox and Srivastava 2006). Larger metacommunities are also less likely to experience either patch-level or metacommunity-wide species extinctions, because the number of patch-level populations of each species will, on average, increase proportionally with the number of patches. Larger overall populations increase the likelihood of a stable population in a patch to allow rescue effects via migration to disturbed patches. The number of patches in the metacommunity also creates opportunities for species to coexist at regional scales that otherwise exclude each other at local scales. For example, increasing the number of patches in the metacommunity can allow for the presence of spatial refugia from predators (McCann et al. 2005, Rooney et al. 2008), and spatial insurance (rescue effect) when disturbances are asynchronous among patches (Loreau, Mouquet, and Gonzalez 2003).

Other aspects of community composition in addition to local richness, such as stochasticity in extinction processes, and evenness of species abundances, are expected to be influenced by metacommunity size. Small metacommunities, defined by fewer patches, can show high beta diversity because rescue effects are less likely, and stochastic processes such as

within-patch ecological drift and trait-independent dispersal play a greater role in determining composition (Chase et al. 2009, Fraterrigo et al. 2009, Jamoneau et al. 2012). Even if species have not yet gone extinct in a patch through local drift, effects may be seen in terms of large differences between abundances of species. Thus, we would expect smaller metacommunities to show less even species abundances. As immigration increases (as in larger metacommunities with more source patches), neutral models predict the number of species to increase while the variance among species abundances in the metacommunity decreases (Bell 2000). Therefore both species richness and evenness of abundances are expected to increase in larger metacommunities, even in the absence of species interactions.

Metacommunity theory also makes predictions about the relationship between regional and local dynamics, for example how alpha (local), and gamma (regional) diversity are related and can determine the amount of species turnover, or beta diversity. Measuring responses of local communities both within, and between metacommunities of similar size can inform how these predictions are supported in empirical systems.

Species may be differentially affected by metacommunity size, depending on traits. A larger metacommunity has an overall greater area of habitat, and higher trophic levels are predicted to be more sensitive to habitat area (Holt et al. 1999); a relationship that can sometimes also be explained by body size or regional abundance (Srivastava et al. 2008). Predators may also forage over several patches (McCann et al. 2005, Pillai et al. 2011). Moving freely between patches may allow the landscape to behave as a single patch, so predators may experience a smaller effective metacommunity than lower trophic levels. Indeed reductions in metacommunity size have been shown to affect top trophic levels more than lower trophic

levels, albeit only in models and experimental mesocosms (Wilson et al. 1998, Davies et al. 2000, Staddon et al. 2010).

The dispersal ability of species can also have a large impact on their response to habitat spatial arrangement (Cottenie 2005, Thompson and Townsend 2006). Dispersal mode (passive or active) and the relative abilities of species can alter whether environmental or spatial aspects of the habitat will structure the community (Hajek et al. 2011). Life history theory also predicts that dispersal traits will “trade off” with other traits that influence local coexistence such as in a colonization-competition trade off (Tilman 1994, Calcagno et al. 2006). Certain species traits may delay the apparent effects of reductions in metacommunity size on local persistence of species. For example this would be the case if species have relatively long life cycles or are only indirectly affected (e.g. if predators are affected via change in their prey base). Such a time lag, or “extinction debt” (Janzen 1986, Tilman et al. 1994, Mouquet et al. 2011) will result in certain species appearing to survive habitat reduction in the short term, but ultimately going extinct.

Finally, there is a growing appreciation of the role of the matrix habitat between patches in influencing fragmented communities, as species can vary dramatically in their use of resources or susceptibility to threats in the matrix (Ricketts 2001, Ewers and Didham 2006, Watling et al. 2011). This variation in qualities of the matrix is reflected in the concept of landscape permeability or, conversely, resistance (Castellon and Sieving 2006). Greater landscape permeability results in greater functional connectivity of patches via dispersing individuals (Severns et al. 2013). In freshwater ponds or phytotelmata, for example, species with completely aquatic life cycles coexist with species with complex life cycles that are obligate users of both aquatic patches and the terrestrial matrix between patches (Wilbur 1980, Schreiber and Rudolf 2008). As a result, functional connectivity may differ among functional groups that,

in turn, respond differently to metacommunity fragmentation depending on their needs for dispersal, reproduction or feeding in the terrestrial matrix (Prugh et al. 2008).

Habitat loss in metacommunities may impact species with obligate dispersal (e.g. insects with complex life cycles) more negatively than those with optional dispersal (as in taxa with simple aquatic life cycles) (Pillai et al. 2011). On the other hand, dispersal between bromeliads is faster for insects, which must oviposit each generation, than for invertebrates with simple life cycles, which rely on rare phoretic events to move between bromeliads (Lopez et al. 2005). Therefore insect populations are more likely to be rescued from extinction. The difference in dispersal strategies between obligate dispersers (insects), and non-obligate dispersers (non-insect invertebrates) has potential implications for the predictability of communities of those taxa with metacommunity size. For example, obligate dispersers may homogenize community composition within metacommunities, while non-obligate dispersers may show more stochastic patterns among bromeliads. If this is the case, we would predict beta diversity to be lower in communities of obligate dispersers than in communities of non-obligate dispersers, and for the effect to increase in larger metacommunities.

In this study, we used bromeliads in a Brazilian restinga to create metacommunities of different numbers of patches, using mesh enclosures, holding the volume and density of bromeliads constant. Bromeliads often have water-filled leaf wells, which support a detritus-based aquatic community of macroinvertebrates with both simple and complex life cycles (SLC and CLC, respectively). Adult insects disperse to oviposit in other bromeliads creating a metacommunity of bromeliad patches. We tested the effects of metacommunity size on aquatic invertebrate community composition. We first compared the enclosed bromeliads to unmanipulated bromeliads in the surrounding forest, to determine if bromeliad-dwelling

invertebrates were sensitive to any reduction in metacommunity size. We then examined the effects of metacommunity size within enclosures. Finally, we used a matrix control treatment to determine whether the number of bromeliads or the amount of terrestrial matrix was more important in driving community patterns.

We predict that in smaller metacommunities, species richness will decline due to increased stochastic local extinctions of smaller populations and lack of some limiting resource requirement not met in small enclosures. In general, insects with complex life cycles are predicted to be more sensitive to metacommunity size than fully aquatic taxa, which may be unaffected by enclosures. We predict that the top trophic level (damselflies), and species with specialized adult feeding requirements such as mosquitoes (Culicidae), and frog-feeding midges (Corethrellidae) will be most negatively affected by enclosures due to lack of these specific food resources in the terrestrial matrix of enclosures. We tested these predictions by enclosing bromeliads in metacommunities for at least one generation of all species and then looking for changes in community composition due to metacommunity size. Results will be discussed in terms of species traits, and the implications for ecosystem function will be considered.

## **METHODS**

### **Experimental Design**

The experiment was conducted on Ilha do Cardoso, Brazil. The study site has many thousands of bromeliads growing as ground cover. We examined two scales of reduction in the number of bromeliads. First, we dramatically reduced the number of bromeliads from the full forest metacommunity by enclosing 10 or fewer bromeliads. Second, we performed a more modest reduction in metacommunity size by comparing enclosures with 1, 3 or 10 bromeliads.

Enclosures were constructed of fine netting (500  $\mu$ m mesh diameter) which prevented immigration/emigration of even the smallest insects (Ceratopogonidae midges). Bromeliads in enclosures were kept at a constant, natural density whereby bromeliads were directly adjacent with leaf tips touching, and enclosure sizes were scaled to just enclose the required number of bromeliads: “small” (1 bromeliad, 0.25 sq m), “medium” (3 bromeliads, 1 sq m), and “large” (10 bromeliads, 4 sq m). All enclosures were 1 m high and the bottom edge of the mesh was buried in the soil to a depth of 5 cm to prevent immigration under enclosures. To test the effect of the number of bromeliads versus the matrix area between patches a fourth treatment, “matrix”, was constructed which was equal in size to large enclosures, but contained only 1 bromeliad.

Length of time of enclosures was determined to span at least the life cycle of the longest lived species, *Leptagrion elongatum* Selys, which is estimated to be 12 months based on studies of another bromeliad-dwelling species in the genus (De Marco Junior and Furieri 2000). Thus, ten replicates of each treatment were constructed in February 2011 and were in place for 14 months. Twice monthly, leaf litter collected on top of enclosures was distributed amongst the bromeliads inside the enclosures to maintain a detritus base for insects and bromeliad nutrient uptake, and bromeliads were watered when necessary to prevent drying out. In April 2012 a single representative bromeliad from each enclosure, plus 10 randomly selected unenclosed “full forest” bromeliads, were dismantled and all surviving aquatic invertebrates were identified to morphospecies. These morphospecies were then assigned to 6 functional groups based on direct observation and published literature: damselfly (*Leptagrion elongatum*; top predator), predator (all insect predators excluding damselflies), shredders, scrapers, gatherers (collectively ‘insect detritivores’), and SLC (Oligochaeta and Ostracoda, which have no terrestrial form).

At the end of the enclosure period when bromeliads were sampled, size measurements (height, width, number of leaves) were taken for each bromeliad, enabling us to calculate maximum water-holding capacity of each plant (using the allometric equation for Brazil given in Chapter 3), hereafter referred to as bromeliad size. Dissolved oxygen and pH (2 wells per bromeliad) and water temperature (one well per bromeliad and one adjacent unenclosed bromeliad) were measured to test the effect of enclosures on aquatic environmental conditions.

## **Analysis**

Biomass was calculated for each morphospecies using dry mass from previous survey data (G.Q. Romero, D.S. Srivastava, unpubl. data). Species richness, overall abundance, and overall biomass were compared using ANOVA and Tukey HSD posthoc tests. Abundance and biomass were both log-transformed to improve residual diagnostics. Shannon-Weiner diversity and Pielou's evenness metrics were calculated for each enclosure and tested between treatments using ANOVA and Tukey HSD posthoc tests. To test for effects of patches versus matrix area Shannon-Weiner diversity and Pielou's evenness of the matrix treatment were also compared to the small and large enclosures using ANOVA.

Differences in the overall composition of communities were tested using NMDS ordination and PERMANOVA (adonis function in vegan package in R) (Oksanen et al. 2012) on a Bray-Curtis dissimilarity matrix. PERMANOVA on community composition among treatments was used to test whether (1) community composition differed between bromeliads in enclosed metacommunities (pooled treatments) and the unenclosed full forest, (2) community composition differed based on enclosure size (small versus medium versus large treatments), and (3) community effects were due to number of bromeliads or amount of terrestrial matrix

(small and large treatments versus matrix treatment). Significance levels were adjusted using the Holm correction for multiple-comparisons.

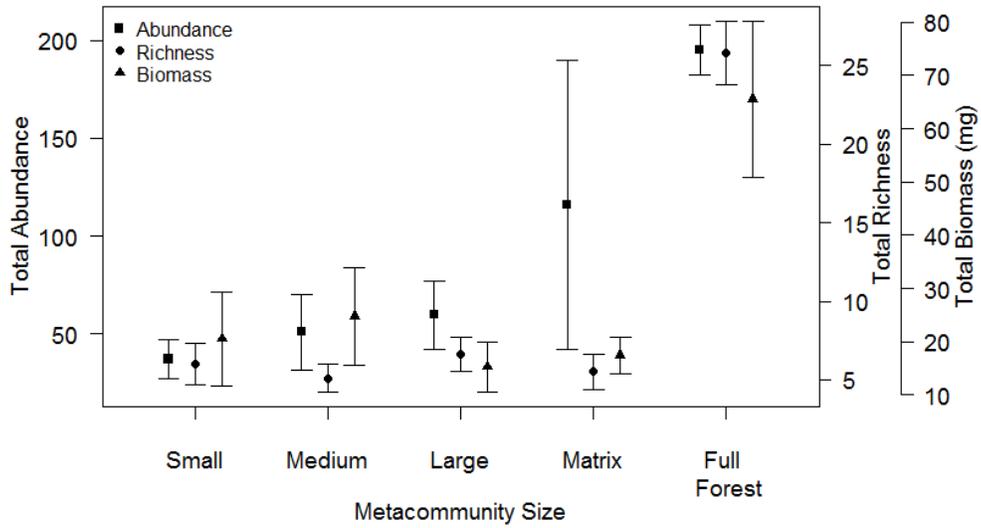
To test for a pattern of increased turnover in community composition we measured beta diversity between metacommunity enclosures as the distance to the group centroid based on dissimilarity coefficients of the communities (betadisper routine in the vegan package for R). Restrictions on feasible sampling effort did not allow us to measure more than one bromeliad per metacommunity enclosure, therefore we were unable to calculate beta diversity within metacommunities, and instead used the dissimilarity between enclosures of the same treatment level as our measure of beta diversity. We compared the effect of enclosure size on beta diversity using ANOVA and Tukey honest significant differences (HSD). To test the effects of species with complex or simple life cycles (CLC and SLC), we repeated the beta diversity analysis on the full community, and on the CLC species community only.

Differences in the abundance and biomass of functional groups were first tested using a linear mixed model with bromeliad identity as a random factor. Pairwise comparisons between treatments for each functional group created immitigable violations of parametric tests, and therefore biomasses were compared using Wilcoxon rank sum tests with Holm adjustment for multiple comparisons, which is slightly less conservative than the Bonferroni correction.

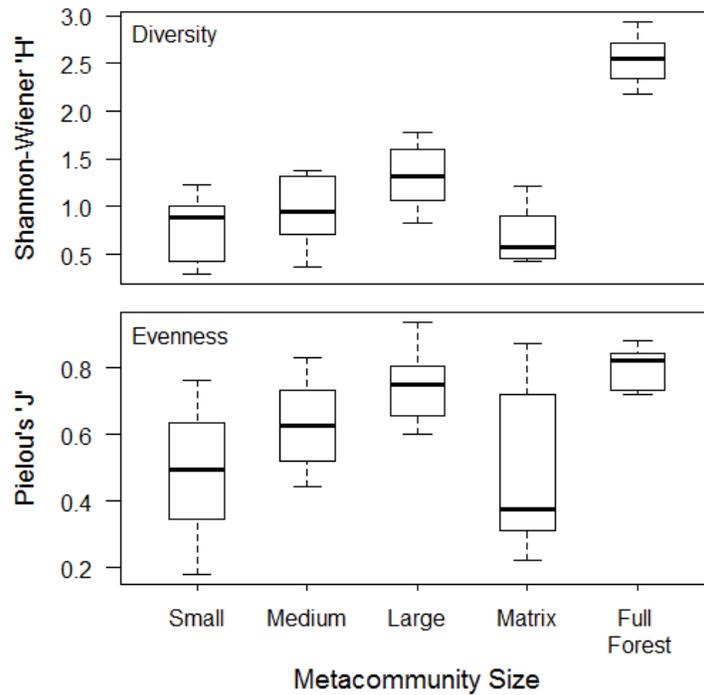
Environmental variables were compared between treatments to test for effects of the enclosures on the aquatic environment. Bromeliad capacity, % O<sub>2</sub> saturation, pH, and temperature difference were tested with ANOVA and Tukey HSD posthoc tests. One low outlier (>2.5 SD from mean) was removed from the pH data to improve residual diagnostics.

## RESULTS

Compared to enclosures, full forest bromeliads had over four times more morphospecies (ANOVA:  $F_{4,44} = 176.41$ ,  $p < 0.0001$ ), almost three times more individuals (ANOVA:  $F_{4,44} = 6.55$ ,  $p = 0.0003$ ), and over three and a half times more biomass (ANOVA:  $F_{4,44} = 11.24$ ,  $p < 0.0001$ ) on average (Fig. 4.1), but none of these metrics were affected by different sizes of enclosed metacommunities (Tukey posthoc:  $p > 0.5$ ). Even our largest enclosures were not large enough to support natural communities. However, Shannon-Weiner diversity ( $H'$ ) and Pielou's evenness ( $J$ ) increased with increasing metacommunity size in enclosures (Fig. 4.2). Both diversity and evenness were significantly greater in large enclosed metacommunities than small (ANOVA, Tukey posthoc:  $p < 0.02$ ), and diversity was consistently lower in enclosures than in full forest bromeliads (ANOVA, Tukey posthoc:  $p < 0.0001$ ). Evenness, however, was similar between bromeliads in large metacommunities and the full forest (ANOVA, Tukey posthoc:  $p = 0.88$ ). Differences in diversity between small and large metacommunities can be attributed more to the number of bromeliads enclosed than the amount of matrix. Specifically, Shannon-Weiner diversity and evenness in matrix treatments did not differ from small enclosures (ANOVA, Tukey posthoc: diversity  $p = 0.88$ , evenness  $p = 0.99$ ), but were significantly different from large enclosed metacommunities (ANOVA, Tukey posthoc: diversity  $p = 0.0007$ , evenness  $p = 0.02$ ).

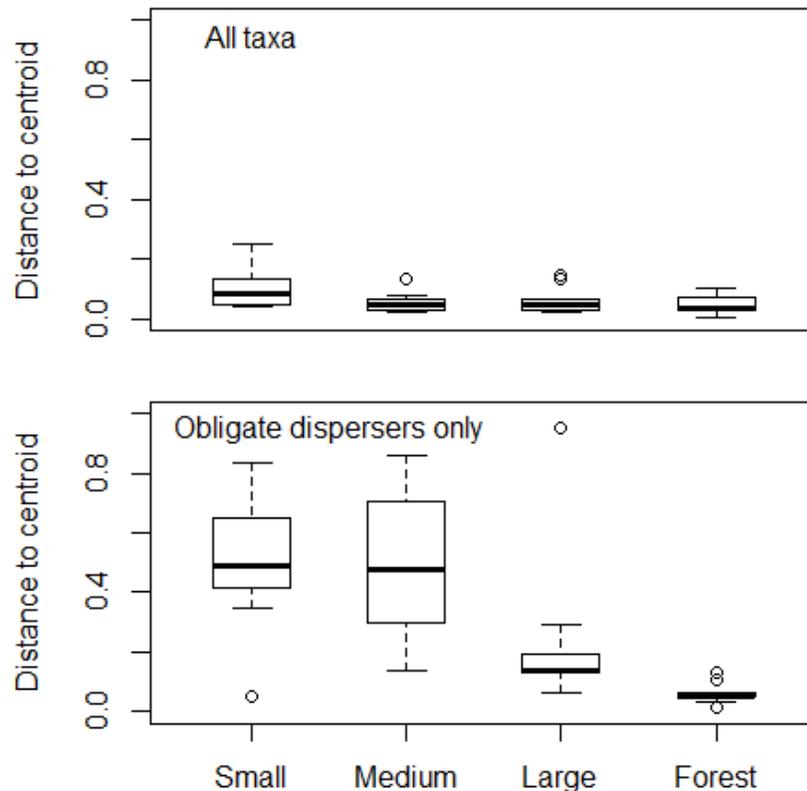


**Figure 4.1.** Overall abundance, richness, and biomass ( $\pm$  95% confidence interval) of all invertebrates per bromeliad in each metacommunity treatment.



**Figure 4.2.** Diversity and evenness of communities in each metacommunity treatment. Boxes represent upper and lower quartiles, and whiskers represent 1.5 x interquartile range.

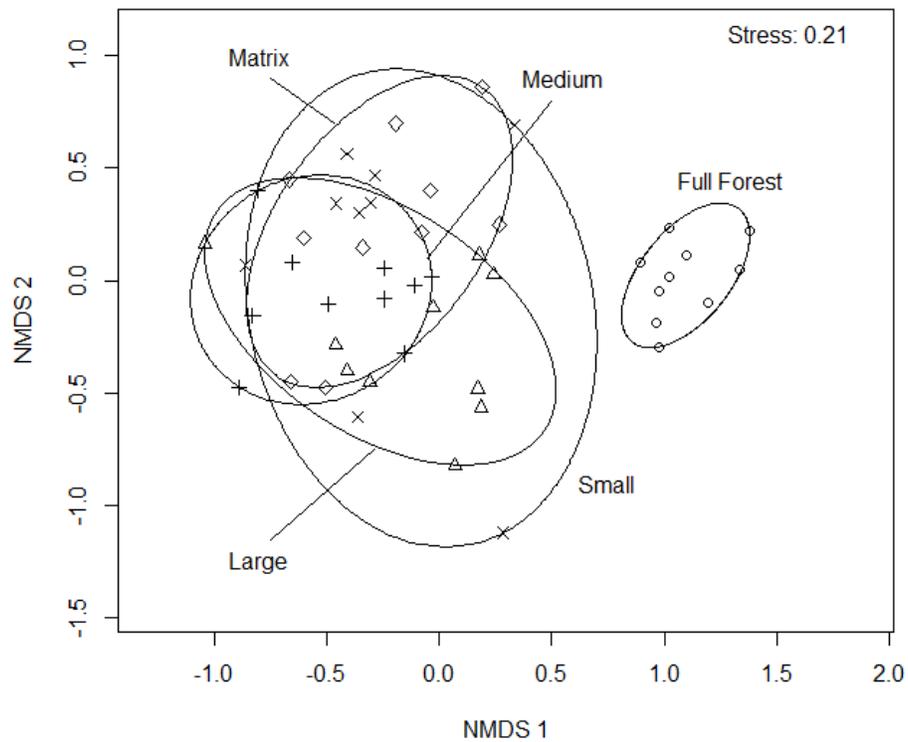
As metacommunity size decreased, so did the predictability of community composition in individual bromeliads. Here we were interested in the degree of divergence between replicate metacommunities, as we examined community turnover between rather than within enclosures. The distance to centroid based on community dissimilarity was marginally significantly greater in small metacommunities than in the unenclosed forest metacommunity (ANOVA  $F_{3,35} = 2.77$ ,  $p = 0.06$ ; Fig. 4.3). When SLC species were removed from the community, beta diversity increased five-fold in small and medium metacommunities, two-fold in large metacommunities, and did not differ in the full forest metacommunity. The difference in beta diversity between small and large metacommunities also became more significant; being significantly greater in small and medium metacommunities than in large and full forest metacommunities (ANOVA  $F_{3,35} = 10.24$ ,  $p < 0.001$ ; Tukey HSD, S vs. L:  $p = 0.03$ , S vs. Forest:  $p < 0.001$ , M vs. L:  $p = 0.04$ , M vs. Forest  $< 0.001$ ; Fig. 4.3).



**Figure 4.3.** Distance to group centroid based on dissimilarity of community data for each metacommunity treatment for the whole community (top panel), and with complex life cycle (CLC) taxa, or obligate dispersers only (bottom panel). Boxes represent upper and lower quartiles, whiskers represent 1.5 x interquartile range, and points represent outliers.

Overall community composition was significantly different in enclosures compared to bromeliads in the full forest (PERMANOVA:  $F_{1,47} = 14.04$ ,  $p = 0.001$ ; Fig. 4.4). Enclosed metacommunity size also had a significant effect on composition; small and large communities were significantly different from each other (PERMANOVA:  $F_{1,17} = 3.27$ , adj.  $p = 0.036$ ), but communities in medium enclosures were intermediate and not different from either small (PERMANOVA:  $F_{1,17} = 1.15$ , adj.  $p = 0.342$ ), or large enclosures (PERMANOVA:  $F_{1,18} = 1.67$ ,

adj.  $p = 0.212$ ). Differences in communities between small and large metacommunities can be attributed to number of bromeliads rather than enclosure size, as communities in the matrix treatment did not differ from those in small enclosures (PERMANOVA:  $F_{1,17} = 0.60$ , adj.  $p = 0.753$ ) but were significantly different from those in large enclosures (PERMANOVA:  $F_{1,18} = 2.81$ , adj.  $p = 0.012$ ).

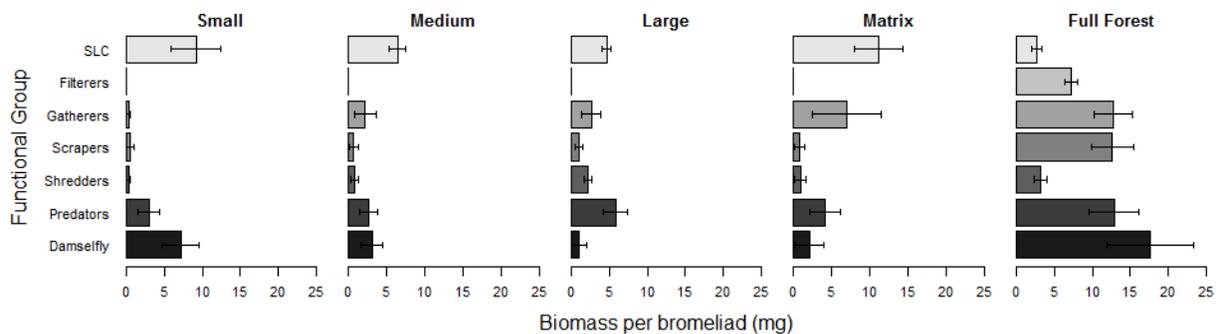


**Figure 4.4.** NMDS plot of invertebrate communities based on a Bray-Curtis dissimilarity matrix of species abundances among all ten replicates of each treatment. Symbols correspond to metacommunity treatments.

Metacommunity size effects on community composition were due to differential responses of functional groups, as evidenced by a significant interaction between metacommunity size and functional group for both abundance (ANOVA:  $F_{1,15} = 8.49$ ,  $p < 0.0001$ ) and biomass (ANOVA:  $F_{1,15} = 5.00$ ,  $p < 0.0001$ ; Fig. 4.5). Damselfly biomass was more

than seven times greater in small enclosed metacommunities than large (Wilcox: 23.5, adj.  $p = 0.07$ ). Biomass of SLC individuals was not significantly different among enclosures, but the mean was almost two times greater in small enclosed metacommunities than large (Wilcox: 34, adj.  $p = 0.40$ ). Conversely, insect detritivore biomass was nearly zero in small enclosures resulting in a predator-heavy community. Insect detritivore biomass tended to increase from small to large metacommunities; large enclosed metacommunities had almost twice the scraper biomass (Wilcox: 52, adj.  $p = 0.46$ ), seven times the shredder biomass (Wilcox: 80.5, adj.  $p = 0.007$ ), and almost ten times the gatherer biomass (Wilcox: 71, adj.  $p = 0.03$ ) compared to small metacommunities. Non-damselfly predator biomass also tended to be greater in large enclosed metacommunities (Wilcox: 57, adj.  $p = 0.34$ ).

Functional groups, however, differed in their response to matrix area or number of bromeliads. Damselfly and gatherer biomass in matrix enclosures was more similar to large metacommunities whereas biomass of SLC taxa was more similar to small metacommunities. Biomass of all other functional groups (predators, shredders, scrapers) in the matrix treatment was intermediate between large and small enclosures (Fig. 4.5).



**Figure 4.5.** Mean biomass per bromeliad of each functional group ( $\pm$  SE) in each metacommunity treatment.

Enclosures had only small effects on environmental conditions in bromeliads. Bromeliad size did not differ between treatments (ANOVA:  $F_{4,44} = 0.85$ ,  $p > 0.5$ ). Water temperature did not differ between bromeliads in enclosures and the full forest (ANOVA:  $F_{4,18} = 0.44$ ,  $p > 0.7$ ). Overall, pH did differ slightly among treatments (ANOVA:  $F_{4,44} = 3.45$ ,  $p = 0.02$ ). All phytotelmata were slightly acidic, and the full forest (mean pH  $\pm$  SE:  $4.76 \pm 0.15$ ) and small ( $4.78 \pm 0.17$ ) metacommunities had marginally higher pH than medium ( $4.32 \pm 0.13$ ) and matrix ( $4.11 \pm 0.21$ ) metacommunities, but pairwise comparisons were not significant (Tukey posthoc:  $0.1 > p > 0.05$ ). Average oxygen saturation in phytotelmata was ~26% lower in full forest bromeliads than in enclosures (Tukey posthoc:  $p < 0.001$ ), but did not differ among enclosed metacommunity sizes (Tukey posthoc:  $p > 0.1$ ). The mesh allowed sufficient light to penetrate to facilitate plant growth over the 14 month period. There was evidence, however, of increased fungal growth on enclosure materials and bromeliads in enclosures, possibly due to increased humidity. One of the single-bromeliad metacommunities did not survive, but there was some additional bromeliad growth in larger enclosures.

## **DISCUSSION**

This study provides evidence from a natural system that isolating smaller metacommunities changes community composition and the relative abundances of functional groups. We demonstrated that metacommunities of even ten bromeliads were unable to support the abundance, species richness and composition typical of bromeliads in the natural metacommunity. This suggests that part of the reason for this site's exceptionally rich bromeliad fauna is the thousands of individual bromeliad plants naturally present in the forest. Reduction

in metacommunity size below ten bromeliads did not further affect species richness and abundance, but still had strong effects on species evenness, predictability and functional group composition. Furthermore, we were able to use species traits and our matrix controls to predict and explain patterns of species extinctions in smaller metacommunities.

The ability to enclose bromeliads in these experimental metacommunities is a valuable tool in ecological research. However, it can also create conditions that have been criticized for resulting in unnatural artefacts of the enclosure, rather than results of ecological interactions (Mac Nally 1997). There is potential for walls of the enclosure to prevent escape of prey and resources which would otherwise emigrate from the area, and thus to artificially intensify resource use in the enclosure (Mac Nally 1997, Mac Nally 2000). These issues need to be considered when interpreting the results from these metacommunity enclosures. However, an isolated metacommunity, by definition, is disconnected from all other patches leaving no option for emigration by species. Based on this concept of isolated metacommunities, enclosures still provide information on how communities will respond to reduction in the number of available patches.

The most surprising result was that total abundance and richness was not affected by the size of enclosed metacommunities, since more connected patches have been shown to support greater species richness in simple models and experimental mesocosms (Bonsall et al. 2002, Staddon et al. 2010, Chisholm et al. 2011). However, the results from the enclosures of our study are similar to one of the few full food-web tests of connectivity. In an oak forest system, in which connectivity was controlled by space between oak trees in a plantation, the food web showed higher complexity (more trophic linkages) in higher connectivity sites, but no difference in abundance or species richness (Murakami et al. 2008). In both our study and the oak forest, it

may be that the range of connectivity is small relative to the natural range, and much larger enclosures in our study system may support intermediate abundances and species richness between the enclosed levels and the full forest.

While overall abundance and species richness did not differ between enclosed metacommunities, smaller metacommunities supported lower diversity, driven by lower evenness in species abundances, which supports our prediction of greater variation among species abundances (Bell 2000). Single-bromeliad communities were often heavily dominated by one species that was often a member of the SLC functional group. Our analysis of dissimilarity between bromeliads within different metacommunity sizes confirms that small metacommunities show greater species turnover, which is an indication of the importance of stochastic processes in community composition (Chase et al. 2009). This supports previous studies showing that stochastic processes are more important in structuring communities in more isolated habitat fragments (Fraterrigo et al. 2009, Jamoneau et al. 2012).

Our beta diversity analysis also demonstrates that the dominance of small metacommunities by SLC taxa actually serves to homogenize the communities. Removing SLC taxa from the community analysis had a greater effect on beta diversity between metacommunities in small treatments than in large. This variation increased the difference in beta diversity among small and large metacommunities, and indicated the importance of SLC taxa survival for maintaining a more homogenous community at lower trophic levels.

While our study focuses on the local aspects of community structure, an important aspect of metacommunity theory is the relationship between local and regional community dynamics, especially partitioning of diversity into alpha, beta, and gamma components. For example, increasing dispersal is predicted to increase alpha (local) diversity, but decrease gamma

(regional) diversity (Hubbell 2001, May et al. 2012). Beta diversity, representing heterogeneity among local communities, also has the potential to differ from within-metacommunity to between-metacommunity scales in the landscape scales (Izsak and Price 2001).

We found evidence for decreasing heterogeneity at two scales: increased evenness of abundances at the within-metacommunity scale, and decreased beta diversity between metacommunities. Due to our sampling constraints, we were unable to calculate beta diversity within metacommunities, but can make some predictions from metacommunity theory. We expect that in larger metacommunities increased area would increase regional or gamma diversity, and our data indicates that within enclosures local (alpha) diversity remained relatively constant. Together these patterns would likely result in increased beta diversity within larger metacommunities (Tuomisto 2010). An interesting extension of this work would be to determine how those opposing forces of increasing within-metacommunity beta diversity and decreasing between-metacommunity beta diversity are balanced.

In the smallest metacommunities, it may seem puzzling that damselfly biomass is fairly dominant in the community. Based on their large body size and high trophic rank, damselfly predators were predicted to be most sensitive to reductions in metacommunity size, and thus to only survive in the largest metacommunities (Cotgreave et al. 1993, Holt et al. 1999, Srivastava et al. 2008). However, the presence of damselflies in small enclosures appears to be a transient effect. All of the *Leptagrion* nymphs found in enclosures were large, late instar nymphs. Small, newly hatched nymphs, found frequently in full forest bromeliads, were absent from all enclosures indicating that *Leptagrion* were not reproducing in enclosures. In this way damselflies represent “the living dead”: hold-overs of long lived, but non-reproducing species in patches in which they will not be replaced when they eventually die (Janzen 1986).

In general, damselflies are known to have a longer larval stage than all other bromeliad-dwelling insects, although the >14 months recorded in this study seems to be exceptional. The decrease in damselfly biomass from small to large enclosures suggests that damselfly larvae have delayed maturation particularly in the small bromeliads, likely due to loss of their prey base as insects with shorter life cycles emerged but did not reproduce in small enclosures (Jimenez-Cortes et al. 2012). The other group surviving well in small enclosures, tiny Ostracoda with simple life cycles, were not often eaten by *Leptagrion* (pers. obs.). In large enclosures, insect detritivore biomass was greater, indicating reproduction in the enclosures and a continued food source for *Leptagrion*. Damselfly nymphs could then mature and emerge normally, at which point they were presumably prevented from reproduction by lack of food or potential mates in the terrestrial matrix.

While life history traits dominated the response of species to reductions in aquatic habitat, effects of the terrestrial matrix may reflect different species traits in the adults such as terrestrial requirements for space, food, and mates (Briers and Gee 2004). For example, mosquito larvae (Diptera: Culicidae), which are among the most abundant species in unenclosed bromeliads, were completely absent from all enclosures, likely due to a lack of vertebrates in enclosures to provide a blood meal for adults to reproduce. Effects of metacommunity size on survival of other detritivore species may be due to adults of certain species requiring fewer terrestrial resources. For example Chironomidae, which have short adult life stages and generally do not feed as adults (Coffman 1984), were found more frequently in enclosures than other insect detritivores, whereas Trichoptera, which spend much longer and may feed as adults (Wiggins 1984), were extremely rare in enclosures.

Within the smaller size range of enclosed metacommunities chironomids were found to respond more to terrestrial matrix space than aquatic patches (Fig. 4.5). Certain chironomid species have been shown not to mate in confined spaces due to lack of space for proper mating swarms (Lloyd et al. 1940, Gibson 1942), and this may be the case in the smaller metacommunity enclosures. It should be noted that due to practical restrictions on the maximum size of enclosures in this study, we can only conclude that terrestrial matrix area is important at the smaller end of potential matrix areas. As terrestrial matrix area increases beyond that studied, it is conceivable that thresholds for various biological processes – such as chironomid swarming or host prevalence – are reached and exceeded. Quantifying such thresholds remains a practical challenge in this system.

The results from the “matrix” enclosures demonstrate that the mechanisms for extinction occurred in both aquatic patches and the terrestrial matrix. The biomass of damselflies was most similar between matrix and large enclosures, indicating a response to the amount of terrestrial space. Since damselflies probably did not reproduce within enclosures, this matrix effect was probably transmitted via the aquatic prey base. Mechanisms in the terrestrial matrix can also include lack of mating space as in the case of chironomids. Biomass of the SLC functional group, with almost no requirements for terrestrial matrix area, was most similar between matrix and small enclosures indicating a response solely to aquatic habitat. We predicted that insects would be more likely to be rescued from extinction due to their dispersal ability, however our results suggest that their reliance on the terrestrial matrix is a stronger factor in their survival, allowing SLC taxa to dominate small metacommunities. Biomass of other functional groups in matrix treatments were generally intermediate between small and large enclosures which could

indicate mechanisms transmitted both via aquatic patches and the terrestrial matrix, as might be expected for species with complex lifecycles that cross ecosystems.

The specific traits of the species in this system can explain how differences in bromeliad number and enclosure size affected community composition. However, the generality to other systems depends on recognizing the broader patterns. Based on these results, we would predict that in general, in any cross ecosystem metacommunity, species with the greatest terrestrial needs would be most sensitive to reduction in metacommunity size, and the corresponding terrestrial matrix. We would also predict that the highest trophic levels would be most sensitive to metacommunity size but that their longer life cycles would create a time lag in observable results.

Reduced abundances, evenness and diversity in smaller metacommunities may result in lower rates of ecological function such as leaf litter loss, and production of fine organic particulates (FPOM). In other studies, the positive relationship between species diversity and ecosystem function has been well established (e.g. Tilman et al. 2001, and reviewed in Cardinale et al. 2006, 2012). In this system, previous experiments have demonstrated the importance of damselflies for decomposition processes, and nitrogen availability for bromeliads (Ngai and Srivastava 2006). As the damselflies were still demonstrating transient dynamics at the end of this study, we did not measure rates of decomposition in our enclosed bromeliads. Instead, we artificially constructed communities that represented the predicted longer-term composition of different metacommunity sizes (i.e. without damselflies). In this parallel study (R.M. LeCraw, unpubl. ms), analogues of small metacommunities showed lower rates of decomposition than communities representing larger metacommunities.

Theory predicts that metacommunities with more connected patches will support a larger food web (Hassell et al. 1991, Wilson et al. 1998), and is supported by simple microcosm experiments (Bonsall et al. 2002, Bonsall et al. 2005). Community composition has also been demonstrated to change based on connectivity in a simple field test of connectivity (Murakami et al. 2008). Our study is one of the first explicit tests of metacommunity size in a natural whole food web, and demonstrates that the number of connected patches in this system affects the evenness and predictability of species composition, the ratio of predators to prey in the food web, the types of functional groups, and may affect ecological function such as decomposition. These results have direct relevance to explaining patterns in other cross-ecosystem environments including other phytotelmata, landscapes of ponds and lakes, oceanic islands, or coastal rock pools. The implications for making testable predictions of local patch diversity based on metacommunity size and species traits extends to any patchy landscapes. We suggest further research based on this field study to specifically test mechanisms of species extinctions and the consequences for ecological functioning.

## **5. BIOGEOGRAPHICAL PATTERNS DRIVE CONTEXT DEPENDENCY OF TOP-DOWN CONTROL IN BROMELIAD-DWELLING COMMUNITIES**

### **INTRODUCTION**

A fundamental question in community ecology is how the structure of local ecological communities affects the functioning of the ecosystem. However, the answer may depend on the geographical area in which the question is posed. Many common study systems are found across large spatial scales, such as forest streams, coastal intertidal pools, salt marshes, and plant phytotelmata, but experiments are most often conducted at a local scale and results may show strong context dependence (Noda 2004). Context dependence in ecological field experiments has been shown to affect diversity-function relationships from scales as little as 20 km apart (Boyer et al. 2009), to as far apart as temperate versus tropical sites (Burkepile and Hay 2006). For example, a few studies replicated across regions within the coastal salt marsh system have shown that both bottom up effects of fertilization on arthropod communities (McCall and Pennings 2012), and top-down effects of arthropods on plant biomass (Pennings and Silliman 2005) can vary among sites within North America. The potential for such geographical variation in studies from different regions means that it is crucial to understand the mechanisms affecting context dependency in community ecology research in order to identify large-scale patterns. Here we use aquatic communities in plant phytotelmata to test how biogeographical and environmental variation within an ecological system can affect patterns of top-down control and rates of ecosystem functioning.

Aquatic systems such as streams and phytotelmata are common sites for studies of community ecology as they are common globally yet are individually a manageable scale for

surveys and manipulations. Studies in these systems often focus on litter decomposition processes (Kitching 2001, Lecerf and Richardson 2009) which have three main drivers: the decomposer community (Graça 2001), leaf litter quality (Cornwell et al. 2008), and climate (Cusack et al. 2009, Boyero et al. 2011), all of which can vary widely over the geographic range of these aquatic study systems. The food web structure (number of links, connectance, trophic ratios) of freshwater aquatic communities can be similar across large geographic ranges, while the taxonomic and functional group composition may vary among sites (Thompson and Townsend 2003). These differences in community composition can have direct effects on rates of litter decomposition or can alter the top-down control of the system by predators.

Certain traits in the macroinvertebrate detritivore community can increase the rate of leaf decomposition, such as the presence and efficiency of leaf shredders, the primary large leaf processors in aquatic systems (Petersen and Cummins 1974). Predators have also been shown to have indirect negative effects on decomposition in streams through consumption of detritivores (Greig and McIntosh 2006, Lecerf and Richardson 2011), but the strength of that top-down control can depend on predator identity and efficiency (Borer et al. 2005, Otto et al. 2008) and traits of prey species such as physical or behavioural predator resistance (Duffy et al. 2007, Edwards et al. 2010, Hines and Gessner 2012).

Differences in the relative abundance of species in the community can also affect litter decomposition, for example when low evenness allows a more efficient leaf-processing species to dominate the community (Dangles and Malmqvist 2004, McKie et al. 2008). Finally, variation in consumer behaviour can affect rates of resource use (Pennings and Silliman 2005), and the strength of top-down control by predators (Dalton et al. 2013).

Environmental differences among sites can also lead to differences in decomposition through climate factors or the quality of leaf litter. For example, increases in temperature and precipitation from temperate forest to tropical rainforest have been shown to increase rates of litter decomposition (Austin and Vitousek 2000, Boyero et al. 2011, Fernandes et al. 2012). Leaf litter quality can also vary across and within ecoregions in terms of leaf toughness (Onoda et al. 2011) and chemistry (Parsons et al. 2012), both of which have strong impacts on decomposition rates (Perez-Harguindeguy et al. 2000, Parsons et al. 2012). The consequences of this environmental variation among sites may be qualitative differences in the relationships between community structure and function (McCall and Pennings 2012, O'Connor and Donohue 2013). Geographically replicated experiments are needed to disentangle the community, climate, and leaf quality mechanisms driving context dependence in these relationships.

We use the natural mesocosm system of bromeliad phytotelmata to test how biogeographical variation within the system can affect decomposition rates and top-down control by predators. Bromeliads are terrestrial or epiphytic plants found in the Americas, from Florida to Argentina, in a range of forest types from montane rainforest to coastal restinga. Water-filled leaf axils support an aquatic invertebrate food web with a detrital resource base of plant litter caught in each axil. Bromeliads are ideal for tests of geographic patterns of community structure and function since biogeographic processes have created variation in the species traits present in the invertebrate community. We studied bromeliad-dwelling macroinvertebrate communities in Puerto Rico, Brazil, and Costa Rica, each with distinct species pools. Specifically, bromeliads on the island of Puerto Rico have a relatively small species pool, and have not been colonized by the largest predator group (damselfly nymphs) (Richardson 1999). The study region in São Paulo state, Brazil, however, is nearer the epicentre

of bromeliad radiation (Givnish et al. 2011) and has the largest species pool of the three sites, including a unique functional group of case-building caddisflies; these shredders, which are resistant to damselfly predation, have not expanded beyond a small range in Brazil and Argentina (Frank and Lounibos 2008).

We combine a cross-site, replicated experiment with analogue communities representing different regions in common sites to disentangle how differences between countries in invertebrate community composition and environmental conditions influence leaf decomposition rates and top-down control. While species overlap among regions is low, the community composition of different regions can be replicated at the family and functional group level. Thus, it is possible to replicate a Puerto Rico analogue community in both Brazil and Costa Rica (although the opposite is not possible). Using this design we address two main questions: 1) Do top-down effects of predators on prey communities and decomposition vary among sites? and 2) Are differences in decomposition and top-down control driven by the site-specific differences in invertebrate community, or by local environmental conditions?

## **METHODS**

Experiments were conducted in the rainiest season at each site: in El Yunque National Forest, Puerto Rico between January and March 2012, in Guanacaste, Costa Rica between October and December 2012, and on Ilha do Cardoso, Brazil between February and May 2011.

### **Treatment and Community Design**

The experiment was designed to replicate detritivore communities representing Brazil (BR), Costa Rica (CR), and Puerto Rico (PR), both in their home countries and as community

analogues in two common sites. The Brazil common site included all three communities (BR, CR, and PR) or their analogues in the cases of CR and PR, assembled with Brazilian fauna. The Costa Rica common site included the CR and PR-analogue communities. Experiments in common sites allowed isolation of the effects of biogeographic differences in community structure. If we assume that similar species in different sites are functionally equivalent (e.g. gatherers in the same genus of Chironomidae, or damselfly predators in different genera) based on the literature on each species and direct observations in the field, comparison of similar communities (e.g. all PR or PR-analogue communities in the three different sites) allows us to control for the effects of community composition and focus on the effects of environmental differences on community and ecological functions. A second PR treatment in Puerto Rico and the Costa Rica common site tested the effect of biomass *per se* by doubling the abundances of all PR taxonomic groups, resulting in initial biomass equal to CR, but relative abundances equal to PR.

The experimental detritivore community was determined by the natural species richness and abundance of each species in 20 mL of water (the scale of one leaf axil or experimental tube) based on previous years of survey data at each field site. Where possible, species of the same genus were used across sites, and where genera did not overlap, species in the same family were used. The BR detritivore community included 26 individuals in 8 taxa, CR included 21 individuals in 7 taxa, and PR included 9 individuals in 5 taxa. Detritivore communities for each site are described in The Appendix (Table S5.1).

Two types of predators were added to detritivore communities: a small bodied chironomid with limited prey options (*Monopelopia* sp: Tanypodinae), and 2 species of odonate generalist predator which are treated as functionally equivalent: (*Mecistogaster modesta* (Selys)

in Costa Rica, and *Leptagrion elongatum* (Selys) in Brazil). Odonate predators are absent from bromeliads in Puerto Rico, so only the chironomid predator treatment was possible. In each predator treatment, one individual predator was added to the detritivore community, reflecting the natural density of predators in surveyed communities, and was replaced if it emerged or died during the experiment.

### **Experimental protocol**

Flow-through enclosures embedded in bromeliads were used as experimental units with replicates across plants. In Costa Rica and Brazil 50 mL plastic centrifuge tubes were used, with 1 cm diameter holes drilled near the base of the tube. In Puerto Rico 15 mL centrifuge tubes were used to accommodate the smaller size of bromeliads, with a single elongate hole cut near the base. Holes were covered with 80  $\mu\text{m}$  Nytex<sup>tm</sup> mesh to prevent movement of invertebrates but allow exchange of water and microorganisms with the bromeliad environment. Tubes were covered with a bag made of 80  $\mu\text{m}$  mesh secured with an elastic band as an emergence trap. While using tubes of different sizes has the potential to affect processes in the experiment (Mallory and Richardson 2005), the tube in each site occupied an entire leaf well, and any differences due to experimental tube size may be interpreted as consequences of natural differences in bromeliad size among sites.

The resource base in each experimental tube was a leaf species representative of the common leaf litter in bromeliads in each site. Leaf species were chosen based on three criteria: they were abundant, naturally found in bromeliads, and rapidly decomposed in bromeliads. I tested several abundant species at each site in leaf packs submerged in bromeliads for a week prior to the experiment, and the species with the greatest loss of leaf mass was used in the

experimental tubes. Leaf species used were *Miconia prasina* (Sw.) in Puerto Rico, *Conostegia xalapensis* (Bonpl.) in Costa Rica, and *Psidium cattleianum* (Sabine) in Brazil. Leaves were oven-dried to constant mass, weighed to 500 mg +/- 50 mg in Costa Rica and Brazil and 250 mg +/- 50 mg in Puerto Rico, reflecting natural density of detritus within bromeliad leaf wells, then rehydrated for 24 hours before the addition of invertebrate communities.

Insect larvae and other macroinvertebrates were collected from bromeliads by collecting leaf litter and water and identifying invertebrates to morphospecies. Ten replicates of each treatment community were initially assembled with half of the total planned invertebrates. Oviposition is continuous in natural bromeliads, so to simulate a new oviposition event, the second half of the communities was added to the tubes after 14 days. Tubes were placed in large unsampled bromeliads, and were partially submerged in each leaf well. Tubes were in bromeliads for a total of 30 days. Emerged adult insects were collected from mesh emergence bags and identified daily. After 30 days all invertebrates remaining in the tubes were recorded, and leaf litter removed. Coarse leaf litter (fragments larger than 850  $\mu\text{m}$ ) and fine particulate organic matter (FPOM; greater than 80  $\mu\text{m}$ ) was oven dried and weighed.

## **Analysis**

The strength of top-down control was measured as the effect of both predator types on the proportional emergence, survival, final biomass and final composition of detritivore communities and on leaf litter loss and FPOM production. Proportional emergence (hereafter referred to as emergence) was calculated as the number of emerged adults divided by the total initial number of insect larvae (non-insect invertebrates complete their life cycle within the bromeliad, and so cannot emerge). Proportional survival (hereafter referred to as survival) was

calculated as the sum of emerged adults and surviving aquatic macroinvertebrates at the end of the experiment divided by the total initial number of macroinvertebrates. Detritivore composition was represented as the proportion of shredders in the community by biomass. Biomass of macroinvertebrates was converted from length of larvae to mg of dry mass, calculated from previous survey data (G.Q. Romero, D.S. Srivastava., unpubl. data). The effects of predators on detritivore communities and decomposition metrics were determined by 2-way ANOVA with predator treatment, site, and a predator X site interaction as fixed explanatory variables. To correct for non-independent multiple comparisons as described in the common site analyses, significance of ANOVA results was assessed using a corrected alpha of 0.007 (See Appendix). To compare the magnitude of top-down control on detritivore community and decomposition metrics by predators among sites we used Hedges' *g* effect size (Hedges and Olkin 1985) with 95% confidence intervals.

After determining the effect of predators on the detritivore community in each site, we tested if the main drivers of decomposition in each site were macroinvertebrate community-based or environmental by (1) determining the degree to which macroinvertebrate community variables explained variation in decomposition within each site, and (2) by comparing decomposition among communities in common sites. The amount of variation in decomposition metrics explained by macroinvertebrate community variables was calculated as the  $R^2$  value of a multiple regression with leaf loss or FPOM as the response variable and final shredder biomass, total macroinvertebrate biomass, macroinvertebrate abundance, and macroinvertebrate species richness as predictor variables. Significance of contributing variables was calculated by repeating the multiple regression with the variable of interest omitted, and comparing the full and reduced models by ANOVA. The proportion of variation not explained by the

macroinvertebrate variables in the regression is assumed to be attributed to environmental factors including forest type and climate, which can influence microbial activity. The inherent differences in leaf and invertebrate species among sites may also emerge as environmental influences outside of macroinvertebrate community composition that affect rates of leaf decomposition among sites.

Theoretically, a strong positive correlation between leaf litter loss and FPOM production is assumed to indicate the contribution of shredding macroinvertebrates to decomposition, whereas leaf litter loss with little corresponding FPOM produced is likely due to other decomposition processes such as microbial activity (Richardson and Neill 1991). We assessed the correlation between leaf litter loss and FPOM (in mg dry mass) using simple linear regression including all replicates across all treatments within a site. The doubled PR treatment in Puerto Rico and Costa Rica was omitted from this analysis as it contained unnaturally high densities of shredders.

We tested for context dependence of results by comparing detritivore emergence and survival, and leaf litter loss and FPOM production in each community between common sites and their home sites. We used 2-way ANOVAs to test for interactions between predator treatment (no predator, chironomid, or damselfly), and either site (by comparing the same type of community across sites), or community type (different community types within the same site) on community and decomposition responses. In total there were seven ANOVA comparisons including common site comparisons and home site comparisons for each response variables, and we corrected for non-independence by using  $\alpha = 0.05/7 = 0.007$ . Full details of each ANOVA are described in The Appendix. Context dependence of top-down control was revealed as

significant predator treatment X site interactions, and differences among communities were revealed as significant predator treatment X community interactions.

We tested the influence of total detritivore biomass (as opposed to community structure) on the performance of the detritivore community and decomposition by comparing responses in the Costa Rica common site among the doubled PR community, and no predator treatments of the PR and CR communities by ANOVA.

## RESULTS

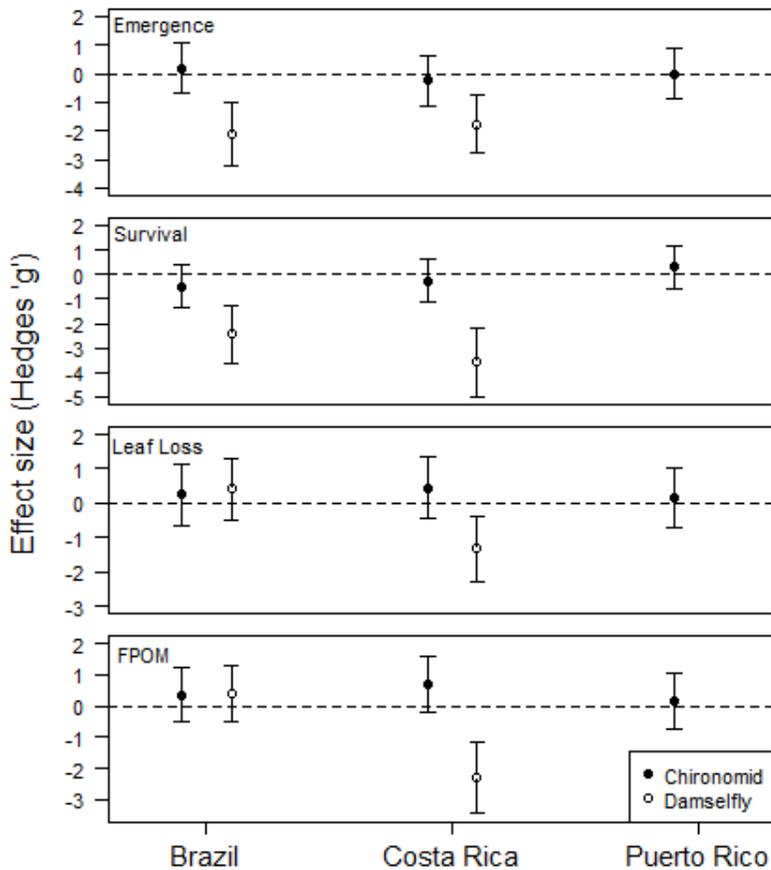
### Top-down control by predators among regions

In this section, we consider only communities in their home site: the BR communities in Brazil, the CR communities in Costa Rica and the PR communities in Puerto Rico. This allows us to establish if sites differ in top-down effects, a necessary first step prior to determining the underlying mechanisms.

#### *Predator effects on detritivore community*

The effect of predators on the survival of the detritivore community was dependent on the predator identity (ANOVA 1 see Appendix, planned contrast between chironomid and damselfly predator treatments:  $F_{3,72} = 68.69$ ,  $p < 0.001$ ), but was consistent among sites (ANOVA 1 site X predator treatment interaction:  $F_{3,72} = 0.94$ ,  $p = 0.43$ ; Fig. 5.1). The predatory chironomid had no effect on the rate of emergence or survival of detritivore communities in any site (Hedges'  $g \pm 95\%$  CI overlaps zero in all sites), but the predatory damselfly significantly reduced both emergence and survival of detritivores in the two sites where it was present (Hedges'  $g \pm 95\%$  CI  $< 0$ ). Due to different effects of predators on survival, there was a

significant interaction effect between predator treatment and site on detritivore biomass (ANOVA 1  $F_{3,72} = 24.46$ ,  $p < 0.001$ ). The presence of damselflies resulted in a 62% loss of detritivore biomass in Brazil (Tukey HSD between damselfly and no predator treatment,  $p = 0.003$ ) and a 99% loss of detritivore biomass in Costa Rica (Tukey HSD between damselfly and no predator treatments,  $p < 0.001$ ). The top predator in Puerto Rico was the Tanypodinae chironomid, which had no effect on detritivore survival, resulting in no significant loss of detritivore biomass due to predators in Puerto Rico (Tukey HSD comparing chironomid and no predator treatment,  $p = 0.98$ ).



**Figure 5.1.** Effect of two types of predators (+/- 95% confidence intervals) directly on emergence and survival of detritivores (top two panels), and indirectly on decomposition (bottom two panels) in communities in their native sites. Confidence bars crossing the dashed line at zero indicate no significant effect of predators while effects below the line with confidence bars that do not overlap the zero line indicate a significant negative effect.

There was also a significant predator treatment X site interaction effect on the proportion of shredders in the detritivore community (ANOVA 1,  $F_{3,72} = 13.59$ ,  $p < 0.001$ ). The caddisfly shredder in Brazil was the only species whose survival was not significantly affected by damselfly predators (Appendix. Fig. S5.1). Consequently the Brazilian detritivore community had a slight but insignificant increase in the proportion of shredders (TukeyHSD between damselfly and no predator treatments, difference = 0.30,  $p = 0.23$ ). In Costa Rica, where all

detritivores are susceptible to predation, predator effects were even stronger and biomass was reduced almost to zero, with no shredders remaining in the community (Tukey HSD between damselfly and no predator treatment, difference = -0.59,  $p < 0.001$ ). In Puerto Rico, however, no taxa were affected by the predatory chironomid, therefore the proportion of shredders remained unchanged (Tukey HSD between chironomid and no predator treatment, difference = 0.1,  $p = 0.99$ ).

### *Predator effects on decomposition*

The cascading effect of predators on leaf litter decomposition rates was dependent on predator identity (ANOVA 1 see Appendix, planned contrast chironomid versus damselfly predator:  $F_{1,72} = 9.87$ ,  $p < 0.001$ ), but differed among countries (ANOVA 1, site X treatment interaction:  $F_{3,72} = 6.00$ ,  $p = 0.001$ , Fig. 5.1). Predatory chironomids had no effect on leaf litter loss or FPOM in any site (Hedges'  $g \pm 95\%$  CI overlaps zero in all sites). Since the chironomid was the top predator in Puerto Rico, this resulted in overall weaker top-down effects on decomposition in that site (Hedges'  $g \pm 95\%$  CI: Leaf loss  $0.14 \pm 0.88$ ; FPOM  $0.16 \pm 0.88$ ). Top-down effects were also weak in Brazil where damselfly predators had no effect on the rate of decomposition (Hedges'  $g \pm 95\%$  CI: Leaf loss  $0.40 \pm 0.89$ ; FPOM  $0.39 \pm 0.88$ ). By contrast, in Costa Rica damselflies significantly reduced both leaf decomposition (Hedges'  $g \pm 95\%$  CI:  $-1.33 \pm 0.97$ ) and the amount of FPOM produced (Hedges'  $g \pm 95\%$  CI:  $-2.28 \pm 1.13$ ).

### **Macroinvertebrate community versus environmental drivers of top-down control**

Analyses in the previous section established that top-down effects on decomposition differ between sites. However, both macroinvertebrate composition and the local environment

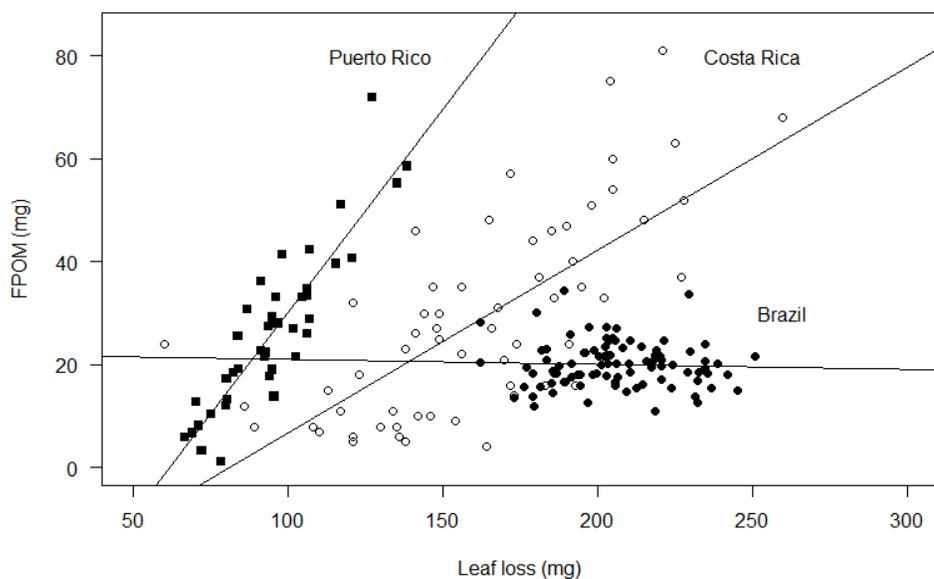
differ between sites, confounding our ability to use replicated experiments to determine the ultimate driver behind these between-site patterns. We now examine the full complement of community treatments (including community analogues of one site that were assembled in a different site) to disentangle the effects of macroinvertebrates and local environment. We first ask whether sites differ in the amount of variation in decomposition that can be explained by macroinvertebrate community structure, and then ask if communities representative of different sites still differ in top-down effects when the local environment is kept constant in a common site.

When all communities were considered, the amount of variation in decomposition rate that could be explained by macroinvertebrate community variables differed among sites (Table 5.1). In Puerto Rico and Costa Rica, both leaf loss and FPOM were strongly and significantly related to community variables. In Brazil, leaf loss was not at all related to community variables, and FPOM had a weak but significant relationship (Table 5.1). In Costa Rica and Brazil the strength of the models differed between decomposition metrics, suggesting a decoupling of leaf loss and FPOM. In fact, leaf loss and FPOM are strongly related in Puerto Rico ( $R^2$ : 0.90,  $p < 0.01$ ), but less so in Costa Rica ( $R^2$ : 0.52,  $p < 0.01$ ) and are not at all correlated in Brazil ( $R^2$ : 0.001,  $p = 0.75$ ; Fig. 5.2).

Of the detritivore community variables, the two contributing most strongly to decomposition were total detritivore biomass and shredder biomass. Total biomass contributed significantly to decomposition in Puerto Rico, but not Costa Rica or Brazil (Table 5.1). Shredder biomass also contributed most strongly to decomposition in Puerto Rico, but not in Costa Rica or Brazil (Table 5.1).

**Table 5.1.** Results of multiple regressions of community-based variables on decomposition responses (FPOM = fine particulate organic material). Single variables were removed in subsequent models to test significance of partial slopes. F and p values reported for single variables refer to the ANOVA comparison between the full model, and the model omitting the given variable. Significant models and contributing variables are shown in bold.

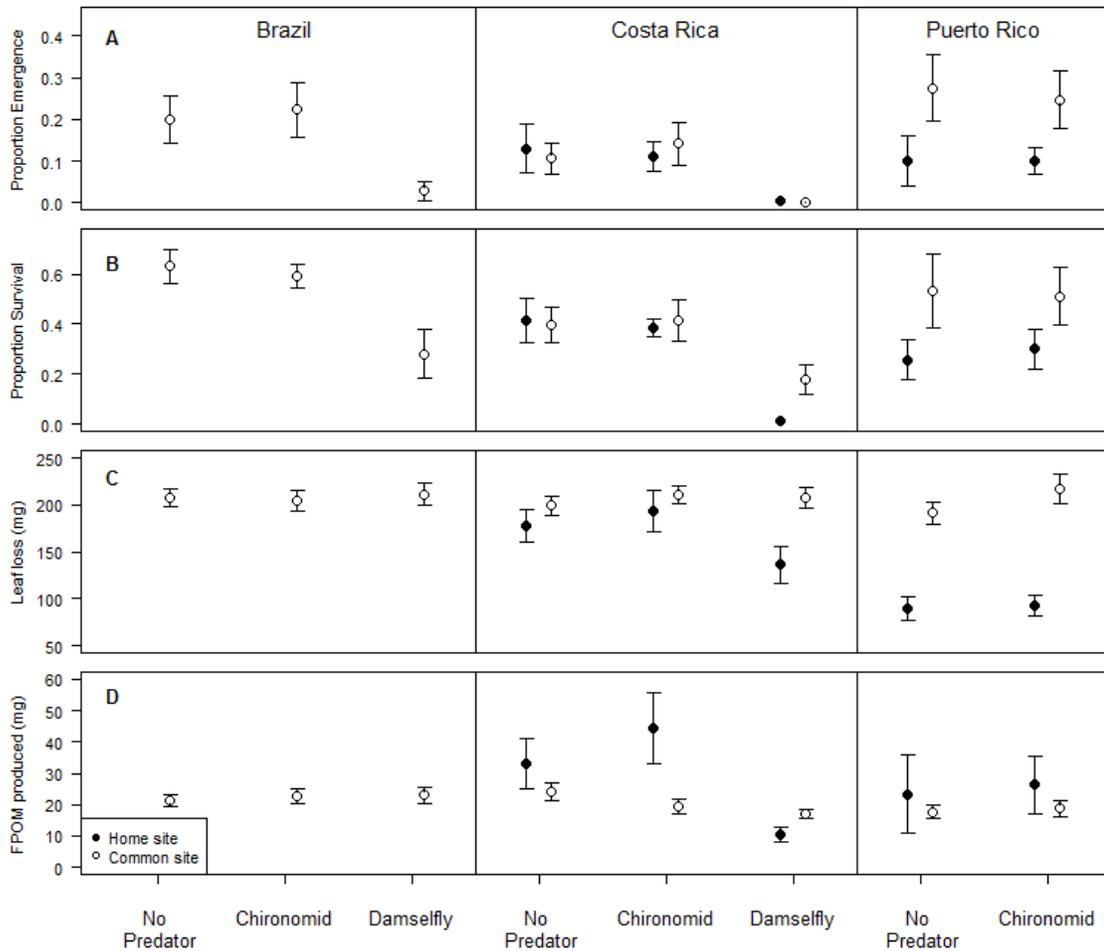
Country	Response	Full Model	Shredder biomass	Total biomass	Abundance	Richness
Puerto Rico	Leaf loss	<b>Adj. R<sup>2</sup>: 0.66</b> <b>p: &lt;0.01</b>	<b>F: 29.01</b> <b>p: &lt;0.01</b>	<b>F: 6.22</b> <b>p: 0.02</b>	<b>F: 11.2</b> <b>p: &lt;0.01</b>	<b>F: 6.23</b> <b>p: 0.02</b>
	FPOM	<b>Adj. R<sup>2</sup>: 0.63</b> <b>p: &lt;0.01</b>	<b>F: 33.20</b> <b>p: &lt;0.01</b>	<b>F: 7.29</b> <b>p: 0.01</b>	<b>F: 7.06</b> <b>p: 0.01</b>	F: 2.17 p: 0.15
Costa Rica	Leaf loss	<b>Adj. R<sup>2</sup>: 0.41</b> <b>p: &lt;0.01</b>	F: 0.18 p: 0.67	F: 2.16 p: 0.15	F: 1.25 p: 0.27	F: 0.06 p: 0.80
	FPOM	<b>Adj. R<sup>2</sup>: 0.78</b> <b>p: &lt;0.01</b>	<b>F: 13.15</b> <b>p: &lt;0.01</b>	F: 1.02 p: 0.32	F: 0.56 p: 0.46	F: 0.98 p: 0.33
Brazil	Leaf loss	Adj. R <sup>2</sup> : -0.03 p: 0.78	F: 0.51 p: 0.48	F: 1.40 p: 0.24	F: 0.16 p: 0.70	F: 1.08 p: 0.30
	FPOM	<b>Adj. R<sup>2</sup>: 0.19</b> <b>p: &lt;0.01</b>	<b>F: 4.13</b> <b>p: 0.05</b>	F: 0.01 p: 0.92	<b>F: 5.96</b> <b>p: 0.02</b>	F: 1.23 p: 0.27



**Figure 5.2.** Scatter plot of leaf loss and fine particulate organic matter (FPOM) from all communities and treatments within each country, omitting control treatments, and doubled Puerto Rico communities as they contain an unnatural density of shredders. The relationships in Puerto Rico and Costa Rica are statistically significant (Linear models  $p < 0.01$ ), and there is no significant relationship in Brazil.

### *Brazil and Costa Rica common sites*

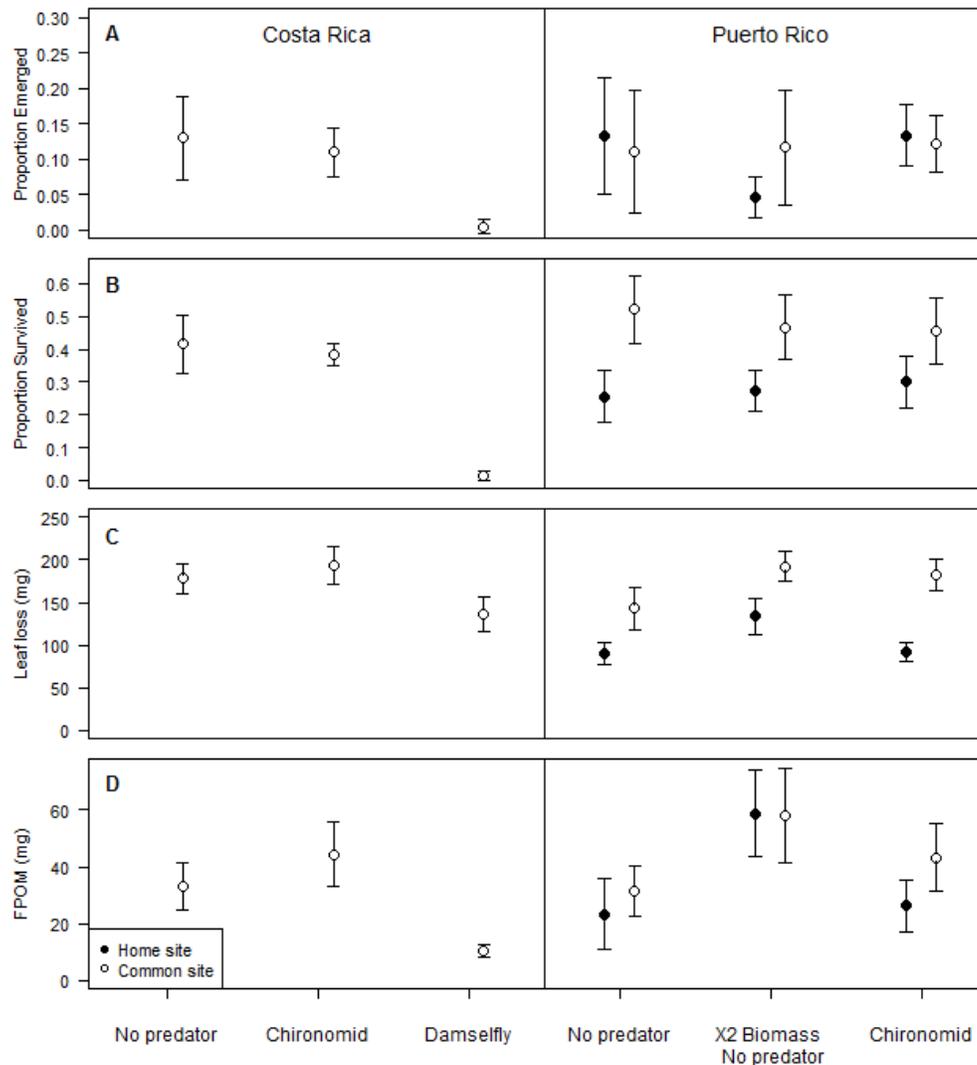
Local environmental conditions can be standardised by creating analogue communities of different sites in a common site; any remaining differences between these analogue communities must be due to differences in macroinvertebrate composition. We attempted to replicate community structure in common sites in both Brazil and Costa Rica. In both common sites, communities representing the same biogeographic site but occurring in different experimental sites showed similar top-down effects of predators on detritivores demonstrated, in most cases, by no significant site X predator treatment interactions. The marginally significant site X predator interaction for survival in the CR community was an exception. (ANOVA 2, PR community, see Appendix, emergence:  $F_{2,54} = 0.21$ ,  $p = 0.81$ ; survival:  $F_{2,54} = 0.59$ ,  $p = 0.56$ ; ANOVA 3, CR community, see Appendix, emergence:  $F_{1,36} = 0.22$ ,  $p = 0.64$ ; survival:  $F_{1,36} = 7.80$ ,  $p = 0.01$ ; Fig. 5.3A,B; Fig. 5.4A,B). These geographically similar results suggest that effects of local environmental conditions on predator functions were minimal in most cases. For example, damselflies in the CR communities in home (Costa Rica) and common (Brazil) sites had similar, significant negative effects on emergence (home: mean Hedges'  $g$  effect size  $\pm$  95% CI:  $-1.76 \pm 1.03$ ; common [Brazil]:  $-2.48 \pm 1.16$ ). However, damselflies had a slightly greater effect on survival in Costa Rica, where detritivore survival was reduced to zero ( $-3.58 \pm 1.41$ ), than in Brazil, where some detritivores were able to survive ( $-2.10 \pm 1.09$ ). In the PR community in both home (Puerto Rico) and common (Brazil and Costa Rica) sites, the predatory chironomid consistently had no significant effect on emergence (home:  $0.00 \pm 0.88$ ; common [Brazil]:  $-0.24 \pm 0.87$ ; common [Costa Rica]:  $0.09 \pm 0.88$ ) or survival (home:  $0.29 \pm 0.88$ ; common [Brazil]:  $-0.05 \pm 0.88$ ; common [Costa Rica]:  $-0.35 \pm 0.88$ ) of the detritivore community.



**Figure 5.3.** Comparison of results for each community (Brazil, Costa Rica, and Puerto Rico) in their home site (filled circles) and the Brazil common site (open circles). As Brazil is the common site, it lacks second data points for home site. Emergence (A) and survival (B) of detritivore community is shown in the top two panels, Leaf loss (C) and fine particulate organic material (FPOM) production (D) represent decomposition in the bottom panels. Error bars indicate 95% confidence intervals.

Top-down effects of particular predators were also generally congruent across communities representative of different biogeographic sites demonstrated by no significant community X predator treatment interactions within both the Brazil common site (ANOVA 4, chironomid predator, see Appendix, emergence:  $F_{3,72} = 1.08$ ,  $p = 0.36$ ; survival:  $F_{3,72} = 0.80$ ,  $p =$

0.50; ANOVA 5, damselfly predator, see Appendix, emergence:  $F_{1,36} = 3.05$ ,  $p = 0.09$ ; survival:  $F_{1,36} = 3.16$ ,  $p = 0.08$ ; Fig. 5.3A,B) and the Costa Rica common site (ANOVA 6, chironomid predator, see Appendix, emergence:  $F_{1,45} = 0.34$ ,  $p = 0.56$ ; survival:  $F_{1,45} = 0.21$ ,  $p = 0.65$ ; Fig. 5.4A,B). For example, regardless of common site location or community origin, damselflies had significant negative effects on detritivore emergence (mean Hedges'  $g$  effect size  $\pm$  95% CI: Brazil common site: BR:  $-2.14 \pm 1.10$ ; CR:  $-2.48 \pm 1.16$ , Costa Rica common site: CR:  $-1.76 \pm 1.03$ ) and survival (Brazil common site: BR:  $-2.44 \pm 1.16$ ; CR:  $-2.10 \pm 1.09$ ; Costa Rica common site: CR:  $-3.58 \pm 1.41$ ). Similarly, regardless of site or community of origin, Tanypodinae chironomids had negligible effects on detritivore emergence (Brazil common site: BR:  $0.20 \pm 0.88$ ; CR:  $0.40 \pm 0.89$ ; PR:  $-0.24 \pm 0.88$ , Costa Rica common site: CR:  $-0.25 \pm 0.88$ ; PR:  $0.09 \pm 0.88$ ) and survival (Brazil common site: BR:  $-0.50 \pm 0.89$ ; CR:  $0.08 \pm 0.88$ ; PR:  $-0.05 \pm 0.88$ , Costa Rica common site: CR:  $-0.26 \pm 0.88$ ; PR:  $-0.35 \pm 0.88$ ).



**Figure 5.4.** Comparison of results for each community (Costa Rica and Puerto Rico) in their home site (filled circles) and the Costa Rica common site (open circles). As Costa Rica is the common site, it lacks second data points for home site. Emergence (A) and survival (B) of detritivore community is shown in the top two panels, Leaf loss (C) and fine particulate organic material (FPOM) (D) represent decomposition in the bottom panels. Error bars indicate 95% confidence intervals.

In contrast to the detritivore responses, the decomposition metrics – especially leaf loss - showed a greater influence of local environmental conditions demonstrated by significant site X predator treatment interactions in some communities (ANOVA 2, PR communities, see

Appendix, Leaf loss:  $F_{2,54} = 2.51$ ,  $p = 0.09$ ; FPOM:  $F_{2,54} = 0.84$ ,  $p = 0.44$ ; ANOVA 3, CR communities, see Appendix, Leaf loss:  $F_{1,36} = 10.28$ ,  $p = 0.003$ ; FPOM:  $F_{1,36} = 11.56$ ,  $p = 0.002$ ; Fig. 5.3 C,D). For example, the PR analogue community had significantly greater leaf loss in Brazil and Costa Rica than in its home site (ANOVA 2, Tukey HSD PR in Puerto Rico vs. PR in Brazil  $p < 0.001$ ; PR in Puerto Rico vs. PR in Costa Rica  $p < 0.001$ ; Fig. 5.4C), and the CR analogue community had greater leaf loss in Brazil than in its home site (ANOVA 3,  $p < 0.001$ ). The importance of local environmental conditions also extended to top-down effects on decomposition. In CR communities, damselflies had a significant negative effect on leaf litter loss and FPOM production at the home site (Costa Rica) (Hedges'  $g$  effect size  $\pm$  95% CI, Leaf loss:  $-1.33 \pm 0.97$ ; FPOM:  $-2.25 \pm 1.13$ ) but had no effect on leaf litter loss in the Brazil common site ( $0.44 \pm 0.89$ ) and a smaller negative effect on FPOM production ( $-1.76 \pm 1.03$ ).

Although decomposition was influenced by local environmental conditions, the common sites revealed that community of origin was sometimes also important. In the Brazil common site, communities representing sites in different biogeographic regions differed slightly in FPOM production (BR > CR > PR; ANOVA 4,  $F_{2,72} = 7.4$ ,  $p = 0.001$ ) but not leaf loss (ANOVA 4,  $F_{2,72} = 0.20$ ,  $p = 0.82$ ). In the Costa Rica common site however, community of origin had no influence on leaf loss (ANOVA 6,  $F_{1,45} = 0.45$ ,  $p = 0.45$ ) or FPOM (ANOVA 6,  $F_{1,45} = 3.66$ ,  $p = 0.06$ ).

#### *Community biomass versus composition*

Macroinvertebrate communities differed between sites not only in composition, but also biomass; for example, CR communities had roughly twice the biomass of PR communities. By including in the Costa Rican common site a treatment that had the same composition as PR

communities but twice the biomass, we were able to assess the degree to which community biomass influenced differences in function between PR and CR communities. This PR doubled community had similar proportional survival and emergence as the PR and CR communities (ANOVA 7, see Appendix, survival:  $F_{2,27} = 1.17$ ,  $p = 0.32$ ; emergence:  $F_{2,27} = 0.06$ ,  $p = 0.94$ ), but marginally higher leaf loss than PR (ANOVA 7,  $F_{2,27} = 6.10$ ,  $p = 0.01$ ; Tukey post hoc PR versus doubled PR:  $p = 0.01$ ) but not CR (Tukey post hoc CR versus doubled PR:  $p = 0.59$ ) suggesting that community biomass differences may underlie site differences in leaf loss (Fig. 5.4). Production of FPOM by the doubled PR community was marginally higher than both the PR and CR community (ANOVA 7,  $F_{2,27} = 6.12$ ,  $p = 0.01$ ; Tukey post hoc, doubled PR versus both PR and CR:  $p = 0.01$ ), indicating a possible important effect of composition here.

## **DISCUSSION**

This study is the first to show how the pathways to decomposition functioning in the bromeliad system differ substantially among three sites in different biogeographic regions, especially in terms of the strength of top-down control. Our geographically replicated and common site experiments show that this variation in decomposition and top-down effects can be explained by both biogeographic patterns in community composition, and geographic variation in environmental conditions, as I explain below.

### **Top-down control of prey community and decomposition**

The strength of top-down control in this system varied by study site and trophic level. The Puerto Rico community showed the weakest top-down control, with undetectable effects of predators on detritivores and decomposition, the Costa Rica community showed strong top-

down control from predators to detritivores to decomposition, and the Brazil community showed moderate top-down control of detritivores that attenuated in terms of detrital decomposition. The mechanisms driving site differences in top-down control were dependent on the trophic level affected.

Differences in predator and detritivore species traits were the primary driver of differences in top-down control of detritivore communities among sites. Predator identity has been documented to influence the strength of trophic cascades (Borer et al. 2005, Bruno and O'Connor 2005, Otto et al. 2008, Shackell et al. 2010), and was a main driver of detritivore community responses in our study. The lack of bromeliad-dwelling damselflies on the island of Puerto Rico meant that the top predator was the much smaller chironomid larva, which universally resulted in much weaker top-down control of prey communities. Predatory damselflies had a strong influence on detritivores in Costa Rica, but that influence was slightly attenuated in Brazil by the presence of predator-resistant detritivore traits (Bell 2002, Duffy et al. 2007, Best and Stachowicz 2012). In our study, the case-building caddisfly shredder *Phylloicus bromelarium* in Brazil was the only taxon whose survival was unaffected by damselfly predators (Appendix Fig. S5.1), which slightly increased overall detritivore survival (Duffy et al. 2007, Edwards et al. 2010) weakening top-down control. Local environmental conditions appeared to have minimal impacts on predator control of detritivores, for top-down effects in a given community were generally similar between common sites and native sites.

Top-down control of decomposition by predators, however, was more affected by site specific conditions driving litter quality and microbial activity, than by predator identity. In Costa Rica, where decomposition was strongly related to the invertebrate community, the odonate predator drove a strong trophic cascade. In Brazil, the presence of the predator-resistant

detritivore could be expected to dampen the trophic cascade (Best and Stachowicz 2012). However, in the Brazil common site there were minimal differences in leaf loss between different community analogues (two of which excluded caddisflies), suggesting that predator resistance was of minor importance in shielding detritus from top-down effects in Brazil. Rather, as we will discuss shortly, poor leaf litter quality and high temperatures in Brazil likely shifted control of decomposition from the invertebrate community to microbes, attenuating the trophic cascade. As shown in other studies, differences in the strength of top-down control at lower trophic levels was therefore influenced by environmental conditions driving basal resource quality (Steiner 2002, Burkepile and Hay 2006, Boyer et al. 2009, O'Connor and Donohue 2013) and rates of biological processes (He et al. 2009, Fernandes et al. 2012).

### **Macroinvertebrate versus environmental drivers of top-down control and decomposition**

Analogue communities in common sites showed that differences in top-down control of leaf litter loss among sites, especially between restinga and rainforest sites, was largely explained by geographic variation in environmental conditions, rather than different patterns in macroinvertebrate community traits. Studies of decomposition across latitudinal gradients have shown that variation in climate variables along these gradients can directly affect rates of biological and chemical processes underlying decomposition, as well as indirectly affect decomposition via effects on the quality of the detritus, and the composition of the invertebrate decomposer community (Garibaldi et al. 2011, Makkonen et al. 2012). Variation in climate can also affect these characteristics among sites within the tropical biome such as between coastal restinga and montane rainforest ecosystems (Goncalves et al. 2006). We suggest that these differences in climate and litter quality among sites resulted in decomposition being driven by

the macroinvertebrate decomposer community in the Puerto Rico and Costa Rica sites, and by microbial activity in the Brazil site. However, given that climatic conditions can vary widely with a small region, it would be valuable to repeat these experiments with replication within a region to test the importance of large scale biogeographical patterns versus site specific climatic conditions.

In the Puerto Rico and Costa Rica sites, where macroinvertebrates were responsible for the majority of leaf litter decomposition, shredder and total detritivore biomass were the greatest contributing factors. Single species trials showed that the main shredder taxa in these two sites, Tipulidae, had the greatest feeding rate, more than three times the next most efficient taxa (Appendix, Fig. S4.2), overshadowing contributions by any other taxa. The common site experiments revealed that differences between Costa Rica and Puerto Rico in decomposition rates were due to local environment, community biomass and indirect effects of predators. In the absence of predators, Costa Rica had higher decomposition rates than Puerto Rico, in part because Costa Rican communities had twice the macroinvertebrate biomass. However, once predators were included in the community, the stronger trophic cascade in Costa Rica resulted in comparable rates of decomposition between sites (Fig. 5.4).

The lack of influence of macroinvertebrates on decomposition in the Brazil site may be due to reduced leaf litter quality. Commonly, studies across latitudinal gradients have found differences in leaf toughness (Onoda et al. 2011), which can reduce their availability to macroinvertebrate herbivores and shredders (Garibaldi et al. 2011). Indeed, tropical leaves have been found to be avoided by shredders in preference for less defended temperate leaves (Graça and Cressa 2010), and consequently their rate of decomposition can be unaffected by the presence of macroinvertebrate shredders (Goncalves et al. 2006, 2007). Common leaves in the

restinga forest on Ilha do Cardoso have been shown to contain a greater proportion of lignin than in the Atlantic rainforest in the same region (Castanho and de Oliveira 2008), and high lignin concentration is often associated with lower rates of decomposition (Schindler and Gessner 2009, Fernandes et al. 2012). These studies support our observation that the invertebrate community had no effect on leaf litter loss at the Brazilian site. Continued studies on differences in the leaf stoichiometry among sites would further clarify how differences in the resource quality may be driving the influence of macroinvertebrates on litter decomposition.

Despite the lack of macroinvertebrate influence on decomposition in Brazil, litter decomposition rates were still high. Because most FPOM in our study was composed of insect fecal material, the decoupling of decomposition metrics (high leaf loss rate without correspondingly high FPOM; Fig. 5.2) indicates a potentially greater influence of microbial decomposition processes than macroinvertebrate activity in Brazil. The higher temperature at the Brazil site (on average 5°C higher than the Costa Rica and Puerto Rico sites) may have enhanced these microbial processes, compensating for the negative effect of leaf quality on macroinvertebrate-facilitated decomposition. Higher temperatures have been shown to increase microbial rates of decomposition (He et al. 2009), and even to reduce the negative effect of lignin content on fungal decomposition (Fernandes et al. 2012).

### **Implications for experiments across sites**

The differences in decomposition and strength of top-down control between home sites and our common sites indicate context dependency of community structure-function relationships in the bromeliad system. Our geographically replicated experiment was able to demonstrate that different mechanisms of context dependence operate at different trophic levels

of the system. We suggest from these conclusions that when studying trophic cascades, it can be misleading to assume all parts of the system are responding to the same elements of the ecosystem. Our study is also based on the assumption of functional equivalence of similar species among sites. Our assignment of species into functional groups was supported by direct observations of behaviour, however even within a species there can be variation in terms of efficiency and specialization which can affect species interactions and community dynamics (Bolnick et al. 2003). It is reasonable to think that this type of variation can also exist within functional groups and that our analogue communities in common sites may not behave identically. While we have convincing evidence for patterns of food web functions across sites while holding functional composition constant, it is possible that some of our environmental influences are the results of variation within functional groups among sites.

The strong context dependence in community-function relationships in this study also indicates that researchers must be aware of broader biogeographical patterns in their study system when interpreting localized experimental results. This may be accomplished through the more frequent use of spatial hierarchies in experimental design which can determine consistency in patterns found at a local scale up to large geographical scales (Noda 2004). International collaborations among researchers in similar systems can also provide a clearer picture of biogeographical patterns. By coordinating local experiments within a working group such as The Bromeliad Working Group (Srivastava 2010), shared data can effectively show spatial hierarchical patterns. In these ways, more general patterns of community drivers of ecosystem function can be uncovered in wide-ranging ecosystems.

## 6. GENERAL CONCLUSIONS

Spatial patterns play a key role in determining the structure and function of ecological communities at several scales. Through experiments and surveys in a natural model system spanning a large geographic range, I have been able to identify mechanisms which at local, regional, and large-scale geographic spatial scales can affect several processes in the aquatic bromeliad-dwelling community. Structural characteristics of the community including functional diversity and trophic structure, and functional characteristics including top-down control by predation and decomposition by macroinvertebrates were sensitive to spatial patterns of habitat. I discovered that the community was not only sensitive to habitat size at the local scale, metacommunity size at the regional scale, and biogeographic differences at a large-scale, but that interactions among spatial scales resulted in context-dependence of results.

At the local scale, habitat size as determined by bromeliad size, affected the rate of decomposition via trophic structure and top-down control. However, large-scale geographic differences in species distributions and climatic conditions affected the shape of the relationship. The presence of a large-bodied predator sensitive to habitat size in Costa Rica resulted in stronger top-down control and lower decomposition rates in larger bromeliads, while the absence of large predators in the community in Puerto Rico allowed detritivores to increase in larger bromeliads, resulting in higher decomposition rates. Climatic differences in Brazil shifted primary decomposition functions from macroinvertebrates to microbes, and as a result the rate of decomposition did not change with habitat size, despite a shift in invertebrate trophic structure. Thus, local habitat size altered ecosystem function differently depending on the geographic context.

At the regional scale, the spatial extent of the metacommunity affected the functional diversity of the local community, driven by traits of functional groups varying in sensitivity to metacommunity size. For example, large-bodied predators and functional groups with required resources in the surrounding terrestrial matrix were most sensitive to changes in the size of the metacommunity. As a result, smaller metacommunities contained less functionally diverse communities, with greater species turnover among replicate metacommunities at the patch level. This variation in local community structure has potential consequences for ecosystem functions, especially in small stochastic metacommunities where certain functional groups may become extinct or dominant depending on traits.

At the largest spatial scale, variation in climate and regional species pools among the three sites, Puerto Rico, Costa Rica, and Brazil, had overarching effects on ecosystem function, but also influenced relationships between habitat and ecosystem function at smaller scales. When considering a cascade of top-down control by predators on detritivore communities and decomposition function, different aspects of geographic variation explained variation in function at different trophic levels. The effects of predators on detritivore community structure were influenced by biogeographic differences in the traits of top predators among sites. In contrast, the top-down effects of predators on decomposition rates were influenced by bioclimatic variation in ecosystem type and resource quality. Geographic variation in characteristics of the bromeliad habitat may have also had an influence on the function of the community; for example ground-dwelling bromeliads in Brazil vs. epiphytic bromeliads in Costa Rica and Puerto Rico, or the species of leaf litter most common as a resource base. As stated above, this biogeographic influence on community function also affected the sensitivity of the community to habitat size at a local scale.

Replicating experiments over such a large geographic range has considerable advantages for determining the generality of patterns across sites, and identifying biogeographic influences on community structure and function. However, it also presents some challenges to control potentially confounding variables such as differences in the timing of seasons and species identity across sites. I was able to control for seasonality by timing my experiments for the rainiest season in each site, not necessarily the same time of year. The greatest challenge in interpreting the data from these studies is that we must draw from slightly different species pools to create ostensibly similar communities. For example, the bromeliad-dwelling community in Costa Rica contains 3 species of collector/gatherer type Chironomidae, but its analogue community in Brazil must be assembled with 3 different, but functionally similar, species of Chironomidae. We need to make the assumption, based on known traits of the species and direct observation of feeding behaviours, that these communities are functionally equivalent, but cannot be certain that differences in species composition do not affect community function.

There is some evidence that communities composed of equivalent functional groups but different species can function equivalently. For example, communities of different species of plants from the same functional groups experience no difference in colonization processes (Gilbert, B. pers. comm.). However, the rate and response of other ecosystem functions remains untested. Therefore the results we present as being most likely the result of environmental differences among sites, could potentially also be influenced by differences in behaviour, feeding efficiency, or interactions of differing species. Indeed, some of the patterns I discovered rely on differences among species of resources, in which leaf litter quality of restinga leaf species in Brazil changes the relationship between invertebrates, decomposition, and bromeliad

size when compared to the rainforest sites of Costa Rica and Puerto Rico. So, while differences in the species used in experiments among sites have the potential to confound some interpretation of environmental effects, they can also explain otherwise puzzling differences in community structure and function relationships.

These results support the idea that community structure and function are influenced by factors at several spatial scales (Ricklefs and Schluter 1993, Krawchuk and Taylor 2003, Banks-Leite et al. 2013, Chase and Knight 2013). By taking advantage of an easily replicated and broad-ranging study system such as bromeliad phytotelmata, I have been able to assemble experimental data showing hierarchical effects of spatial scale on the local community in a common ecosystem. Spatial patterns in habitat influenced different community processes at different scales that determined the community structure and function. Local habitat size influenced the trophic structure of the community through differences in predator colonization, which affected decomposition rate. Regional metacommunity size influenced dispersal, cross-ecosystem dynamics and metapopulation persistence, which determined overall functional structure of the community. Large-scale geographic differences in climate and continental connectivity influenced resource use and biogeographic patterns in species pools that affected both top-down control of the community, and the relationships between community structure and function at smaller scales.

Understanding the mechanisms at each spatial scale that influence the relationship between community structure and function is crucial to identify general patterns that can be applied over large geographic ranges (Noda 2004). These studies are a first step, identifying the response of a few community and ecosystem functions to spatial patterns in habitat, and the interactive effects at the local and large geographic scale. Further research to test these patterns

in other ecosystems would broaden the applicability of the relationships. For example, other aquatic habitats with a similar structure to the bromeliad system such as freshwater ponds or intertidal pools, or even terrestrial systems with differences in species composition, such as temperate forests in which small mammalian predators live, but large carnivores are present (e.g. in Canada) or absent (e.g. in New Zealand, or the U.K.). These other types of ecosystems can be used to test if local habitat size affects trophic structure and function in the same manner across environmental scales, and if differences in function are due to initial community structure or underlying environmental differences. Additionally, more hierarchical experiments designed to test for interactions between other spatial scales (e.g. metacommunity size and local patch size) would increase our knowledge of how local communities are influenced by the landscape in which they are found. This collection of experimental studies is an important beginning step to describing the important relationships between habitat structure, community structure, ecosystem function and spatial scale.

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## APPENDIX

**Table S5.1.** Abundance of each species in experimental communities. Top heading designates the community type, and second heading designates the field site in which it was assembled.

Species	BR		CR		PR		
	Brazil	Brazil	Costa Rica	Puerto Rico	Brazil	Costa Rica	Puerto Rico
Oligochaete			3			1	
Ostracoda, <i>Elpidium</i> sp. <sup>1</sup>	13	3		3	1		1
Diptera, Culicidae, <i>Culex</i> sp.	3	2	2	2	3	3	3
Diptera, Chironomidae, <i>Chironomus</i> sp.	3	5	5		2	2	
Diptera, Chironomidae, <i>Polypedilum</i> sp. 1 <sup>2</sup>	1	2	2		1	1	
Diptera, Chironomidae, <i>Polypedilum</i> sp. 2	1	2					
Diptera, Chironomidae, Orthocladiinae			2	2			1
Diptera, Chironomidae, <i>Tanytarsus</i> sp.				5			2
Diptera, Ceratopogonidae				2			
Diptera, Tipulidae, <i>Trentepholia</i> sp.		3	3	3	2	2	2
Diptera, psychodidae, <i>Sciaridae</i> sp. <sup>3</sup>	1						
Coleoptera, Scirtidae	2	4	4	4			
Trichoptera, <i>Phylloicus bromelarium</i> <sup>3</sup>	2						
<b>Total Individuals</b>	<b>26</b>	<b>21</b>	<b>21</b>	<b>21</b>	<b>9</b>	<b>9</b>	<b>9</b>

<sup>1</sup>Not found in the Costa Rica field site

<sup>2</sup> *Polypedilum* is extremely rare in the Puerto Rico field site

<sup>3</sup> Only found at the Brazil field site

## ANOVA design, chapter 5

Three experiments were conducted, one in each site. Communities were constructed representative of different biogeographic origins, either Brazil (BR), Costa Rica (CR) or Puerto Rico (PR). We also included a PR community with doubled abundances (2xPR). Either no predator was included (No), or a Tanypodinae chironomid (C) or a damselfly (D). These experiments were analysed with seven partially overlapping ANOVAs (red boldface font shows treatments included in each ANOVA), and so significance was assessed with Bonferonni adjustment of alpha ( $\alpha=0.05/7$  tests = 0.007)

### ANOVA 1:

		Origin			
		BR	CR	PR	2xPR
Site	Brazil	<b>No, C, D</b>	No, C, D	No, C	
	Costa Rica		<b>No, C, D</b>	No, C	No
	Puerto Rico			<b>No, C</b>	No

### ANOVA 2

		Origin			
		BR	CR	PR	2xPR
Site	Brazil	No, C, D	No, C, D	<b>No, C</b>	
	Costa Rica		No, C, D	<b>No, C</b>	No
	Puerto Rico			<b>No, C</b>	No

### ANOVA 3

		Origin			
		BR	CR	PR	2xPR
Site	Brazil	No, C, D	<b>No, C, D</b>	No, C	
	Costa Rica		<b>No, C, D</b>	No, C	No
	Puerto Rico			No, C	No

**ANOVA 4**

		Origin			
		BR	CR	PR	2xPR
Site	Brazil	<b>No, C, D</b>	<b>No, C, D</b>	<b>No, C</b>	
	Costa Rica		No, C, D	No, C	No
	Puerto Rico			No, C	No

**ANOVA 5**

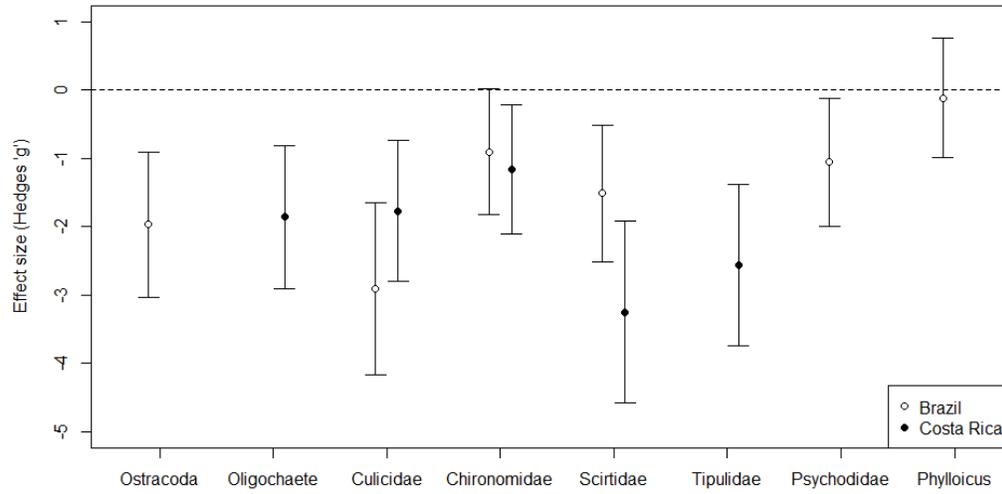
		Origin			
		BR	CR	PR	2xPR
Site	Brazil	<b>No, C, D</b>	<b>No, C, D</b>	No, C	
	Costa Rica		No, C, D	No, C	No
	Puerto Rico			No, C	No

**ANOVA 6**

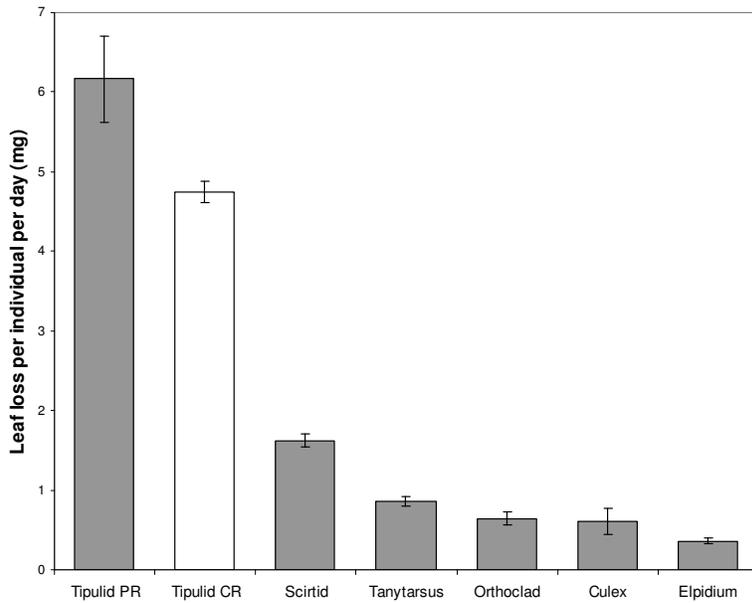
		Origin			
		BR	CR	PR	2xPR
Site	Brazil	No, C, D	No, C, D	No, C	
	Costa Rica		<b>No, C, D</b>	<b>No, C</b>	No
	Puerto Rico			No, C	No

**ANOVA 7**

		Origin			
		BR	CR	PR	2xPR
Site	Brazil	No, C, D	No, C, D	No, C	
	Costa Rica		<b>No, C, D</b>	<b>No, C</b>	<b>No</b>
	Puerto Rico			No, C	No



**Figure S5.1.** Effect of damselfly predators (+/- 95% confidence interval) on the survival of taxa in detritivore communities in Brazil and Costa Rica. Confidence bars crossing zero (dashed line) indicate no effect on survival, and effects below zero indicate a significant reduction in survival in the presence of damselfly predators.



**Figure S5.2.** Mean per-individual, per-day feeding rates from single species trials in Puerto Rico (grey bars) and Costa Rica (white bar)