INVERTEBRATE CONSUMER INFLUENCES ON ECOSYSTEM PROCESSES IN A
RAINFOREST UNDERSTORY

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by

Chelse M. Prather

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Gary Belovsky, Director

Graduate Program in Biology
Notre Dame, Indiana
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Abstract

by

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Consumer organisms are frequently considered passive components of tropical forests with negligible effects on ecosystem processes. However, non-tropical consumers play known important roles by changing resources available to detrital food webs. In rainforests, plants sequester most nutrients, and microbes facilitate important nutrient transformations. Consequently, only plants and microbes are assumed to affect how rainforests function. If tropical consumers alter detrital resources like their non-tropical counterparts, they may also have important effects on rainforest functioning, particularly in light gaps, where increased resources due to rapid plant growth and litterfall lead to higher consumption rates.

This dissertation examines how common herbivores (walking sticks, Lamponius portoricensis) and detritivores (snails, Megalomastoma croceum) affect a Puerto Rican rainforest under two different canopy covers. I hypothesized that herbivores prefer faster decomposing plants would shift plants to a slower decomposing plant community. This shift would reduce resource quality for decomposers, consequently reducing decomposition, nutrient availability and plant production. I predicted that detritivores
would accelerate decomposition by fragmenting litter, consequently increasing nutrient availability and primary production. Lastly, I expected consumer effects to be greatest in light gaps because of higher feeding rates. To test these hypotheses, I conducted enclosure experiments manipulating canopy, herbivore and detritivore presence. I measured consumer effects on plant growth, nutrient cycling, and decomposition. These data were used to parameterize a trophic interaction model, which examined the role of trophic interactions on nutrient cycling in this rainforest.

The experiments and models show that consumers significantly affect this rainforest, but almost exclusively in light gaps. Herbivores increased plant growth and nutrient availability, but decreased litter decomposition rates by driving a shift to a slower decomposing plant community. This shift supplied poorer quality resources to microbial decomposers, leading to less abundant and rich litter bacteria. Detritivores reduced plant growth and nutrient availability, but did not affect decomposition rates. These detritivores may selectively feed on microbial groups crucial to N-cycling, thus reducing nutrient availability. These results challenge the common assumption that consumers are unimportant to rainforest functioning by providing evidence that consumers alter rainforest processes, particularly after disturbances.
This is for my parents, who have supported me along every step of the way.
## CONTENTS

Figures................................................................................................................................ vi

Tables......................................................................................................................................... ix

Acknowledgments.............................................................................................................. xi

Chapter 1: Introduction ....................................................................................................... 1
  1.1. Literature review ........................................................................................................... 2
  1.2. The role of species in ecosystem functioning ................................................................. 4
      1.2.1. Herbivore and detritivore effects on ecosystems .............................................. 7
  1.3. Tropical disturbances and consumers ................................................................................ 9
  1.4. Dissertation overview ................................................................................................... 10
  1.5. Study system and species ............................................................................................. 11
  1.6. Experimental enclosure study ...................................................................................... 12
  1.7. Literature cited ............................................................................................................. 13

Chapter 2: Consumers alter plant production in a rainforest understory ...................... 18
  2.1. Abstract .......................................................................................................................... 18
  2.2. Introduction .................................................................................................................... 19
  2.3. Methods .......................................................................................................................... 23
      2.3.1. Study site and species ...................................................................................... 23
      2.3.2. Experimental design .......................................................................................... 26
      2.3.3. Data analysis ......................................................................................................... 29
  2.4. Results ............................................................................................................................. 30
      2.4.1. Plant species differences ..................................................................................... 32
      2.4.2. Canopy cover effects ......................................................................................... 32
      2.4.3. Enclosure effects .................................................................................................. 34
      2.4.4. Herbivore effects ................................................................................................. 35
      2.4.5. Detritivore effects ............................................................................................... 38
      2.4.6. Herbivore + detritivore interactions ................................................................... 39
  2.5. Discussion ......................................................................................................................... 40
      2.5.1. Herbivore impacts ............................................................................................... 40
      2.5.2. Detritivore impacts ............................................................................................. 41
      2.5.3. Enclosure effects ................................................................................................. 42
      2.5.4. Conclusions: Implications for rainforest functioning ......................................... 43
  2.6. Acknowledgments ............................................................................................................ 43
  2.7. Literature cited ................................................................................................................. 44
Chapter 5: Synthesizing consumer influences on ecosystem processes: A trophic interaction model

5.1. Abstract
5.2. Introduction
5.3. Methods
  5.3.1. Modeling
  5.3.2. Model Parameterization
5.4. Results
  5.4.1. Model validation
  5.4.2. Model sensitivity
  5.4.3. Response to trophic dynamics
5.5. Discussion
5.6. Acknowledgments
5.7. Literature cited

Chapter 6: Conclusions

6.1. An unconvential view of rainforest functioning: the role of trophic interactions
  6.1.1. Herbivore impacts to rainforest ecosystems
  6.1.2. Detritivore impacts to rainforest ecosystems
  6.1.3. Interaction of different consumer trophic levels
  6.1.4. Future research questions
6.2. Final words
6.3. Literature cited
FIGURES

Figure 1.1 The mechanisms by which herbivores and detritivores affect ecosystem processes. ................................................................. 7

Figure 2.1 Study organisms. Top panels are plant species: A) the slow decomposing plant, *Miconia prasina*, and B) the fast decomposing plant, *Piper glabrescens*. Bottom panels are consumer organisms: C) the detritivore, a litter snail, *Megalomastoma croceum*, and D) the herbivore, a walking stick, *Lamponius portoricensis*. These consumers are the most common macro-detritivore and herbivore in the understory of this Puerto Rican rainforest. ................................. 25

Figure 2.2 Pictures of experimental system. The top panel shows experimental enclosures from above. The bottom panel shows one experimental enclosure (left) and an un-enclosed forest baseline plot (right). ........................................... 26

Figure 2.3 Consumer impacts on plant biomass of plant species in light gaps over time. 34

Figure 2.4 Plant community succession one year after treatments had been removed showing A) enclosure impacts, and B) detritivore past presence. Small inset panels show treatment impacts on total plant biomass, and large panels show the total biomass divided into plant life forms. .......................................................... 37

Figure 2.5 Ratio of aboveground to belowground biomass showing A) herbivore treatments and B) detritivore treatments. ................................. 38

Figure 2.6 Percent difference in plant biomass comparing treatment effects to total exclusion enclosures in light gaps................................................. 39

Figure 3.1 Graphical depiction of the components of a simplified nitrogen budget in enclosures. There are 10 components of this simplified nitrogen budget: (1) soil, (2) initial litter, (3) *P. glabrescens* leaves, (4) *P. glabrescens* wood, (5) *P. glabrescens* litter, (6) *M. prasina* leaves, (7) *M. prasina* wood, (8) *M. prasina* litter, (9) herbivore, and (10) detritivore. ................................................. 56
Figure 3.2 Detritivore impacts on the total amount of N (g N / m²) in both closed canopy sites (left) and light gaps (right).

Figure 3.3 Nutrient distribution in treatments: bars depict means ± standard deviation. Horizontally hatched bars are detritivore treatments, vertically hatched bars are herbivore treatments, solid black bars are herbivore + detritivore, and white bars are total exclusion treatments.

Figure 3.4 Treatment effects on the percent change in available nutrients (NH₄, NO₃ and PO₃) between the end and the beginning of the experiment.

Figure 3.5 Herbivore impacts on aboveground plant biomass (left) and plant N (right) of both plant species. Graphs depict the change in biomass or plant N (g / m²) over time as the difference between herbivore treatments and exclusion treatments.

Figure 4.1 Experimental enclosures were replicated in two canopy covers, represented by white and black shading. Un-caged control areas were set-up (see Methods). The first litterbag experiment was replicated in all treatments (LB1), and while the second was not (LB2) was not.

Figure 4.2 Treatment effects on decomposition rates from LB1. Bars represent mean k values (± 1 SE). A) Litter sources and mesh size effect. B) Disturbance effect. C) Consumer effects.

Figure 4.3 Experimental results of ratios of fast (P. glabrescens) litter to slow (M. prasina) litter. Dashed lines represent a 1:1 ratio of fast:slow litter, and points represent the mean ratios (± 1 SE) of fast:slow litter biomass. A) Pooled herbivore effects. Consumer effects across: B) closed canopy sites, and C) light gaps.

Figure 4.4 Herbivore effects on bacterial richness and abundance across herbivore treatments. Bars represent mean ± 1 SE. Richness (top panels) was measured as the total number of significant TRFLP peaks (over 50 FU) in a given sample, and abundance (bottom panels) was measured as the total area underneath significant peaks of the electropherogram.

Figure 4.5 Proposed graphical hypotheses for consumer alteration of decomposition. Arrows represent the movement of biomass from one component to another, and the circle represents the rate of decomposition, where the left panel is without herbivores and the right panel is with herbivores. Thick arrows represent the important pathways of material movement observed in this study.
Figure 5.1 Graphical depiction of concepts used in the Trophic Interaction Model. Solid arrows indicate biomass being built, and dashed lines represent biomass being lost by plants via litterfall, or decomposition. Detritivores are not explicitly built into the model, as they had no significant impacts on decomposition rates. 112

Figure 5.2 The observed and expected average values of each component within each experimental treatment. Gray lines are observed values and black lines are predicted values. “*” denotes significant differences between the observed and expected values, as determined by paired t-tests at each point. 120

Figure 5.3 Main ecosystem components for average enclosures when no consumers (top panel), herbivores (middle panel), and predators (bottom panel) are present. ... 122

Figure 5.4 Main ecosystem components for average enclosures when herbivore feeding preferences are switched from fast decomposing (left) to slow decomposing plants (right). ................................................................. 124
Tables

Table 1.1  Literature review of how consumers affect processes across ecosystems, biomes & taxons. .......................................................... 6

Table 2.1  Regressions estimating total aboveground biomass of plants. ................. 31

Table 2.3  Results from fully-crossed repeated-measures ANOVA on plant biomass with 4 factors (canopy cover, herbivore and Detritivore presence, and plant species), and time as the repeated measure. .......................................................... 33

Table 2.4  Results from a fully-crossed ANOVA on the arcsin squared transformed ratio of aboveground: belowground biomass. .......................................................... 36

Table 2.5  Results from a fully-crossed ANOVA on the plant community biomass a year after consumer treatments had been removed. .................................................. 36

Table 3.1  Percent N used in nitrogen budget. Leaf and soil N are averages of values used because dynamic values were used in the budget, while the other values are static values for the budget. .......................................................... 59

Table 3.2  Fully-crossed Repeated measures ANOVA results for amount of total N (g per m²) in treatments. .......................................................... 60

Table 3.3  Mean LN response ES ± standard deviation of treatments enclosure (E), detritivore (D) and herbivore (H) effects on N in each component.................................. 63

Table 4.1  Mixed species litterbag composition. ......................................................... 84

Table 4.2  k value analysis results from fully-crossed ANOVA. .............................. 89

Table 4.3  Frass and initial litter chemistry of different litter types (Means with SE) ......... 91

Table 4.4  Total litter (g/m² dry weight) analysis results from fully crossed repeated-measures ANOVA. .......................................................... 93
Table 4.5  Results from repeated-measures ANOVA on fast: slow litter. .......................... 94

Table 4.6  Results from a 3 x 2 ANOVA on bacterial TRFLP richness and abundance. 95

Table 5.1  Model parameters. .......................................................................................... 121
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CHAPTER 1:
INTRODUCTION

“If we and the rest of the backbone animals were to disappear overnight the rest of the world would get along pretty well. But if they (the invertebrates) were to disappear, the land’s ecosystems would collapse.” (Attenborough 2005)

The biotic components that construct an ecosystem are known as ecosystem structure. A question that has driven ecological research for decades is: how do different components of an ecosystem’s structure affect how that ecosystem functions? While investigating this question, ecologists have discovered that microbes fill a variety of roles, including providing essential nutrients to primary producers (van der Heijden et al. 2008). In turn, primary producers are essential to ecosystems at global scales because they bridge solar and biological energy (Field et al. 1998; Jobbagy & Jackson 2000). Subsequently, primary consumer organisms (i.e., herbivores and detritivores) convert primary production into energy and resources that are critical to higher trophic levels and other food webs (Hairston et al. 1960; Polis & Strong 1996).

Although there are many examples of herbivores and detritivores altering primary production, nutrient cycles and decomposition in a variety of ecosystems, how important consumer impacts are to ecosystems globally remains uncertain (Huntly 1995). Several significant reviews have attempted to answer this question (Weisser and Seimann 2005). However, few studies have quantified consumer impacts to the most complex and highly
productive systems on Earth: tropical rainforests. So the question remains: do consumers significantly affect the functioning of the complex and highly productive rainforests? If so, do consumers affect tropical rainforests by the same mechanisms that they do in non-tropical ecosystems? And lastly, because many tropical systems are frequently disturbed, does disturbance alter consumer impacts to rainforest ecosystems? These are the major questions that I attempt to answer in this dissertation.

In this introduction, I use a literature search to show that very few studies have examined consumers’ impacts to terrestrial tropical ecosystems. I then describe the mechanisms by which consumers have been shown to impact the functioning of other ecosystems. Lastly, I describe how I quantify rainforest consumer impacts and examine the potential mechanisms of their impacts in this dissertation.

1.1. Literature review

To look at how research regarding consumers’ effects on ecosystem processes is distributed across different ecosystem types, biomes, and taxonomic consumer groups, I conducted several Web of Science searches (7-11-2010). I ran a total of 12 topical searches for two primary consumer trophic groups (herbivores OR detritivores) and their combination (herbivores AND detritivores), and either the general term “ecosystem process” or one of three specific ecosystem processes (primary production, nutrient cycling OR decomposition). I recorded all hits, and then looked at each publication producing a hit. Only those publications that directly measured how an herbivore or detritivore (or their combination) affect ecosystem processes were used. For each paper
used, I recorded the ecosystem type, biome, and the general consumer taxonomic group (invertebrate, bird, amphibian or mammal) that was studied.

This literature search highlights some of the current gaps in knowledge regarding how consumers affect their ecosystems. Out of a total of 415 hits on these 12 different searches, roughly $\frac{1}{4}$ (93 manuscripts) directly measured a consumer’s impact on an ecosystem process (Table 1.1; see Appendix A for a full list of the references used in this table). This result is likely due to many ecosystem level studies “black-boxing” consumer effects on ecosystems (i.e. avoiding the internal complexity in consumer trophic levels), which was especially prevalent in early ecosystem ecology. The studies that do directly measure consumer effects often measure how a particular trophic level affects the ecosystem process that involves the material that the consumer feeds on (i.e., researchers tend to study how herbivores affect primary production and detritivores affect decomposition). Only one study looked at the effects of herbivores and detritivores in combination with one another (Mysterud et al. 2005).

In general, most research on this topic looks at how invertebrate consumers influence temperate forest ecosystem processes. Only 17% of these studies occurred in tropical systems, and most tropical studies examine detritivore impacts on decomposition or herbivore impacts on plant production. Only 2 studies looked at the effect of terrestrial consumers on tropical forest ecosystems (Feeley & Terborgh 2005; Fonte & Schowalter 2005), and only one study examined how herbivores impact decomposition (Fonte and Schowalter 2005). This research occurred at my study site and served as the basis for my predictions. None of the tropical studies in my literature search looked at herbivores and detritivores in combination with one another.
The vast biodiversity in tropical forest ecosystems makes the description of the ecosystem structure in these systems very difficult, which is probably why consumer impacts in these ecosystems are so understudied. A general conceptual framework for regarding how primary consumers (i.e., herbivores and detritivores) affect non-tropical ecosystem functioning has emerged, and this is described below. Because such little research has examined consumer impacts to tropical forest processes, these trophically complex ecosystems provide excellent tests of this conceptual framework.

1.2. The role of species in ecosystem functioning

The role of species in maintaining an ecosystem’s functioning has been pondered since the beginnings of ecology, when natural historians like Charles Darwin noted that sediment bioturbation by earthworms can have dramatic effects on soil morphology at large scales (1896). As ecology became a more formal discipline, one of the early and important concepts that emerged was the important role that plants play in the facilitation of succession after disturbances (Cowles 1899; Connell & Slatyer 1977). In the past several decades, with the recognition of alarmingly rapid declines of biodiversity in many systems (World Resources Institute 2003), the role of species in their respective ecosystems has become a hot topic of ecological debate (e.g., Loreau et al 2001; Hooper et al 2005; Loreau et al 2010). Countless studies have looked at how plant diversity affects ecosystem functioning (e.g., Naeem et al 1994). A special issue of Bioscience was dedicated to how consumers affect ecosystems several decades ago (1984, Volume 34, Number 3). More recently, researchers have examined the effect of both consumer
diversity (e.g., Duffy et al 2003) and species functional traits on ecosystem processes (e.g., Boulton et al 2008).

Some organisms have impacts to their ecosystems that are more apparent than others. Ecosystem engineers (sensu Jones et al. 1994) are organisms that alter their physical surroundings thereby modifying the habitats in which they live. Classic examples of ecosystem engineers include beavers, which build dams that alter the flow of water, sediments and nutrients in freshwater systems and termites that build large biogenic nesting structures, creating localized patches of fertility.

Many consumers, though, do not change the physical structure of the habitats that they live in, but still have important impacts to ecosystem functioning. Although several researchers have claimed that consumers play a crucial role in maintaining the functioning of ecosystems globally (Wilson 1987; Kellert 1993; Wardle 2002; Weisser & Siemann 2004), the potentially important role of consumers is not still well understood or accepted across all ecosystems.
# TABLE 1.1

LITERATURE REVIEW OF HOW CONSUMERS\(^1\) AFFECT PROCESSES ACROSS ECOSYSTEMS\(^2\), BIOMES\(^3\) & TAXONS\(^4\).

<table>
<thead>
<tr>
<th>Group</th>
<th>Process</th>
<th>Hits Used</th>
<th>Ecosystem</th>
<th>Biome</th>
<th>Consumers</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>FOR GL FW WL MAR SV TEM TRO TUN</td>
<td>MAR</td>
<td>BOB</td>
</tr>
<tr>
<td>D</td>
<td>Decomposition</td>
<td>16</td>
<td>11</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td></td>
<td>Primary production</td>
<td>14</td>
<td>29</td>
<td>(1)</td>
<td>(2)</td>
</tr>
<tr>
<td>H</td>
<td>Decomposition</td>
<td>85</td>
<td>8</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td></td>
<td>Nutrient cycling</td>
<td>55</td>
<td>16</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td></td>
<td>Primary production</td>
<td>37</td>
<td>41</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td>H + D</td>
<td>Decomposition</td>
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<td>0</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td></td>
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<td>0</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td></td>
<td>Primary production</td>
<td>0</td>
<td>0</td>
<td>(0)</td>
<td>(0)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>415</td>
<td>93</td>
<td>(31)</td>
<td>(0)</td>
</tr>
</tbody>
</table>

\(^1\) Herbivores = H and detritivores = D

\(^2\) Forests = FOR, grasslands = GL, freshwater systems = FW, wetlands = WL, marine systems = MAR, savannahs = SV

\(^3\) Temperate = TEM, marine = MAR, tropical = TRO, tundra = TUN, boreal = BOR, polar = POL, desert = DES, and alpine systems = ALP

\(^4\) Invertebrates = INV, mammals = MAM, birds, and herps
1.2.1. Herbivore and detritivore effects on ecosystems

In this dissertation, I use concepts largely developed in temperate systems to build hypotheses about how tropical consumers affect ecosystem processes. In general, herbivores and detritivores have impacts on ecosystem functioning by: 1) physically altering plant and litter material through the act of feeding; 2) the production of nutrient-rich frass; and 3) preferential feeding on plants and litter or microbes. Figure 1.1 shows the main mechanisms by which herbivores and detritivores affect primary production, nutrient cycling and decomposition, and these mechanisms are described in detail below.

Figure 1.1 The mechanisms by which herbivores and detritivores affect ecosystem processes.
Herbivore effects

Herbivore feeding decreases the standing stock biomass of plants, and can stimulate plants to reallocate biomass belowground (Dyer 1993). Herbivores may also increase greenfall, the premature abscission of green leaf material, through inefficient feeding (Schowalter 2000). Although invertebrate herbivore frass is more nutrient rich than most other detritus, frass may either stimulate (Sirotnak & Huntly 2000; Fonte & Schowalter 2005) or inhibit soil nutrient availability (Hanlon & Anderson 1979). Selective feeding by herbivores can also either increase or decrease decomposition rates and nutrient release from litter. The direction of the change depends on the nutrient content and quality of the herbivores’ preferred foliage. For example, if herbivores prefer to consume fast decomposing plants, then the abundance of these plants decreases, creating a slow decomposing plant community. Decomposers subsequently respond adversely to the increase in slow-decomposing, poor quality litter, and rates of decomposition and litter nutrient release decline resulting in a reduction of plant nutrient availability and ultimately primary production (Pastor et al. 1988; Brown & Gange 1992; de Mazancourt & Loreau 2000; Schmitz et al. 2000; Feeley & Terborgh 2005). Alternatively, herbivores selectively feeding on slow decomposing plants may increase primary production by increasing high quality resources to decomposers and plant nutrient availability (McNaughton 1985; Holland 1995; Belovsky & Slade 2000).

Detritivore effects

Detritivores comminute litter (i.e., break it into smaller pieces), thus accelerating decomposition by exposing more surface area to litter microbial activity. This
acceleration of decomposition by detritivores has been shown to occur in tropical forests (Gonzalez & Seastedt 2001). Increased decomposition rates may lead to greater nutrients available to plants and thus increased plant production (Swift et al. 1979). Beyond litter comminution, detritivores may increase decomposition rates and nutrient availability by acting as dispersal agents of fungal and bacterial propagules within the litter (Behan & Hill 1978) while adding inputs of detritivore frass, which act similarly to herbivore frass inputs. Detritivores may also alter decomposition and nutrient cycling by selectively feeding on microbial groups that are important to these processes. Selective feeding by detritivores has seldomly been explored in terrestrial systems (but see Moore et al. 1988; Wardle et al. 2002). If terrestrial detritivores selectively feed on microbes and alter microbial functional composition, nutrient transformation rates may either increase or decrease depending on the functional role of the preferred microbial group.

In this dissertation, I will explore whether the mechanisms that have been demonstrated in non-tropical ecosystems occur in tropical rainforests. All of the mechanisms described above act concurrently, so I consider the net effect of these mechanisms on my study system.

1.3. Tropical disturbances and consumers

Because consumer species have been understudied in tropical systems, the current understanding of tropical forest functioning does not include consumer effects. However, disturbance is one of the main drivers of changes to rainforest ecosystem structure, with thousands of publications dedicated to the subject of tropical gap dynamics (e.g., Brokaw and Grear 1991, Foster et al 1998). In light gaps, plants grow rapidly, and new foliage is
often an ideal resource for herbivores. Since plant growth is rapid, litterfall is elevated, resulting in increased resources for detritivores, also. With increased resources, consumption rates are higher, so any impacts that consumers have on ecosystem processes may be amplified. Additionally, because herbivores often prefer gap specialists compared to shade tolerant plants, their impacts to plants may be especially amplified in light gaps (Coley & Barone 1996, Angulo-Sandoval & Aide 2000; Spiller & Agrawal 2003).

1.4. Dissertation overview

Do consumers significantly affect how tropical forests function? In this dissertation, I seek to answer this question in a Puerto Rican rainforest understory using field experiments coupled with analytical chemistry, molecular biology, and theoretical modeling techniques. I use a reductionist approach to examine how the most common herbivores and detritivores affect rainforest functioning: first, I ask how consumers alter primary production, a complex phenomenon, and then examine whether consumer impacts to primary production can be reduced to simpler mechanisms involving other ecosystem processes. Specifically:

1. In Chapter 2, I ask: do invertebrate herbivores and detritivores impact the growth and production of two different plants in a rainforest understory? To answer this, I measured the biomass of plants within experimental treatments annually until plants were harvested at the end of the experiment. Upon final harvest, I used dimensional analysis to examine the impact of these two consumers on the plant biomass over time.

2. Next, in Chapter 3, I ask: can differences in primary production between consumer treatments be attributed to their alteration of nutrient distribution or availability? I investigated how snails and walking sticks affect nutrient
availability in the soil and the distribution of nutrient within different components of nutrient budgets using analytical chemistry techniques.

3. In Chapter 4, I ask: can consumer impacts on nutrient distribution and availability be explained by these consumers’ effects on litter decomposition and the litter microbial community? I measured litter decomposition rates and quantified the litter microbial community using litterbag experiments coupled with molecular biology techniques.

4. Lastly, in Chapter 5, I ask: can proposed mechanisms of consumer impacts be supported with predictions from a model? I developed a general model of rainforest functioning and examined whether my proposed mechanisms for consumer ecosystem-level effects were supported by the predictions of this model. I then used this model to develop hypotheses about how additional trophic complexity may affect rainforest functioning.

1.5. Study system and species

This study was conducted at the Luquillo Long Term Ecological Research site (LUQ LTER; described in Odum & Pigeon 1970). LUQ is located in the Northeastern corner of Puerto Rico (18° 19' N, 65° 45' W). This forest is frequently hit by tropical storms, which create large light gaps in the forest, and consequently the forest is in an almost constant state of secondary succession (Waide & Lugo 1992). Therefore, the ecosystem structure of LUQ is driven by disturbances. This insular forest has a relatively low floral and faunal richness compared with mainland tropical sites, and consequently LUQ is one of the only tropical forests where the food web has been described in detail (Waide & Reagan 1996). Thus, this forest is an ideal location to begin to examine the role of consumers in rainforest systems because there is a basic understanding of the important components of this system’s food web.

*Miconia prasina* and *Piper glabrescens* were chosen as representatives of the understory plant community for this experiment because these genera are abundant across
the neotropics (Molina & Alemany 1997). *M. prasina* is a small shrub-like tree (Loigier 1995), and is an important early colonizer at LUQ (Aide et al. 1996). *P. glabrescens* is a common understory shrub in Puerto Rico that decomposes faster than *M. prasina* (Prather, Chapter 4). The invertebrate consumers used in this experiment were *Megalomastoma croceum*, which is the most abundant detritivorous litter snail at LUQ (Prather, unpublished) and *Lamponius portoricensis*, which is the most abundant generalist herbivore in the forest (Willig et al. 1986; Willig et al. 1993). These plants and consumers were chosen because they are abundant, commonly studied, and easy to transport and manipulate.

1.6. Experimental enclosure study

This experiment used a fully crossed, 3 x 2 factorial ANOVA design that manipulated herbivore, detritivore, and canopy cover presence to test consumer impacts on ecosystem processes. Enclosures and controls were replicated in 3 light gaps and 3 closed canopy sites. Light gaps and closed canopy sites were located in close proximity to one another. Data from this experiment was analyzed in Chapters 2-4, and was used to paramaterize the model in Chapter 5.

*In this dissertation, I hope to further elucidate the potentially important roles of invertebrate consumers on the functioning of rainforest ecosystems. If consumer roles are important in the understory of this forest, studies seeking to better understand how*
ecosystem processes operate in tropical rainforests must explicitly consider the role of consumer organisms.

1.7. Literature cited


CHAPTER 2:
CONSUMERS ALTER PLANT PRODUCTION IN A RAINFOREST UNDERSTORY

2.1. Abstract

Consumer effects on tropical forest primary production are often considered negligible because herbivores and detritivores usually consume a small fraction of annual plant and litter production. I examined how an invertebrate herbivore (walking stick) and detritivore (snail) affect the production of two understory plants in light gaps and closed canopy sites in a Puerto Rican rainforest using an enclosure experiment. Aboveground biomass was estimated annually and belowground biomass was measured at the end of the experiment. One year after the consumer treatments were removed, the biomass and composition of the succeeding plant community were measured by harvesting plants growing from the seed bank. Consumers had no significant effects on plant growth in closed canopy sites. Furthermore, consumers only had significant effects in light gaps, where nutrients, not light, are limiting to plant growth. In light gaps, herbivores increased plant growth, but detritivores decreased plant growth. However, with both consumers present, plant biomass increased suggesting that herbivore impacts outweigh

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5 I gratefully acknowledge my coauthor, Gary Belovsky. This manuscript is in preparation for Oecologia.
detritivore impacts. Also, plants stored more biomass belowground with detritivores present, but the ratio of aboveground to belowground plant biomass was not different between herbivore treatments. Detritivore-induced reductions of aboveground plant biomass in light gaps persisted for a year after detritivore treatments were removed, but former detritivore presence did not impact plant composition. Additionally, former herbivore presence had no lasting impact on plant biomass or composition. This study demonstrates that invertebrate consumers can alter understory primary production in rainforests, and underscores the need for more research to understand the potentially important impacts of consumers on tropical ecosystem processes.

2.2. Introduction

Rainforests are some of the most highly productive and diverse ecosystems on Earth. Many factors influence their rapid plant growth and diverse community structure, with disturbances known to be very important (e.g., Brokaw and Grear 1991, Foster et al 1998). However, the potential impacts of rainforest consumers (i.e., trophic groups above primary producers) on plant growth and communities have not been thoroughly studied because of the low biomass of consumers compared to primary producers (Feeley and Terborgh 2005). Additionally, the high levels of biodiversity make the food webs of tropical rainforests hard to describe, which has further led to the pervasive view that consumers are not important to rates of primary production in these systems.

As is typical of other ecosystems, herbivores in these forests generally consume a small fraction of net primary production (11% of leaf material in tropical forests; Coley and Barone 1996), and macro-detritivores consume small amounts of total litterfall. Even
without consuming large quantities of biomass, herbivores and detritivores in other systems alter decomposition rates, nutrients available to plants, and plant production by altering the resources provided to the detrital food web. Although seldom examined (except for one study with a mammalian herbivore: Feeley and Terborgh 2005), consumers may exercise important control over the nutrients available to plants in tropical forests. Additionally, although invertebrate herbivores and detritivores can significantly interact to impact plant production (e.g., Poveda et al. 2005), there have been no studies examining of the interaction of these two trophic groups on plants in the tropics.

Disturbances can drive plant growth and alter community composition in many tropical forests, and subsequently consumer impacts on plants may also be altered by disturbances. Tropical light gaps promote the rapid growth of new leaves thus increasing litterfall (Angulo-Sandoval and Aide 2000; Spiller and Agrawal 2003) and the abundance of gap specialist plants, which are often preferred by herbivores (Coley and Barone 1996). Thus, consumer impacts to plants may be amplified in light gaps where herbivores and detritivores have increased leaves and litter available for consumption. In this study, I use a manipulative enclosure experiment to test if consumers impact aboveground and belowground plant growth in a Puerto Rican rainforest like they do in non-tropical systems, and if light gaps alter their potential impacts.

Studies in non-tropical systems have shown that herbivores and detritivores may impact plants and the nutrients that support primary production by several different mechanisms: 1) the physical effects of feeding on plant and litter structure, 2) the production of feces or frass, and 3) selectively feeding on plants and litter or microbes,
thereby changing the functional composition of the plant and litter microbial communities. These mechanisms are described below for both trophic groups.

Herbivores negatively impact aboveground plant biomass by directly feeding on leaf tissues (Weisser and Siemann 2004), but foliage loss to herbivores may stimulate plants to reallocate biomass belowground (Dyer 1993). Invertebrate herbivore frass that falls to the forest floor may either stimulate (Fonte and Schowalter 2005; Frost and Hunter 2004; Rinker et al. 2001; Sirotnak and Huntly 2000) or inhibit nutrient availability (Hanlon and Anderson 1979). Selective feeding by herbivores may cause a plant community shift, which in turn either increases or decreases nutrient release from litter, depending on the nutrient content of the preferred species. For example, herbivores that prefer highly palatable, fast decomposing plants may shift the plant community to less palatable, slower decomposing plants. Decomposers respond negatively to the influx of poor quality litter produced by slow decomposing plants, which consequently reduces nutrient release from litter and the nutrients available to plants (Pastor et al. 1988; Brown and Gange 1992; de Mazancourt and Loreau 2000; Feeley and Terborgh 2005). Alternatively, herbivores selectively feeding on slower decomposing plants may increase primary production by increasing high quality resources to decomposers and ultimately plant nutrient availability (McNaughton 1985; Holland 1995; Belovsky and Slade 2000, 2002).

Detritivores that directly feed on litter or litter microbes may increase the nutrients available to plants by accelerating decomposition rates through their comminution of litter (i.e., fragmenting it into smaller pieces), thus exposing more surface area to litter microbial activity (Swift et al. 1979). This has been shown to occur in tropical forests.
Detritivores can increase nutrient availability by inputs of detritivore frass, as described above for herbivores. Also, detritivore selective feeding on litter microbial groups may alter nutrient availability, but this mechanism has rarely been explored in terrestrial systems (but see Moore et al. 1988; Wardle et al. 2002). The direction of change to nutrient availability would depend on the functional role of the preferred microbial group. These described mechanisms of consumer impacts on plant production act concurrently, so it is important to look at the net effects of consumer presence on plant production.

In this study, I used an enclosure experiment manipulating the presence of herbivores (walking sticks—*Lamponius portoricensis*) and detritivores (snails—*Megalomastoma croceum*) in light gaps and closed canopy sites to look at consumer impacts to aboveground and belowground plant growth over time. I also measured plant community succession one year after consumer treatments had been removed to see if past consumer presence altered the biomass and composition of the succeeding plant community. I predicted that herbivore presence would decrease primary production since my focal herbivore prefers to consume faster decomposing plants (Sandlin 1989; Sandlin and Willig 1993; Prather unpublished data), and that detritivore presence would increase primary production by increasing nutrient availability to plants through their litter comminution. I also predicted that herbivore consumption would mediate detritivore impacts by altering the quantity and quality of the resources reaching the detrital food web: detritivore feeding should decrease with herbivores present because of lower quality resources. Additionally, I predicted that light gaps would amplify the effects of both groups by providing them with plentiful resources. This study is part of a larger study.
looking at the impact of these consumers on primary production, nutrient cycling and decomposition (Prather, Chapter 3 and 4, this volume).

2.3. Methods

2.3.1. Study site and species

This study was conducted at the Luquillo Long Term Ecological Research site (LUQ LTER), located in the Northeastern corner of Puerto Rico (18°10’N, 65°30’W). LUQ is a subtropical montane wet forest receiving approximately 3,500 mm of rain annually (Thompson et al. 2004). This study was conducted at around 300 m above sea level in the Tabonuco forest, named for the dominant tree, Tabonuco (Dacroydes excelsa Vahl; Brown et al. 1983). LUQ is in a constant state of secondary succession because the forest is frequently hit by tropical storms (Waide and Lugo 1992). This insular forest has a relatively low floral and faunal richness compared with mainland tropical sites; and therefore, LUQ is one of the only tropical forests where the food web has been described in detail (Waide and Reagan 1996). Thus, this forest is an ideal location to begin to examine the role of consumers in rainforest systems because there is a basic understanding of the important components of this food web.

Miconia prasina and Piper glabrescens were chosen for this experiment because they are representative of the understory plant community (Figure 2.1, A and B). The Miconia (Melostomaceae) and Piper (Piperaceae) genera are extremely speciose in the neotropics with 19 and 12 species, respectively, in the Caribbean (Molina and Alemany 1997). Species of these genera have been studied together in several Neotropical
rainforests because they are abundant in these systems (Baldwin and Schultz 1988; Denslow et al. 1987). *M. prasina* is a shrub-like tree (Loigier 1995) that is an important early colonizer at LUQ (Aide et al. 1996). *P. glabrescens* is a common understory shrub that is relatively faster decomposing than *M. prasina* (Prather, Chapter 4, this volume). The focal invertebrate consumers in this experiment (Figure 2.1, C and D) were *M. croceum*, which is the most abundant detritivorous litter snail at LUQ (Prather, unpublished) and *L. portoricensis* is the most abundant generalist herbivore at LUQ (Willig et al. 1986; Willig et al. 1993). These plants and consumers were chosen because they are abundant in the understory, commonly studied, and easy to transport and manipulate.
Figure 2.1 Study organisms. Top panels are plant species: A) the slow decomposing plant, *Miconia prasina*, and B) the fast decomposing plant, *Piper glabrescens*. Bottom panels are consumer organisms: C) the detritivore, a litter snail, *Megalomastoma croceum*, and D) the herbivore, a walking stick, *Lamponius portoricensis*. These consumers are the most common macro-detritivore and herbivore in the understory of this Puerto Rican rainforest.
2.3.2. Experimental design

This experiment was a fully crossed, 3 x 2 factorial design, manipulating herbivore, detritivore, and canopy cover presence (light gaps and closed canopy sites). I used un-enclosed control plots to test the effect of the enclosure. Enclosures and controls were replicated in 3 light gaps (< 10% canopy cover) and 3 closed canopy sites (> 90% canopy cover), which were located in close proximity to one another (< 1000 m) to account for environmental differences. Each site contained 4 enclosures, and 1 control for a total of 24 enclosures and 6 controls (see Figure 2.2 for pictures of experiments).

Figure 2.2 Pictures of experimental system. The top panel shows experimental enclosures from above. The bottom panel shows one experimental enclosure (left) and an un-enclosed forest baseline plot (right).
Mesh enclosures (0.15 mm from Bioquip) were supported by a 3.34 m² PVC frame (Figure 2.2), and trenched into the ground to keep out soil organisms. All litter and visible organisms (including plants) were initially removed from inside enclosures and controls. In both controls and enclosures, non-focal plants and macro-organisms were removed during the experiment: on five occasions, predators (spiders, frogs or lizards) were observed in the enclosures and were removed. Litter was collected from 36 – 1.6 m x 1.6 m areas near the study sites, air dried, homogenized and the average amount of dry litter in each area (1050 ± 50 g) was added to plots to create a similar litter layer.

All consumers were stocked at natural abundances determined by the following methods. Herbivore biomass was determined by marking 50 individuals of both \textit{M. prasina} and \textit{P. glabrescens} and recording the number, weight, sex and size of \textit{L. portoricensis} individuals on each plant every other night for consecutive 2 weeks. Herbivore treatments were subsequently based on the average biomass of these observations: \( \approx 3.6 \text{ g of walking sticks per treatment (} \approx 1.8 \text{ g / m}^2 \text{)}. \) These treatments consisted of generally 6 individuals: 2 adult males, 1 adult female, 2 juveniles and 1 nymph individual. Detritivore biomass was determined by the average biomass of snails in 36-2 m² areas of litter close to study sites. Treatments were based on the average biomass: \( \approx 11.4 \text{ g of snail per treatment (} \approx 5.7 \text{ g / m}^2 \text{; generally 9 individuals}). \) These abundances are higher than previously recorded abundances of \textit{M. croceum} (Secrest 1995; Willig and Camilo 1991) because previous studies only recorded individuals on top of the litter, not inside the litter. Enclosures were stocked with consumers over 2 weeks in August of 2005. Thereafter, herbivores and detritivores in treatments were sampled every 4 months and treatment biomasses were held constant over time.
Individuals of each plant species (0.35 to 0.75 m tall) were located in the forest, transplanted into seedling bags, and grown for 3 months under similar light conditions in common homogenized forest soil. Ten understory plants (5 individuals of each species) were randomly chosen for each enclosure and control. This is a naturally occurring density of understory plants in this forest. Individuals were planted in PVC pipes (10.16 cm diameter, \(\approx 0.25\) m tall), with 12-2 cm diameter holes to allow the exchange of nutrients and water with the soil. Plants were watered with rainwater collected near plots for three consecutive days after being planted and then left to establish.

The number, length and width of several plant variables (listed below) were measured on each individual when they were initially transplanted into enclosures (August, 2005) and annually thereafter in the dry season at LUQ (January of 2006-2008). Plant variables measured were: stems, new (unflushed) and old (completely flushed) leaves, branches and reproductive parts. Plant survival was measured annually and plant abundances were held constant (i.e., when a plant died, it was replaced). All plants were harvested at the end of the experiment in August of 2008 and the dimensional variables described above were again measured. Constituent parts (stem, leaves and branches) were separated, dried and weighed to obtain dry biomass that was used to perform dimensional analysis (King 1991).

Because roots had grown outside the plant pipes, I was not able to extract the total belowground biomass. To estimate belowground biomass, I randomly chose one individual of each plant species in each enclosure upon final harvest. For these individuals, I removed all soil from the PVC pipes in which the plants were growing and weighed the entire mass. Each soil mass, containing soil, roots, and rocks, was placed in
a mesh bag (0.4 µm—which is fine enough to catch fine roots) and soaked overnight in water. The soil was then washed from the bags, leaving only rocks and roots. Rocks were separated from the roots, and I obtained an estimate of the belowground biomass per unit mass of soil.

To look at consumer effects on plant community succession, a year after the experiment had ended (i.e., experimental plants had been harvested and consumer treatments had been removed from enclosures), I harvested all the plants that grew up from the seed bank in enclosures and controls (June 2009) to determine if consumer treatments altered the succession of plants. I separated these plants by plant life form (grasses, herbs, shrubs / saplings, ferns, vines, and mosses) and determined the pooled biomass of each life form.

2.3.3. Data analysis

Any data that were not normally distributed as determined by a Kolomagrov-Smirnoff test were transformed using an appropriate transformation. All statistical analyses were completed with Systat 10 (SPSS, Chicago, Illinois, USA). P-values less than 0.05 were considered significant.

Dimensional analysis was used to estimate total aboveground biomass at each time point. I used multiple forward linear regression using one randomly selected individual from each enclosure and control to develop regression models for each plant species. I used plant dimensional variables as independent variables and final aboveground biomass as the dependent variable.
I assessed treatment effects on changes in plant biomass over time (the summed biomass of all plant individuals of each species in one plot) with a fully-crossed, fixed-effects, repeated measures ANOVA with three main factors (plant species, canopy cover, herbivore and detritivore presence), plant species nested within consumer treatments, and time as the repeated measure \((t = 4: 2005-2008)\). Hereafter, these factors are referred to as T (time), C (canopy cover), H (herbivore presence), D (detritivore presence) and S (plant species). Also, to examine significant H + D interactions, I calculated the percent difference between each consumer treatment plant biomass (H present, D present, and H + D present) and plant biomass with no consumers present (total exclusion = TE) at each time period. I assessed treatment effects on final root biomass per unit soil and the ratio of aboveground: belowground biomass using a 4 x 2 ANOVA (C, H, D, and S). I used a 4-way ANOVA (plant life-form, C, H and D) to determine effects on plant succession after consumer treatments.

Since the H and D treatments consisted of a natural abundance of organisms, H + D enclosures should most closely represent the whole forest but with the enclosure present. I compared control plots (enclosure absent) to the H + D enclosures to determine enclosure impacts on each response variable. Consequently, each statistical test described above was repeated, replacing consumer treatment factors (H and D presence) with an enclosure presence factor (enclosure presence).

### 2.4. Results

Using dimensional analysis, I was able to determine allometric equations to predict plant biomass for each species (Table 2.1).
TABLE 2.1
REGRESSIONS ESTIMATING TOTAL ABOVEGROUND BIOMASS OF PLANTS.  

<table>
<thead>
<tr>
<th>Species</th>
<th>Regression</th>
<th>df</th>
<th>F</th>
<th>P</th>
<th>Adjusted R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. prasina</td>
<td>0.229*(stem diameter) + 0.36*(height) + 0.562*(number of fruit) + 0.493*(new leaf length) – 0.75*(branch length)</td>
<td>10, 15</td>
<td>4459.99</td>
<td>&lt;0.001</td>
<td>0.766</td>
</tr>
<tr>
<td>P. glabrecens</td>
<td>0.329*(stem diameter) + 0.215*(number of new leaves) - 0.359*(number old leaves) + 0.426*(number of branches) + 0.549*(old leaf length)</td>
<td>11, 16</td>
<td>42.59</td>
<td>&lt;0.001</td>
<td>0.642</td>
</tr>
</tbody>
</table>

6 Forward multiple regression was used with dimensional plant variables as independent variables and total aboveground biomass as the dependent variable.
2.4.1. Plant species differences

*M. prasina* individuals grew ~ 90% larger aboveground than *P. glabrescens* individuals across all treatments (Table 2.2 and Figure 2.3), and *M. prasina* had larger root masses than *P. glabrescens* (S, F = 6.20, df = 1, 29, P = 0.014). However, *M. prasina* stored much less biomass belowground (aboveground: belowground biomass—2.278 ± 0.31; Table 2.4) compared to *P. glabrescens* (aboveground: belowground biomass—1.288 ± 0.28). One year after consumer treatments had been removed, the dominant plant life forms were shrubs / saplings (especially a *Desmodium spp.*, *Miconia racemosum*, and *Mecranium amygdalinum*), and grasses (Table 2.4, Figure 2.4).

2.4.2. Canopy cover effects

Aboveground plant biomass increased in light gaps and decreased in closed canopy sites during the experiment in both treatments and controls (Table 2.2). At the end of the experiment, both above- and belowground plant biomass was an order of magnitude higher in light gaps than closed canopy sites (Table 2.3). However, more biomass was stored belowground in closed canopy sites (aboveground: belowground biomass—0.467 ± 0.15) than light gaps (1.268 ± 0.18; Table 2.3 and Figure 2.5), and this pattern held for both plant species. One year after the experiment ended, plants growing up from the seed bank also grew larger in light gaps than closed canopy sites (Table 2.4).
TABLE 2.2
RESULTS FROM FULLY-CROSSED REPEATED-MEASURES ANOVA ON PLANT BIOMASS WITH 4 FACTORS (CANOPY COVER, HERBIVORE AND DETRITIVORE PRESENCE, AND PLANT SPECIES), AND TIME AS THE REPEATED MEASURE. 7

<table>
<thead>
<tr>
<th>Source</th>
<th>ss</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>372356.06</td>
<td>1 372356.06</td>
<td>11.89</td>
<td>0.002</td>
</tr>
<tr>
<td>Time * Canopy cover (C)</td>
<td>442179.29</td>
<td>1 442179.29</td>
<td>14.12</td>
<td>0.001</td>
</tr>
<tr>
<td>Time * Herbivore (H)</td>
<td>1708.35</td>
<td>1 1708.35</td>
<td>0.06</td>
<td>0.817</td>
</tr>
<tr>
<td>Time * Detritivore (D)</td>
<td>21834.82</td>
<td>1 21834.82</td>
<td>0.70</td>
<td>0.411</td>
</tr>
<tr>
<td>Time * Species (S)</td>
<td>368384.88</td>
<td>1 368384.88</td>
<td>11.77</td>
<td>0.002</td>
</tr>
<tr>
<td>Time * C * D</td>
<td>250175.82</td>
<td>1 250175.82</td>
<td>7.99</td>
<td>0.027</td>
</tr>
<tr>
<td>Time * C * S</td>
<td>383353.70</td>
<td>1 383353.70</td>
<td>12.24</td>
<td>0.002</td>
</tr>
<tr>
<td>Time * D * S</td>
<td>94872.68</td>
<td>1 94872.68</td>
<td>3.03</td>
<td>0.163</td>
</tr>
<tr>
<td>Time * C * H * S</td>
<td>182856.92</td>
<td>1 182856.92</td>
<td>5.84</td>
<td>0.042</td>
</tr>
<tr>
<td>Time * C * H * D * S</td>
<td>197573.15</td>
<td>1 197573.15</td>
<td>6.31</td>
<td>0.039</td>
</tr>
<tr>
<td>Error</td>
<td>814089.04</td>
<td>26 31311.12</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Between subjects</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy cover (C)</td>
<td>401299.58</td>
<td>1 401299.58</td>
<td>15.37</td>
<td>0.001</td>
</tr>
<tr>
<td>Herbivore (H)</td>
<td>10174.02</td>
<td>1 10174.02</td>
<td>0.39</td>
<td>0.538</td>
</tr>
<tr>
<td>Detritivore (D)</td>
<td>11968.40</td>
<td>1 11968.40</td>
<td>0.46</td>
<td>0.504</td>
</tr>
<tr>
<td>Species (S)</td>
<td>433914.62</td>
<td>1 433914.62</td>
<td>16.62</td>
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</tr>
<tr>
<td>C * S</td>
<td>337702.95</td>
<td>1 337702.95</td>
<td>12.94</td>
<td>0.001</td>
</tr>
<tr>
<td>Error</td>
<td>678732.56</td>
<td>26 26105.10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

7 Only interactions with $P < 0.2$ are reported.
2.4.3. Enclosure effects

*P. glabrescens* individuals were smaller in controls compared to inside enclosures (enclosure * species, $F = 3.46$, df = 1, 12, $P = 0.044$) while *M. prasina* biomass did not differ inside and outside the enclosures. Root biomass was not different between controls and enclosures (enclosure, $F = 0.968$, df = 1, 14, $P = 0.342$). One year after treatments were removed, plant biomass in light gaps was lower outside enclosures ($457 \pm 87$ g) compared to inside ($317 \pm 76$ g; top panel of Figure 2.3; enclosure * C, $F = 16.84$, df = 1,48, $P < 0.001$). However, plant life-form composition was not different inside and
outside enclosures (top panel of Figure 6; enclosure * plant life-form, $F = 1.138$, df = 5, 48, $P = 0.353$).

2.4.4. Herbivore effects

Herbivores significantly altered patterns of aboveground plant biomass over time, but only in light gaps (Table 2.2, Figure 2.3); herbivore presence had no significant effect on aboveground or belowground plant growth in closed canopy sites. In the presence of herbivores, aboveground $M. prasina$ biomass increased and $P. glabrescens$ biomass decreased, but only in light gaps. Herbivores did not impact belowground production (Table 2.3) or the biomass or composition of succeeding plants a year after the experiment had ended (Table 2.4).
### TABLE 2.3

RESULTS FROM A FULLY-CROSSED ANOVA ON THE ARCSIN SQUARED TRANSFORMED RATIO OF ABOVEGROUND: BELOWGROUND BIOMASS.  

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover (C)</td>
<td>7.04</td>
<td>1</td>
<td>7.04</td>
<td>28.89</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Herbivore (H)</td>
<td>0.46</td>
<td>1</td>
<td>0.46</td>
<td>1.88</td>
<td>0.36</td>
</tr>
<tr>
<td>Detritivore (D)</td>
<td>0.67</td>
<td>1</td>
<td>0.67</td>
<td>2.74</td>
<td>0.24</td>
</tr>
<tr>
<td>Species (S)</td>
<td>8.55</td>
<td>1</td>
<td>8.55</td>
<td>35.05</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>C * D</td>
<td>1.86</td>
<td>1</td>
<td>1.86</td>
<td>7.64</td>
<td>0.019</td>
</tr>
<tr>
<td>C * S</td>
<td>1.62</td>
<td>1</td>
<td>1.62</td>
<td>6.64</td>
<td>0.015</td>
</tr>
<tr>
<td>D * S</td>
<td>1.77</td>
<td>1</td>
<td>1.77</td>
<td>7.27</td>
<td>0.023</td>
</tr>
<tr>
<td>C * D * S</td>
<td>1.23</td>
<td>1</td>
<td>1.23</td>
<td>5.04</td>
<td>0.078</td>
</tr>
<tr>
<td>Error</td>
<td>7.07</td>
<td>29</td>
<td>0.24</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

### TABLE 2.4

RESULTS FROM A FULLY-CROSSED ANOVA ON THE PLANT COMMUNITY BIOMASS A YEAR AFTER CONSUMER TREATMENTS HAD BEEN REMOVED.  

<table>
<thead>
<tr>
<th>Source</th>
<th>SS</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover (C)</td>
<td>124124.65</td>
<td>1</td>
<td>124124.65</td>
<td>40.10</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Herbivore (H)</td>
<td>633.85</td>
<td>1</td>
<td>633.85</td>
<td>0.21</td>
<td>0.65</td>
</tr>
<tr>
<td>Detritivore (D)</td>
<td>8790.8792</td>
<td>1</td>
<td>8790.8792</td>
<td>2.84</td>
<td>0.186</td>
</tr>
<tr>
<td>Plant life-form (P)</td>
<td>216620.01</td>
<td>14</td>
<td>43324.00</td>
<td>14.00</td>
<td>0.00</td>
</tr>
<tr>
<td>C * D</td>
<td>18324.6496</td>
<td>1</td>
<td>18324.6496</td>
<td>5.92</td>
<td>0.039</td>
</tr>
<tr>
<td>C * P</td>
<td>216611.12</td>
<td>5</td>
<td>43322.22</td>
<td>14.00</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Error</td>
<td>297156.51</td>
<td>240</td>
<td>3095.38</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

---

8 Only interactions with \( P < 0.2 \) are reported.

9 Only interactions with \( P < 0.2 \) are reported.
Figure 2.4 Plant community succession one year after treatments had been removed showing A) enclosure impacts, and B) detritivore past presence. Small inset panels show treatment impacts on total plant biomass, and large panels show the total biomass divided into plant life forms.
2.4.5. Detritivore effects

Like herbivores, detritivores had no significant effects on aboveground or belowground plant growth in closed canopy sites. However, in light gaps detritivores decreased aboveground biomass of both plant species over the course of the experiment (Table 2.2, Figure 2.3). Also, both plant species stored more biomass belowground in the presence of detritivores (Figure 2.5). This pattern was stronger in *M. prasina* than *P. glabrescens* individuals. One year after treatments were removed, plant community biomass was much lower where detritivores had been present in light gaps (see bottom
panel of Figure 2.6; $C * D, P = 0.039$). However, detritivores did not impact plant life-form composition.

2.4.6. Herbivore + detritivore interactions

There was a significant one significant herbivore + detritivore interaction: for plant biomass, the $T \times C \times H \times D \times S$ interaction was significant (Table 2.2). To look more closely at this interaction, I compared the relative magnitude of consumer treatments by calculating the percent difference between each consumer treatment’s plant biomass compared to the plant biomass with no consumers present at each time period. The pattern of change in plant biomass of the $H + D$ treatment mimicked the $H$ treatments (i.e., plant biomass increased over time relative to total exclusion), but differed directionally from $D$ treatments. This result suggests that detritivore impacts on plant growth were overwhelmed by herbivore impacts.

![Figure 2.6 Percent difference in plant biomass comparing treatment effects to total exclusion enclosures in light gaps.](image-url)
2.5. Discussion

This is the first study that demonstrates invertebrate consumers can alter patterns of plant growth in a rainforest, similar to their non-tropical counterparts. I predicted that consumer impacts would be amplified in light gaps because of increased resource availability to consumers, and, interestingly, both snails and walking sticks altered plant growth only in light gaps. In this particular forest, plant and consumer populations are driven by frequent disturbances (Waide and Lugo 1992). Herbivory is known to increase after hurricanes at LUQ (Angulo-Sandoval et al 2000) and in other tropical systems (Spiller and Agrawal 2003) because increased light resources lead to high levels of new leaves available to herbivores. Because consumers have the potential to alter patterns of plant production in light gaps of this forest, this study shows that consumer presence may be important in rainforest successional processes.

2.5.1. Herbivore impacts

Wardle and Bardgett (2005) predict that herbivory will have important ecosystem level consequences in systems where primary production is high and when grazing promotes a less palatable plant community. I observed that herbivore consumption promoted a shift to a less palatable, slower-decomposing plant community in this highly productive system, fitting Wardle and Bardgett’s criteria. My original prediction that herbivore selective feeding on fast decomposing plants would reduce aboveground plant growth was based upon the assumption that my two focal plant species had similar foliar nutrient contents. However, chemical analyses show that P. glabrescens has much higher foliar nitrogen (N) than M. prasina (Prather, Chapter 3, this volume). The herbivore’s
consumption of fast-decomposing, high N plants released nutrients stored in the faster decomposing plant tissues to the litter and soil. I hypothesize that as nutrients became available to slow decomposing, low N plants, these plants are able to build greater amounts of plant tissue per unit N over time, thus increasing total plant production.

However, the herbivore-induced increases in plant production observed in this study are likely temporary. This shift to a lower quality, less palatable plant community should eventually decrease the quality of resources available to decomposers, decreasing decomposition rates and ultimately reducing nutrients available. However, these changes likely occur on a time scale than my experiment ran. In order to see a reduction in primary production, the experiment would have needed to run until herbivore consumption decreased the biomass of preferred host plants (*P. glabrescens*) to very low levels. Therefore, it is likely that had I measured plant biomass at year five, I would have seen the growth of *M. prasina* level off due to decreased nutrient availability. Shifts to unpalatable plants communities have been shown to decrease nutrient availability and reduce primary production over time in other systems (Pastor and Naiman 1992; de Mazancourt and Loreau 2000; Feeley and Terborgh 2005).

2.5.2. Detritivore impacts

Like herbivore impacts, detritivore impacts to plants were only observed in light gaps. These detritivore alterations of plant production patterns were not surprising since tropical production is primarily thought to be driven by nutrients derived from detrital decomposition. However, the detritivore-induced reduction of aboveground biomass was unexpected because I predicted that detritivores would increase primary production.
through their litter comminution increasing nutrient availability to plants. Also, detritivores stimulated belowground biomass. This result may indicate a decline in soil nutrients if plants need greater root mass to more efficiently acquire soil nutrients at low concentrations.

In fact, total soil N concentration decreased with detritivores present (Prather, Chapter 3, this volume). One possible mechanism for the detritivore reduction of soil N and plant production may be that snails selectively feed on some important microbial group, which alters the functional composition of the litter microbial community and consequently reduces nutrients available for plant growth. Invertebrate detritivores (such as Collembola) in other systems selectively feed on certain microbial groups and decrease nitrogen and phosphorus in the soil, ultimately reducing aboveground plant biomass (Warnock et al. 1982). Additionally, there are more fungal feeding macro-organisms than pure detrital feeders in tropical systems (Takeda and Abe 2001), suggesting that the role of macro-detritivores as microbivores may be more important than their fragmentation of litter.

2.5.3. Enclosure effects

Although there were differences in the growth of one plant species growth with enclosures present, this is not surprising because these experiments were designed to isolate the impacts of understory two consumers on understory plant production. These differences may be explained by some other biotic mechanism. I hypothesize that *P. glabrescens* individuals were smaller outside enclosures because other herbivores besides *L. portoricensis* were feeding on these highly palatable plants. If true, the presence of
non-focal rainforest herbivores would only quicken the plant community shift that was
driven by the herbivores in my study system. Given this proposed mechanism, the results
of this study are realistic for understory dynamics.

2.5.4. Conclusions: Implications for rainforest functioning

In this study, I show that similar to non-tropical systems, rainforest consumers can
have important consequences for ecosystem functioning. In this forest, herbivore and
detritivore impacts are especially important to understory plants growing in disturbed
areas. Herbivore selective consumption supersedes any impacts of detritivores on plant
production by altering the quality of resources entering the decomposer subsystem
(Figure 2.6), similar to pathways shown in non-tropical systems (e.g., Pastor et al 1988;
Wardle and Bardgett 2005). Herbivore mediation of detrital food webs has important
consequences for tropical ecosystems, which are commonly thought to be driven by
detrital dynamics. Because this study demonstrates impacts of consumers on tropical
ecosystem and successional processes, these results underscore the need for future
research on tropical primary production and plant succession to explicitly consider
impacts of the diverse consumer biota.

2.6. Acknowledgments

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interpretation, including H. Mahon, M. Michel and D. Flagel who read earlier drafts of
This manuscript. C. Prather was supported on a University of Notre Dame Environmental Research Center (UNDERC) Fellowship for three summers, a Pollard Fellowship from the Department of Biological Sciences, and a Bayer Fellowship from Center for Environmental Science and Technology at the University of Notre Dame. This work is supported by NSF LTER grant numbers DEB-0218039 and DEB-0620910 to Belovsky.

2.7. Literature cited


CHAPTER 3:
CONSUMERS ALTER NUTRIENT DISTRIBUTIONS AND AVAILABILITY IN A RAINFOREST UNDERSTORY\textsuperscript{10}

3.1. Abstract

Consumers, such as herbivores and detritivores, have known impacts on the distribution and availability of nutrients in many ecosystems, but this has not been well studied in tropical rainforests. However, recent studies have shown that consumers can alter rates of rainforest primary production, suggesting that these groups alter nutrient availability to plants. Nutrient cycling in tropical forests is driven by disturbance, so any consumer impacts to nutrient cycling may be altered by disturbances. I examined if consumer alterations of plant growth can be explained by their alterations of nutrient cycles. To test these ideas, I used a 3-year enclosure experiment, manipulating herbivore, detritivore, and canopy cover presence. Every year, I measured the biomass and nutrient content of aboveground and belowground plant tissue, litter, and soil in these experiments to determine the total nutrients in all components of these simplified ecosystems. I also measured soil nutrient availability (NO\textsubscript{3}, NH\textsubscript{4} and PO\textsubscript{4}) with resin bags. Herbivore presence increased the availability of NH\textsubscript{4} in the soil, and shifted the distribution of

\textsuperscript{10} I gratefully acknowledge my coauthor, Gary Belovsky. This manuscript is in preparation for Biotropica.
nitrogen from litter to sequestration in the aboveground tissue of slowly decomposing plants. Detritivore presence reduced the availability of NH₄ and NO₃, and decreased total N in enclosures, mainly through reductions in soil nitrogen and nitrogen stored in aboveground plant tissues. The consumer impacts to nutrient cycling are aide in examining consumer alterations of primary production. Because consumers had significant impacts on nutrient cycling in this rainforest, future ecosystem-level research should consider the impacts of both herbivorous and detritivorous consumers on the distribution and availability of nutrients in tropical forests.

3.2. Introduction

Rapid and efficient internal nutrient cycles support high primary production in rainforests (Vitousek 1984). Although many different factors have been shown to be important to rainforest nutrient cycles, including disturbance (e.g., Steudler et al 1991), the potential role of consumers in these nutrient cycles has been largely ignored (Feeley and Terborgh 2005). Consumers, such as herbivores and detritivores, have important impacts to the distribution and availability of nutrients in many different ecosystems (e.g., marshes--Abrahamson and McCrea 1986, temperate and tropical streams--Covich et al. 1999, grasslands--Belovsky and Slade 2000, 2002, mangroves--Feller 2002, temperate forests--Yang 2004). In these ecosystems, consumers affect nutrient cycles through the consumption of plants and detritus, and by physically altering the structure of materials (reviewed in Weisser and Siemann 2004). If invertebrate consumers perform similar redistributions of nutrients in tropical rainforests, they may play important active roles in the nutrient cycling of these systems. Recent studies have shown that consumers
impact understory plant growth and composition, and here I examine whether these consumer alterations of plant communities can be explained by their impacts to nutrient cycles.

Research from non-tropical sites has shown that a consumer’s trophic level impacts the type of effects they have on nutrient cycles. Herbivore frass that falls to the forest floor may either stimulate (Fonte and Schowalter 2005; Frost and Hunter 2004; Rinker et al. 2001; Sirotnak and Huntly 2000) or inhibit nutrient availability due slow release of nutrients because of resistant frass (Hanlon and Anderson 1979). Also, through selective feeding, herbivores can increase or decrease decomposition and subsequent nutrient release from litter depending on the quality of preferred foliage (a framework which was developed by McNaughton 1985, Pastor et al. 1988, DeAngelis 1992, and empirically demonstrated in Holland 1995, Belovsky and Slade 2000, 2002).

Detritivores can alter nutrient distribution and availability through: frass production, similar to herbivore frass; fragmenting detritus into fine particles that are easily used by microorganisms, thus increasing nutrient release from litter (Swift et al. 1979); and selectively feeding on litter or soil microbial groups that are important to the processes of decomposition and nutrient cycling. Although this last mechanism has been often shown in marine systems (e.g., Phillips 1984), it has been seldomly explored in terrestrial systems (but see Moore et al 1988, Wardle 2002). If detritivores selectively feed on microbes and subsequently alter microbial functional composition, their presence may either inhibit or accelerate nutrient transformation rates, depending on the functional role of the preferred microbial group.
A few studies have examined the effect of single consumer trophic levels on nutrient cycling in tropical forests: herbivore effects have been examined in two studies (Feeley and Terborgh 2005, Fonte and Schowalter 2005) and detritivores effects have been examined by several studies (e.g., Heneghan et al. 1998, 1999, Gonzalez 1999, Milton and Kaspari 2007). In combination, herbivores and detritivores have fairly complex interactions on nutrient cycling in non-tropical systems (Scheu et al. 1999, Poveda et al. 2005, Classen et al. 2006, Classen et al. 2007). However, no studies have examined the effect of both herbivores and detritivores in combination on nutrient cycling in tropical systems.

In many tropical forests, forest structure and nutrient cycles are driven by disturbances. Consumers effects on the distribution and availability of nutrients may be amplified in light gaps because: 1) understory plant growth and litterfall is more rapid in light gaps where plants are not limited by light (Kobe 2006), 2) herbivores often prefer gap specialist plants compared to shade tolerant plants in tropical forests (Coley and Barone 1996), and 3) these increased high quality resources may amplify consumer feeding rates (Angulo-Sandoval and Aide 2000, Spiller and Agrawal 2003). Therefore, this study was conducted under two levels of canopy cover to determine if disturbance alters how consumers affect rainforest nutrient cycling.

Here, I seek to examine how representatives from these two trophic groups affect the distribution of nutrients in a simplified rainforest ecosystem, consisting of aboveground and belowground plant biomass, litter, and soil. I used experimental enclosures in light gaps and closed canopy sites of a Puerto Rican rainforest to manipulate herbivore and detritivore presence. I predicted that herbivore feeding would
increase the nutrients stored in slower decomposing plants. I expected this result because my focal herbivore preferentially consumes faster decomposing plants, which shifts plant communities to abundant slower decomposing, less palatable plants. However, I predicted that detritivores, which reduced aboveground plant production, would also reduce nutrients available to plants. I also predicted that the impacts of both consumers to nutrient cycling would only be observed in light gaps because both groups only impacted plant growth in light gaps. Lastly, I expected that herbivore impacts would override any detritivore impacts to nutrient availability and distribution because herbivores affect the resources provided to the detrital food web.

3.3. Methods

3.3.1. Study site and species characteristics

This study was conducted at the Luquillo Long Term Ecological Research site (LUQ LTER; described in Odum and Pigeon 1970). LUQ is located in the Northeastern corner of Puerto Rico (18° 19' N, 65° 45' W) and contains soils that are mainly clays and silty loams (Utisols of the Los Guineos series), which are characteristically highly weathered and acidic (Waide and Reagan 1996). LUQ is frequently hit by tropical storms that create large light gaps (Scatena and Larsen 1991) and is therefore constantly in a state of secondary succession (Waide and Lugo 1992). Consequently, the ecosystem structure at LUQ is largely driven by disturbances. This insular forest has a relatively low floral and faunal richness compared with mainland tropical sites. Accordingly, LUQ is one of the only tropical forests where the food web has been described in detail (Waide
& Reagan 1996), so this forest is an ideal location to begin to examine the role of consumers in rainforest systems because there is a basic understanding of the important ecosystem components.

This study is part of a larger experiment that examines the impact of these consumers on several ecosystem processes so the focal species and experimental design of this study have been previously described (Prather, Chapter 2, this volume). *Miconia prasina* and *Piper glabrescens* were chosen as fast and slow decomposing representatives of the understory plant community, respectively, because these genera are abundant across the Neotropics (Molina and Alemany 1997) and have been previously studied together (Denslow et al. 1987, Baldwin and Schultz 1988). The invertebrate consumers used in this experiment were the most abundant detritivorous litter snail, *Megalomastoma croceum*, and the most abundant generalist herbivore, *Lamponius portoricensis* (a walking stick). *L. portoricensis* has been shown to preferentially consume faster decomposing plants (Prather, Chapter 2). These plants and consumers were chosen because they are abundant, commonly studied, and easy to transport and manipulate.

3.3.2. Experimental design and data collection

I used a fully-crossed 3 x 2 factorial designed enclosure experiment, manipulating herbivore, detritivore and canopy cover presence with 3 replicates of each treatment. A 3.34 m² PVC frame supported mesh enclosures (0.15 cm from Bioquip). To look at the effect of the enclosure, I setup un-caged controls at each study site (6 controls total). I removed all litter and visible organisms from enclosures, and added ≈ 315 g/m² of a common forest litter collected near study sites to each enclosure and control. Treatments
were implemented in August of 2005 and consisted of a naturally occurring biomass of consumers: for detritivore treatments, $\approx 5.7 \text{ g/m}^2$ (about 9 individuals), and herbivore treatments $\approx 1.8 \text{ g/m}^2$ (about 6 individuals). The biomass of herbivores and detritivores in treatments was sampled every 4 months and initial consumer biomass was held constant over time.

Plants of each species (0.35 to 0.75m in height) were located in the forest, transplanted into seedling bags, and grown for at least 3 months under similar light conditions in common forest soil. Five individuals of each species were randomly chosen for each enclosure and control, and planted into PVC pipes in the ground with holes to allow the exchange of nutrients and water with the soil. Plants were harvested at the end of the experiment in 2008.

3.3.3. Nutrient availability and pools

To determine treatment effects on soil nutrient availability, I filled unbleached nylon bags with 10 g of Rexyn 300 (H-OH) analytical grade resin beads. I placed 2 bags 10 cm beneath the surface of the soil in each enclosure and control (Binkley and Matson 1983, Fonte and Schowalter 2005). The bags were retrieved from the field and replaced with a new set of bags every six months. Upon retrieval, I froze the bags, and later extracted half of the rexyn for nitrogen and half for phosphorus using standard extraction methods. I then analyzed NH$_4$, NO$_3$ and PO$_3$ availability from each bag on a gas chromatograph.

There are ten components (i.e., biotic components forming an ecosystem) of this simplified ecosystem structure, which each make up a pool (i.e., standing stock of
nutrients) within the nutrient budget: (1) soil, (2) initial litter, (3) aboveground P. glabrescens tissues, (4) belowground P. glabrescens tissues, (5) P. glabrescens litter, (6) aboveground M. prasina tissues, (7) belowground M. prasina tissues, (8) M. prasina litter, (9) herbivores and (10) detritivores (Figure 3.1). The nutrient content of each ecosystem component was measured in the following manner. Soil, foliar, and litter samples were taken annually in July in each enclosure (2005-2008), and stems and roots were sampled at the end of the experiment. To account for soil heterogeneity, two replicate soil cores were pooled and homogenized for each enclosure. One leaf was taken from each individual plant, and these leaves pooled by species within each enclosure. Litter was separated into litter from each plant species and weighed (Prather, Chapter 4, this volume). Stem and root samples of each species were taken from one individual from each enclosure at the end of the experiment. All samples were dried for at least 24 hours at 60°C and ground through 60 micron mesh. Annual foliar, soil, litter, and final stem and root N contents were determined on an Elemental Analyzer (Costech Elemental Analyzer 4010, Valencia, CA, U.S.A.).

Pools were calculated by the time-specific biomass of each of these ecosystem components, multiplied by time-specific (when appropriate) N content of each of these pools. The measurement/estimation of biomass is described in Chapter 2 (aboveground and belowground plant biomass) and Chapter 4 (litter biomass). I added the total N in each pool together to obtain the total N in each enclosure and converted this amount to g/m².
Figure 3.1 Graphical depiction of the components of a simplified nitrogen budget in enclosures. There are 10 components of this simplified nitrogen budget: (1) soil, (2) initial litter, (3) *P. glabrescens* leaves, (4) *P. glabrescens* wood, (5) *P. glabrescens* litter, (6) *M. prasina* leaves, (7) *M. prasina* wood, (8) *M. prasina* litter, (9) herbivore, and (10) detritivore.

3.3.4. Statistical analyses

I analyzed differences in soil nutrient availability (the arcsine-square root transformed percent change in NO₃, NH₄, and PO₄ availability from the beginning to the end of the experiment) using a 3 x 2 ANOVA (with factors herbivore, detritivore and canopy cover presence). I analyzed treatment effects on the total N in each enclosure using repeated measures ANOVA with 3 factors (canopy cover, herbivore and detritivore presence) and time as the repeated measure (t = 4: 2005-2008). I examined treatment effects (herbivore, detritivore and herbivore + detritivore) on the distribution of nutrients.
among different pools using effect sizes. Effect sizes (ES) were calculated as log response ratios of $g N / m^2$ in each ecosystem component using the following equation:

$$ES = \ln \left( \frac{\text{treatment}}{\text{control}} \right)$$

where treatment refers to enclosures with organisms present and control refers to no consumers present (total exclusion enclosures).

Since the herbivore + detritivore enclosures consisted of natural abundance of focal consumers, these enclosures should most closely represent the whole forest. I compared controls (enclosure absent) to the herbivore + detritivore enclosures (enclosure present) to determine the effect that enclosures had on each response variable (soil nutrient availability, N in each component pool, and total N). Consequently, each statistical test described above was repeated, replacing consumer treatment factors (herbivore and detritivore presence) with an enclosure presence factor.

3.4. Results

3.4.1. Overall patterns

There were no significant consumer effects on available phosphorus (P); therefore, total P pools were not determined. The average N content used to calculate the amount of N in each component is reported in Table 3.1. The leaves and litter of *P. glabrescens* have higher N than *M. prasina*. However, *M. prasina*’s wood and roots contain higher N. Overall, the total N in plots did not change over time (Table 3.2, Table 3.3, Figure 3.2). The largest pool of N in this system resides in the soil, and the second
largest pool resides in belowground plant tissue. Much more aboveground N is stored in
*M. prasina* tissues compared to *P. glabrescens* tissues. However, belowground more N
is stored in *P. glabrescens* tissues than *M. prasina* tissues (Figure 3.3).
TABLE 3.1
PERCENT N USED IN NITROGEN BUDGET.  

<table>
<thead>
<tr>
<th>Component</th>
<th>Species</th>
<th>Site</th>
<th>% N</th>
<th>SE</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaves</td>
<td><em>M. prasina</em></td>
<td>Closed canopy</td>
<td>1.76</td>
<td>0.19</td>
<td>65</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>1.52</td>
<td>0.22</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td><em>P. glabrescens</em></td>
<td>Closed canopy</td>
<td>2.37</td>
<td>0.17</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>2.37</td>
<td>0.18</td>
<td>60</td>
</tr>
<tr>
<td>Wood</td>
<td><em>M. prasina</em></td>
<td>Closed canopy</td>
<td>1.52</td>
<td>0.26</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>1.37</td>
<td>0.11</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td><em>P. glabrescens</em></td>
<td>Closed canopy</td>
<td>1.31</td>
<td>0.15</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>1.37</td>
<td>0.11</td>
<td>6</td>
</tr>
<tr>
<td>Litter</td>
<td><em>M. prasina</em></td>
<td>Both</td>
<td>1.14</td>
<td>0.09</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td><em>P. glabrescens</em></td>
<td>Both</td>
<td>1.99</td>
<td>0.12</td>
<td>36</td>
</tr>
<tr>
<td></td>
<td>Other</td>
<td>Both</td>
<td>0.91</td>
<td>0.21</td>
<td>36</td>
</tr>
<tr>
<td>Soil</td>
<td></td>
<td>Closed canopy</td>
<td>0.3</td>
<td>0.03</td>
<td>122</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>0.27</td>
<td>0.06</td>
<td>118</td>
</tr>
<tr>
<td>Roots</td>
<td><em>M. prasina</em></td>
<td>Closed canopy</td>
<td>1.41</td>
<td>0.10</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>1.52</td>
<td>0.07</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td><em>P. glabrescens</em></td>
<td>Closed canopy</td>
<td>1.36</td>
<td>0.18</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Light gap</td>
<td>1.38</td>
<td>0.23</td>
<td>6</td>
</tr>
</tbody>
</table>


---

11 Leaf and soil N are averages of values used because dynamic values were used in the budget, while the other values are static values for the budget.
TABLE 3.2
FULLY-CROSSED REPEATED MEASURES ANOVA RESULTS FOR AMOUNT OF TOTAL N (G PER M² ) IN TREATMENTS. ¹²

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Within subjects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>T</td>
<td>1, 20</td>
<td>1.287</td>
<td>0.270</td>
</tr>
<tr>
<td>T * C</td>
<td>1, 20</td>
<td>20.208</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>T * C * D</td>
<td>1, 20</td>
<td>5.252</td>
<td>0.033</td>
</tr>
<tr>
<td>Between subjects</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>1, 20</td>
<td>19.452</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>H</td>
<td>1, 20</td>
<td>5.055</td>
<td>0.138</td>
</tr>
<tr>
<td>D</td>
<td>1, 20</td>
<td>9.689</td>
<td>0.637</td>
</tr>
</tbody>
</table>

¹² T = time, C = canopy cover, H = herbivore, and D = detrivore. Only interactions with P < 0.20 are reported.
Figure 3.2 Detritivore impacts on the total amount of N (g N / m²) in both closed canopy sites (left) and light gaps (right).
Figure 3.3 Nutrient distribution in treatments: bars depict means ± standard deviation. Horizontally hatched bars are detritivore treatments, vertically hatched bars are herbivore treatments, solid black bars are herbivore + detritivore, and white bars are total exclusion treatments.
<table>
<thead>
<tr>
<th>N pool</th>
<th>Forest</th>
<th>Effect</th>
<th>Year 0</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aboveground</td>
<td>Closed canopy</td>
<td>E</td>
<td>-0.062 ± 0.059 *</td>
<td></td>
<td>1.779 ± 1.414 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>H</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Light gap</td>
<td>E</td>
<td></td>
<td></td>
<td>-0.451 ± 0.422 *</td>
<td>-0.310 ± 0.247 *</td>
</tr>
<tr>
<td>Aboveground</td>
<td>Closed canopy</td>
<td>E</td>
<td></td>
<td>0.561 ± 0.517 *</td>
<td>1.047 ± 1.032 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>H</td>
<td></td>
<td>-0.249 ± 0.240 *</td>
<td>-0.502 ± 0.284 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Light gap</td>
<td>D</td>
<td>0.486 ± 0.423 *</td>
<td></td>
<td></td>
<td>0.391 ± 0.312 *</td>
</tr>
<tr>
<td></td>
<td></td>
<td>D + H</td>
<td>-0.854 ± 0.178 **</td>
<td>-0.590 ± 0.519 *</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Litter</td>
<td>Closed canopy</td>
<td>E</td>
<td></td>
<td>3.218 ± 2.337 **</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>-0.684 ± 0.008 **</td>
<td>-4.890 ± 0.874 **</td>
<td>-2.953 ± 0.338 **</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>H</td>
<td>-0.670 ± 0.019 **</td>
<td>-3.992 ± 3.015 **</td>
<td>-2.798 ± 0.556 **</td>
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</tr>
<tr>
<td></td>
<td></td>
<td>D + H</td>
<td>-0.685 ± 0.019 **</td>
<td>-5.712 ± 1.005 **</td>
<td>-3.323 ± 0.409 **</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Light gap</td>
<td>E</td>
<td></td>
<td></td>
<td>0.391 ± 0.312 *</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>D</td>
<td>-0.612 ± 0.080 **</td>
<td>-2.619 ± 1.252 **</td>
<td>-2.701 ± 0.430 **</td>
<td></td>
</tr>
</tbody>
</table>

13 Only ES significantly different from 0 are reported. Those that are significantly greater than 0 are denoted with “*”, and those significantly greater than 0.5 are denoted with “**”.
<table>
<thead>
<tr>
<th>N pool</th>
<th>Forest</th>
<th>Effect</th>
<th>Year 0</th>
<th>Year 1</th>
<th>Year 2</th>
<th>Year 3</th>
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<tr>
<td></td>
<td></td>
<td>H</td>
<td>-0.658 ± 0.028 **</td>
<td>-3.611 ± 0.985 **</td>
<td>-2.827 ± 0.334 **</td>
<td></td>
</tr>
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<td></td>
<td>D + H</td>
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<td>-3.255 ± 1.66 **</td>
<td>-3.272 ± 1.113 **</td>
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<tr>
<td>Soil</td>
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<td>0.376 ± 0.112 *</td>
<td>0.338 ± 0.218 *</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>D</td>
<td>-0.389 ± 0.190 *</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>D + H</td>
<td>-0.133 ± 0.101 *</td>
<td></td>
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<tr>
<td></td>
<td>Light gap</td>
<td></td>
<td>None significantly differ from 0</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Belowground MP</td>
<td>Closed canopy</td>
<td>D</td>
<td>0.803 ± 0.728 *</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>H</td>
<td>0.712 ± 0.629 *</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>D + H</td>
<td>1.401 ± 1.219 *</td>
<td></td>
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<tr>
<td></td>
<td>Light gap</td>
<td>D</td>
<td>0.487 ± 0.415 *</td>
<td>-0.523 ± 0.487 *</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>H</td>
<td>0.330 ± 0.302 *</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>D + H</td>
<td>1.335 ± 0.688 **</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Belowground PG</td>
<td>Closed canopy</td>
<td>D</td>
<td>-0.106 ± 0.077 *</td>
<td></td>
<td>2.537 ± 0.709 **</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>D + H</td>
<td>3.250 ± 2.168 **</td>
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<td>D</td>
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<tr>
<td></td>
<td></td>
<td>H</td>
<td>-1.687 ± 1.541 *</td>
<td>-1.866 ± 1.648 *</td>
<td>-1.671 ± 1.415 *</td>
<td></td>
</tr>
</tbody>
</table>
3.4.2. Herbivore effects

Herbivores stimulated the availability of NH$_4$ increased by about 20% in both canopy covers ($F = 7.04$, df = 1, 16, $P = 0.014$; Figure 3.4). However, herbivores did not affect the availability of NO$_3$ or PO$_4$, or the total N in enclosures (Table 3.2, Figure 3.2). Also, herbivores caused an increase in the N stored in aboveground *M. prasina* tissues over time, especially in light gaps, but decreased the N stored in both aboveground and belowground *P. glabrescens* tissues. Herbivores had no significant impact on soil N.

![Figure 3.4](image)

**Figure 3.4** Treatment effects on the percent change in available nutrients (NH$_4$, NO$_3$, and PO$_4$) between the end and the beginning of the experiment.

3.4.3. Detritivore effects

In the presence of detritivores, the availability of both NO$_3$ ($F = 9.72$, df = 1, 16, $P = 0.005$) and NH$_4$ ($F = 5.06$, df = 1, 16, $P = 0.032$) in the soil declined, but PO$_4$
availability did not change (Figure 3.4). Detritivores did not affect total N in closed canopy sites, but reduced the total N in light gaps (Table 3.2, Figure 3.2). Soil N and the N stored in aboveground *M. prasina* tissues declined in response to detritivores in light gaps, but not in closed canopy sites. However, detritivores increased the N in belowground *P. glabrescens* tissues.

3.4.4. Herbivore + detritivore interactions

There were no significant herbivore + detritivore interaction effects on the availability of any nutrients measured, or on the total amount of N (Table 3.2). However, there was higher variability in the loge response ratios for most ecosystem components when both consumers were present (Table 3.3).

3.4.5. Canopy cover effects

Canopy cover did not significantly affect the availability of any soil nutrients, other than the interactions with consumers, described above. The total N in plots decreased over time in closed canopy sites, but increased over time in light gaps (Table 3.2, Figure 3.2). Much more N is stored in plant tissues in light gaps than in closed canopy sites due to higher plant biomass in light gaps (Table 3.3, Figure 3): there was approximately an order of magnitude more N in aboveground *M. prasina* tissues; ~ 5 times as much N in aboveground *P. glabrescens* tissues; ~ 4 times more N in belowground *M. prasina* tissues; and about twice as much in belowground *P. glabrescens* tissues.
3.4.6. Enclosure effects

Uncaged controls in this experiment allowed canopy inputs to reach the forest floor, whereas the enclosures excluded these inputs. NH$_4$ availability was higher outside enclosures in both light gaps and closed canopy sites compared to inside enclosures. Enclosure presence did not have a significant impact on NO$_3$ or PO$_4$. The enclosures had several significant impacts on different components of the N budget. Total N was higher outside enclosures compared to inside enclosures, mainly due to the exclusion of canopy litter inputs: the amount of N stored in litter increased outside enclosures, but decreased inside enclosures regardless of canopy cover or consumer treatments.

3.5. Discussion

Consumers actively change the distribution and nutrients available to plants, and these impacts can be modified by disturbance. The results of this study help to describe how consumer impacts on the N cycle cause previously observed consumer alterations of plant growth.

3.5.1. Herbivore effects

The most significant herbivore-induced change in N distribution was the increase in aboveground slow plant N and decreased above- and belowground fast plant N. These changes are coupled with increased N availability in the soil. The herbivore-induced shift in aboveground plant N from fast decomposing to slow decomposing plant tissues explains herbivore-induced increase in plant production (Prather, Chapter 2, this volume). The walking sticks’ consumption of higher N, fast decomposing plants decreased these
plants. The nutrients released from this nitrogen-rich plant tissue were released to the soil, demonstrated by the increase in NH$_4$ in the soil, and were acquired by slowly decomposing plants. These nutrients transfer into a higher biomass of plants per unit of nitrogen because of the lower N in slower decomposing tissues. This difference can be visualized with Figure 3.5. The dramatic difference in the size of the arrows representing absolute changes in plant biomass between plant species (left) compared to the similarly sized arrows depicting the change in plant N demonstrate how a change in similar amounts of N result in large differences between the biomass of plants.

![Graph of herbivore impacts on aboveground plant biomass and plant N](image)

**Figure 3.5** Herbivore impacts on aboveground plant biomass (left) and plant N (right) of both plant species. Graphs depict the change in biomass or plant N (g/m$^2$) over time as the difference between herbivore treatments and exclusion treatments.

### 3.5.2 Detritivore effects

The unexpected detritivore-induced reduction of plant growth is explained by the decrease in the soil N pool and N availability over the course of this experiment. However, the exact mechanism of the reduction in soil total N, NH$_4$ and NO$_3$ is not currently known, but there could be several explanations for this result. First, detritivores could alter N availability by preferentially consuming a microbial group that is important
in N-cycling (e.g., nitrifying bacteria or mycorrhizal fungi). However, there is little documentation of the preferential feeding of detritivores on microbes in terrestrial studies. Also, snail movements may alter the physical structure of the detrital layer and/or the soil (i.e., bioturbate the litter and soil), which has been shown to increase leaching rates in other ecosystems (Gardner et al. 1987, Meysman et al. 2006, Volkenborn et al. 2007). Further study would be needed to determine if some combination of these mechanisms is driving the detritivore effects on nutrient cycling in this study.

3.5.3. Herbivore + detritivore effects

Although previous literature suggests that tropical forest production is driven by nutrients derived from detrital food webs (e.g., Milton and Kaspari 2007), herbivores may alter the detrital food web through changes in the quality of resources reaching decomposers (Wardle and Bardgett 2005). In this study, herbivore only and herbivore + detritivore treatments both exhibit a similar shift in aboveground plant N from fast decomposing to slow decomposing plants. However, there are not similar patterns between detritivore only and herbivore + detritivore treatments. This result suggests that the herbivores mediate the effect of detritivores on nutrient cycling in these systems. Shifts to less palatable plant communities by herbivores have been shown to adversely impact decomposers in other systems (e.g., Pastor et al. 1988). These results counter the prevailing assumption that rainforest processes are mainly driven by the detrital food web.
3.5.4. Implications for rainforest nutrient cycling

Consumer effects on the N cycle help to explain the mechanisms of observed consumer alterations of plant growth, which were also largely seen in light gaps. Even though consumers may not influence the distribution of nutrients in areas of less-disturbed forest, their impacts in light gaps may signify that they alter how forest successional processes proceed. This may be especially true for herbivores that shift the composition of plant communities by selectively feeding on one type of plant over another. Since I have shown that consumers function as an active component of rainforest ecosystem structure, future ecosystem-level research should consider the impacts of both herbivorous and detritivorous consumers on nutrient cycling in tropical forests.

3.6. Acknowledgments

C. Prather’s committee members Todd Crowl, Jessica Hellman and Jeanne Romero-Severson helped tremendously with experimental design. Erik Jansen, Kunal Mandal, David Dang and Rick and Donna Prather were crucial in constructing the enclosures and other fieldwork. John Loftus and Suzyanne Guzicki were extremely helpful in teaching C. Prather analytical methods. Chemistry lab work was completed at the Center from Environmental Science and Technology at the University of Notre Dame. This work is supported by NSF LTER DEB-0218039 and DEB-0620910 grants to Belovsky. C. Prather was supported on an UNDERC fellowship for two summers and a Bayer Fellowship from the Center from Environmental Science and Technology at the University of Notre Dame.
3.7. Literature cited.


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CHAPTER 4: TROPICAL CONSUMERS ALTER DECOMPOSITION RATES BY MODIFYING RESOURCES AVAILABLE TO MICROBIAL COMMUNITIES

4.1. Abstract

Consumers are often considered to have negligible effects on decomposition in tropical forests, despite conflicting evidence in non-tropical systems. Recent studies have shown that herbivores and detritivores alter primary production and nitrogen (N) cycling through their selective feeding on vegetation and litter microbes. Additionally, disturbances modify these impacts. Here, I examine whether consumers have important impacts on litter quality, microbial communities and decomposition rates, and if so, if those impacts explain previously observed consumer effects on other ecosystem processes. I examined how natural abundances of an invertebrate detritivore (snail, *Megalomastoma croceum*) and a generalist herbivore (walking stick, *Lamponius portoricensis*) affect decomposition rates in sites with and without canopy cover. I conducted a 3 x 2 factorial experiment, manipulating herbivore, detritivore, and canopy cover presence in a Puerto Rican rainforest understory. I measured the effects of litter chemistry, disturbance and consumer treatments on decomposition rates, and subsequently quantified the effects of these treatments on the composition of litter fungal

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14 I gratefully acknowledge my coauthors, Gary Belovsky, Sharon Cantrell, and Grizelle Gonzalez. This manuscript is in preparation for Ecology.
and bacterial communities. Decomposition rates were not different between light gaps and closed canopy sites, and consumer effects on decomposition were not amplified in light gaps. Detritivores did not alter decomposition rates or litter abundance. However, herbivores significantly reduced leaf decomposition rates and the abundance of high quality litter as well as bacterial richness and abundance, but did not affect fungal communities. These results help to support hypothesized mechanisms about how these consumers impact primary production and nutrient cycling. This study documents previously unreported impacts of tropical consumers on the process of decomposition, and specifically how tropical herbivores affect litter microbial communities, demonstrating an important effect of consumers on ecosystem functioning in tropical rainforests.

4.2. Introduction

The decomposition of plant material provides most of the nutrients required for plant growth and accounts for approximately 14% of annual global carbon fluxes (Schlesinger 1997). Reviews on decomposition indicate a hierarchical relationship between three important factors that influence variability in decomposition rates: climate, geology and biota, with climate being most important and the biota being least important (Swift et al. 1979, Lavelle et al. 1993, Aerts 1997). In tropical climates, however, temperature and humidity are near optimal for high decomposition rates, and geologic factors generally have negligible effects (e.g., high amounts of iron that render clays inactive for adsorption of nutrients). With optimal climatic conditions and geologic factors not as important to tropical litter decomposition compared to other systems, biotic
components of ecosystem structure (like consumers) may be more important to tropical
decomposition compared to other systems (Lavelle et al. 1993, Fonte and Schowalter
2005). Nonetheless, consumer impacts on tropical decomposition remain largely
unexplored. Additionally, results from recent studies also suggest that tropical
collectors have significant impacts to primary production and nitrogen (N) cycles, and
that these impacts are amplified in light gaps (Prather, Chapter 2 and 3, this volume).
Here, I examine the impact of two common rainforest consumers to tropical
decomposition in light gaps and closed canopy sites, and ask whether observed consumer
impacts to other ecosystem processes can be explained by their effects on litter
decomposition.

Consumer impacts on decomposition have generally been divided into two
categories: (1) changes to litter quality and quantity through consumer selective feeding,
and (2) high quality inputs of frass. Changes to plant and litter composition involve more
recalcitrant substrates, whose nutrients are sequestered for longer periods of time, and
consequently these are called the *inputs to the slow cycle of decomposition*. Frass,
however, decomposes relatively quickly, and thus frass-related inputs are known as
*inputs to the fast cycle of decomposition* (sensu McNaughton et al 1988). Consumer
frass-related inputs to ecosystem processes have been shown for consumers in this forest,
including predators (Beard et al. 2003) and herbivores (Fonte and Schowalter 2005), but
inputs to the slow cycle have not been examined in any tropical forest.

Consumers have different impacts on decomposition based on their tropical level.
Herbivore frass inputs to the fast cycle of decomposition have been shown to increase
nitrogen cycling (Sirotnak and Huntly 2000, Rinker et al. 2001), stimulate microbial
activity (Frost and Hunter 2004) and ultimately increase decomposition rates (Fonte and Schowalter 2005). However, a few studies have shown that even though frass is a higher quality nutrient source than litter (higher nitrogen and lower C: N), nutrients may not be readily released to microbes because frass has a low internal porosity, thus inhibiting microbial activity and reducing decomposition rates (e.g., Hanlon and Anderson 1979).

Herbivore inputs to the slow cycle of decomposition (selective feeding) may increase or decrease rates of decomposition depending on the nutrient content and quality of the herbivores’ preferred foliage. For example, if herbivores prefer to eat faster decomposing plants, then less high quality, fast decomposing litter reaches the forest floor. In turn, slower decomposing, poorer quality plants increase in abundance, resulting in poorer quality litter for decomposers, and ultimately decreasing decomposition rates (Pastor et al. 1988, Brown and Gange 1992, de Mazancourt and Loreau 2000, Schmitz et al. 2000, Feeley and Terborgh 2005). The opposite pathway can also occur: herbivore preference for slower decomposing plants could increase rates of decomposition (McNaughton 1985, Holland 1995, Belovsky and Slade 2000, 2002).

Detritivores can facilitate decomposition by feeding directly on litter material and breaking it into smaller pieces, increasing surface area available for microbes (shown at my study site: Heneghan et al. 1998, Gonzalez and Seastedt 2000, Gonzalez et al. 2001). Beyond comminution, detritivore frass inputs may accelerate or inhibit decomposition depending on frass quality and porosity, as described for herbivores. Detritivores may also impact decomposition through inputs to the slow cycle of decomposition by: selectively feeding on microbial functional groups within the litter layer, a seldomly examined mechanism (but see Moore et al. 1988, Wardle et al. 2002); and acting as
dispersal agents for fungal and bacterial propagules while traveling through the litter layer (Behan and Hill 1978).

All of these consumer impacts to decomposition can be altered by disturbance. Gap dynamics have been indicated as the main mechanism for maintaining tropical forest successional processes (e.g., Brokaw and Grear 1991, Foster et al. 1998), and disturbances cause microclimatic changes that affect decomposition rates (Zhang and Zak 1995, Vasconcelos and Laurance 2005), and. In light gaps, plants grow rapidly due to release from light limitation. Large amounts of new foliage and high leaf turnover rates provide areas of abundant resources for herbivores and detritivores. Additionally, consumption rates may be higher in light gaps because large numbers of highly palatable plants occur here (Coley and Barone 1996). Thus, increased consumption by herbivores and detritivores in light gaps may amplify consumer impacts on decomposition rates.

In this study, I examine the impact of the most abundant invertebrate detritivores (litter snails, Megalomastoma croceum) and herbivores (walking stick, Lamponius portoricensis rehn) on the decomposition rates, production, and microbial communities of litter using a field enclosure experiment in light gaps and closed canopy sites. I predicted that the detritivore (M. croceum) should increase decomposition rates by fragmenting litter and increasing surface area available for microbial enzymatic activity. The focal herbivore (L. portoricensis) prefers to eat faster decomposing plants with more nutritious foliage (Prather, unpublished data. I predicted that because my focal herbivore prefers to consume faster decomposing foliage, less high quality litter will fall to the forest floor, and more slowly decomposing, poorer quality litter should accumulate in the detrital layer, decreasing the ratio of fast: slow litter. The reduction of litter quality by herbivores
would result in a less abundant and active decomposer community, and ultimately decrease decomposition rates.

Herbivores have been shown to mediate detritivore impacts by altering the quantity and quality of the resources reaching the detrital food web in this study system (Prather, Chapter 2 and 3, this volume). Thus, herbivores should cancel out any stimulating effects from the detritivore’s comminution of litter. I also predicted that in disturbance-driven forests, like my study site in Puerto Rico, disturbances that produce large amounts of leaves and litter that increase rates of consumer consumption will amplify invertebrate effects on decomposition.

4.3. Methods

4.3.1. Study site and species characteristics

This study was conducted at the Luquillo Long Term Ecological Research site (LUQ LTER; described in Odum and Pigeon 1970). LUQ is located in the Northeastern corner of Puerto Rico (18° 19' N, 65° 45' W) and has an average annual rainfall of over 3500 mm (Thompson et al. 2004). Puerto Rico is frequently hit by tropical storms that create large light gaps, and consequently the forest is in a constant state of secondary succession. This insular forest has a relatively low floral and faunal richness compared with mainland tropical sites. Therefore, LUQ is one of the only tropical forests where the food web has been described in detail (Waide and Reagan 1996), so this forest is an ideal location to begin to examine the role of consumers in rainforest systems because there is a basic understanding of the important components of the LUQ food web.
The focal species and experimental design of this study have been described as part of a larger study examining these consumers’ impacts to primary production, nutrient cycling and decomposition (Prather, Chapter 2 and 3, this volume). *Miconia prasina* and *Piper glabrescens* were chosen as representatives of the understory plant community for this experiment because these genera are abundant across the Neotropics (Molina and Alemany 1997) and have been studied together in several Neotropical rainforests (Denslow et al. 1987, Baldwin and Schultz 1988). The invertebrate consumers used in this experiment were *M. croceum*, which is the most abundant detritivorous litter snail at LUQ (Prather, unpublished) and *L. portoricensis*, which is the most abundant generalist herbivore in the forest (Willig et al. 1986). These plants and consumers were chosen because they are abundant, commonly studied, and easy to transport and manipulate.

4.3.2. Enclosure study

I used a fully-crossed 3 x 2 factorial enclosure experiment and manipulated herbivore, detritivore, and canopy cover presence (light gaps: < 10% canopy cover, and forest sites: > 90% canopy cover) in replicates of 3. Mesh enclosures (0.15 mm made by Bioquip) were supported by a 3.34 m² PVC frame. I setup 3 un-enclosed controls to test the effect of the enclosure. Control plots had the same dimensions as enclosures, but were unenclosed and plants that grew up from the seed bank during the experiment were removed to treat the control plots like experimental enclosures. I removed all litter and visible organisms from enclosures and controls, and added 1050 g (± 50 g) of a homogenized forest litter that was collected near study sites to create a similar litter layer. Treatments consisted of natural abundances of consumer organisms and were implemented in August of 2005. Plants of both species were grown for at least 3 months.
under similar conditions. Individual plants were planted into PVC pipes in the ground in each enclosure (10.16 cm diameter and ≈ 0.25 m tall).

4.3.3. Decomposition rates

To determine consumer effects on rates of leaf decomposition and the role of the micro-arthropod community on decomposition, a litterbag experiment was implemented in 2006, one year after the enclosure study was established (LB1, Figure 4.1). I replicated 1 set each of 6 types of litterbags: two different mesh sizes (1 large mm mesh which allows micro-arthropod access to the litter, and small 500 micron mesh which excludes most micro-arthropods), crossed with 3 different leaf litter types (described below) in each enclosure (LB1, Figure 4.1). Different litterbag mesh sizes allowed me to see if treatments altered microarthropod community influences on decomposition rates. A preliminary experiment to test whether the litter in the two litterbag mesh types had effects on litter moisture content showed no significant differences between the two bag types after one week in the field (Prather, unpublished data). I used three different litter types to determine if consumer effects were altered by different litter sources. Newly senescent leaves of three litter types were collected from the forest floor: (1) *M. prasina*, (2) *P. glabrescens*, and (3) mixed-species litter. Mixed litterbags were composed of the top 11 plant species as determined from natural litterfall rates near experimental sites (see Table 4.1; Zalamea and Gonzalez 2008).

Each litterbag (8 cm x 16 cm) contained 4 g (± 0.5 g) of one of the 3 different litter types. Each litterbag set consisted of 4 litterbags retrieved at 4 consecutive time intervals: time 0 (to account for handling losses), 2, 5 and 8 months, for a total of 24 litterbags in each enclosure and 720 litterbags total. Upon retrieving litterbags, any live
plant material or soil was carefully removed from bags. Micro-arthropods were extracted from litter using Berlese funnels and sorted to family (but this data is not reported here). The litter was dried for at least 24 hours at 60°C until reaching a constant weight, then weighed to determine leaf mass lost from each bag. \( k \) values for each litterbag set were determined using Olson’s \( k \): \( \frac{X_t}{X_0} = e^{kt} \), where \( X_0 \) is the initial mass of litter, \( X_t \) is the mass of litter at time \( t \), and \( k \) is the decay rate constant (Olson 1963).
Figure 4.1 Experimental enclosures were replicated in two canopy covers, represented by white and black shading. Un-caged control areas were set-up (see Methods). The first litterbag experiment was replicated in all treatments (LB1), and while the second was not (LB2) was not.

TABLE 4.1
MIXED SPECIES LITTERBAG COMPOSITION.\textsuperscript{15}

<table>
<thead>
<tr>
<th>Plant species</th>
<th>% of litter</th>
<th>Amount in litterbag (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dacryodes excelsa</td>
<td>34.37</td>
<td>1.37</td>
</tr>
<tr>
<td>Manilkara bidentata</td>
<td>19.96</td>
<td>0.68</td>
</tr>
<tr>
<td>Prestoea montana</td>
<td>12.95</td>
<td>0.52</td>
</tr>
<tr>
<td>Buchenavia tetraphylla</td>
<td>9.13</td>
<td>0.37</td>
</tr>
<tr>
<td>Homalium racemosum</td>
<td>7.97</td>
<td>0.32</td>
</tr>
<tr>
<td>Rourea surinamensis</td>
<td>3.55</td>
<td>0.14</td>
</tr>
<tr>
<td>Sloanea berteriana</td>
<td>3.29</td>
<td>0.13</td>
</tr>
<tr>
<td>Cyrilla racemiflora</td>
<td>2.96</td>
<td>0.12</td>
</tr>
<tr>
<td>Tetrakastris balsamifera</td>
<td>2.96</td>
<td>0.12</td>
</tr>
<tr>
<td>Schefflara mortorioni</td>
<td>2.96</td>
<td>0.12</td>
</tr>
<tr>
<td>Matayba domingensis</td>
<td>2.74</td>
<td>0.11</td>
</tr>
</tbody>
</table>

\textsuperscript{15} All of these plants are trees, except for \textit{R. surinamensis}, which is a common liana.
4.3.4. Litter chemistry and abundance

Senescent leaves were saved from time zero of the first litterbag experiment for litter chemistry. Frass was collected from feeding trials with *L. portoricensis* feeding on *P. glabrescens* and *M. prasina*. Carbon: nitrogen (C: N) of senescent leaves of each litter type and herbivore frass were determined on an Elemental Analyzer (Costech Elemental Analyzer 4010, Valencia, CA). Fiber analysis to determine percent non-fibrous material, cellulose, hemicellulose and lignin of single species litter and herbivore frass was completed by M. Strickland at University of Georgia, Athens. To determine the relative abundance of different litter types in each enclosure and control, once annually (May, 2006-2008), all litter was carefully removed from the plots, sorted, weighed and put back into the experiment. Litter was removed only when litterbag experiments were not occurring.

4.3.5. Litter microbial community

A second litterbag experiment was conducted in 2007-2008 to assess consumer treatment impacts on the litter microbial communities (Figure 4.1, LB2). To test the mechanism behind any consumer effects on decomposition rates, the second litterbag experiment was only replicated in consumer treatments that significantly altered decomposition rates. I used single species, senescent litter in large mesh litterbags (1 mm mesh). Ten g of newly senescent leaves were placed in each litterbag and sewn shut. Sets of 3 litterbags of each single species litter were placed in each enclosure, and subsequently retrieved at 2, 5, and 8 months.

Upon retrieval, litterbags were placed in a cooler and kept chilled until DNA extraction. After removing any green plant material and soil, litter was thoroughly
homogenized. DNA was extracted from 0.3 g of litter from each litterbag using a MoBio Ultraclean DNA Soil Extraction Kit (Carlsbad, CA). DNA concentration and quality was determined for each extract with a biophotometer (Eppendorf, Westbury, USA).

The bacterial 16S rDNA and the fungal ITS1-5.8S-ITS2 rDNA were amplified using universal Eubacteria primers 27F-FAM/1525R (Lane 1991) and ITS1-FAM/ITS4 (White et al. 1990). PCR was performed using a mixture of 25µl JumpStart REDTaq ReadyMix (Sigma-Aldrich, Saint Louis, MO, USA), 0.5 µM of each primer and 10-50 ng DNA, and the following cycling parameters: initial cycle of denaturation at 94°C for 5 min, followed by 30 cycles of 94°C for 30 s, 52°C for 30 s, and 72°C for 1.5 min, and lastly a final cycle with an extension time of 10 min at 72°C. Positive and negative controls were used for quality assurance. PCR products were checked for amplification on a 1% agarose gel.

Terminal restriction fragment length polymorphism (TRFLP: Osborn et al. 2000, Buchan et al. 2003, Haynes et al. 2003) was run for each sample. Amplicons were enzymatically digested with HaeIII (fungi) and MnlI (bacteria) following the manufacturer’s protocols. Samples were precipitated with ethanol to eliminate impurities and dried. The samples were re-suspended in formamide with a GenScan 500 Liz size standard (ABI, Warrington, UK) and run on an ABI 3130 Genetic Analyzer (ABI, Foster City, CA). Samples were analyzed and TRFLP profiles were generated using GeneMapper Software version 4.0 (ABI, Foster City, CA). Bacterial and fungal richness were determined by counting the number of significant peaks over 50 FU (fluorescent units), and each significant peak was considered an operational taxonomic unit (OTU).
Total abundance in each sample was estimated by the summation of the total area underneath all significant peaks in the electropherogram.

4.3.6. Statistical analyses

Appropriate transformations were performed for any variables that were not normally distributed as determined by a Kolomagrov Smirnoff test ($P < 0.05$). $P$-values less than 0.05 were considered significant. All statistical analyses were completed with Systat 10 (SPSS, Chicago, Illinois, USA).

Differences in $k$ were examined using a multi-factorial, fixed effects model ANOVA with 5 factors (canopy cover, litter type, mesh size, herbivore and detritivore presence), and differences between different litter types were determined with a Tukey’s test. Hereafter, these factors are referred to as M (mesh), C (canopy cover), H (herbivore presence), D (detritivore presence) and L (litter type). Treatment effects on C: N were analyzed with a 2-way ANOVA (with factors M and L). I used repeated measures ANOVA with 3 factors (C, H and D) and time as the repeated measure ($t = 3$, 2006-2008) to evaluate treatment effects on total litter amount and the ratio of fast: slow decomposing litter ($P. glabrescens$: $M. prasina$ litter biomass) in each enclosure. I examined treatment effects on bacterial and fungal abundance and richness using a multi-way ANOVA (with factors C, L, and H). I could not use repeated measures ANOVA for this data because amplification of DNA for TRFLP analysis was not sufficient at all time points (see results).

I determined the effect that the enclosure had on each response variable measured by comparing control plots to the herbivore + detritivore (H+D) treatment. The H+D enclosures should most closely represent the whole forest because natural abundances of
consumers were added to treatments, although enclosures excluded canopy inputs. Consequently, each statistical test described above was repeated, replacing consumer treatment factors (herbivore and detritivore presence) and with an enclosure factor (enclosure presence).

4.4. Results

4.4.1. Litter type effects

Sources of litter differed in their decomposition rates: *P. glabrescens* litter decomposed ~35% faster than *M. prasina* litter, and mixed litter decomposed the slowest (Table 4.2, Figure 4.2 A). Litter in the large mesh litterbags, which allowed micro-arthropod access, decomposed about twice as fast as litter in the small mesh litterbags, which excluded most non-microbial biota. Both types of single species litter decomposed much faster in the large mesh litterbags. However, because there were no significant interactions between either consumer treatment and microarthropod presence, microarthropod data are not described here.

*C*: *N* was significantly different among litter types (Table 4.3). Fiber content analyses were only conducted on single species litter—percent hemicellulose (*t* = 4.517, df = 5, *P* < 0.01), cellulose (*t* = 5.52, df = 5, *P* < 0.005) and lignin (*t* = 6.42, df = 5, *P* < 0.002) were different between *P. glabrescens* and *M. prasina*, while percent non-fibrous material was not different (*P* > 0.05). *L. portoricensis* frass contained less non-fibrous material and hemicellulose, and more nitrogen, and a lower *C*: *N* than both types of litter.
<table>
<thead>
<tr>
<th>Source</th>
<th>ss</th>
<th>df</th>
<th>MS</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Canopy cover (C)</td>
<td>12.60</td>
<td>1</td>
<td>12.60</td>
<td>3.92</td>
<td>0.08</td>
</tr>
<tr>
<td>Mesh size (M)</td>
<td>41.85</td>
<td>1</td>
<td>41.85</td>
<td>15.09</td>
<td>&lt; .001</td>
</tr>
<tr>
<td>Herbivore presence (H)</td>
<td>16.10</td>
<td>1</td>
<td>16.10</td>
<td>5.80</td>
<td>0.043</td>
</tr>
<tr>
<td>Detritivore presence (D)</td>
<td>5.09</td>
<td>1</td>
<td>5.09</td>
<td>1.84</td>
<td>0.184</td>
</tr>
<tr>
<td>Litter type (L)</td>
<td>25.78</td>
<td>2</td>
<td>12.89</td>
<td>4.65</td>
<td>0.036</td>
</tr>
<tr>
<td>C x M</td>
<td>7.40</td>
<td>1</td>
<td>7.40</td>
<td>2.67</td>
<td>0.111</td>
</tr>
<tr>
<td>C x L</td>
<td>15.47</td>
<td>2</td>
<td>7.74</td>
<td>2.79</td>
<td>0.075</td>
</tr>
<tr>
<td>M x D</td>
<td>10.90</td>
<td>1</td>
<td>10.90</td>
<td>3.93</td>
<td>0.055</td>
</tr>
<tr>
<td>M x L</td>
<td>39.23</td>
<td>2</td>
<td>19.61</td>
<td>7.07</td>
<td>0.003</td>
</tr>
<tr>
<td>H x D</td>
<td>4.80</td>
<td>1</td>
<td>4.80</td>
<td>1.73</td>
<td>0.197</td>
</tr>
<tr>
<td>D x L</td>
<td>15.52</td>
<td>2</td>
<td>7.76</td>
<td>2.80</td>
<td>0.074</td>
</tr>
<tr>
<td>C x M x H</td>
<td>6.59</td>
<td>1</td>
<td>6.59</td>
<td>2.40</td>
<td>0.132</td>
</tr>
<tr>
<td>C x M x D</td>
<td>8.10</td>
<td>1</td>
<td>8.10</td>
<td>2.92</td>
<td>0.073</td>
</tr>
<tr>
<td>C x H x D</td>
<td>9.77</td>
<td>1</td>
<td>9.77</td>
<td>3.52</td>
<td>0.069</td>
</tr>
<tr>
<td>M x D x L</td>
<td>9.04</td>
<td>1</td>
<td>9.04</td>
<td>3.26</td>
<td>0.079</td>
</tr>
<tr>
<td>C x H x D x L</td>
<td>13.49</td>
<td>1</td>
<td>13.49</td>
<td>4.86</td>
<td>0.084</td>
</tr>
<tr>
<td>Error</td>
<td>99.86</td>
<td>36</td>
<td>2.77</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^{16}$ Only interactions with $P < 0.2$ are reported.
Figure 4.2 Treatment effects on decomposition rates from LB1. Bars represent mean $k$ values ($\pm$ 1 SE). A) Litter sources and mesh size effect. B) Disturbance effect. C) Consumer effects.
<table>
<thead>
<tr>
<th></th>
<th>C (%)</th>
<th>SE</th>
<th>N (%)</th>
<th>SE</th>
<th>C: N</th>
<th>SE</th>
<th>Non-fibrous (%)</th>
<th>SE</th>
<th>Hemim-cellulose (%)</th>
<th>SE</th>
<th>Cellulose (%)</th>
<th>SE</th>
<th>Lignin (%)</th>
<th>SE</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. glabrescens</strong></td>
<td>37.48</td>
<td>0.57</td>
<td>1.99</td>
<td>0.19</td>
<td>19.26</td>
<td>1.54</td>
<td>56.98</td>
<td>1.63</td>
<td>13.99</td>
<td>1.17</td>
<td>11.16</td>
<td>0.45</td>
<td>17.87</td>
<td>0.36</td>
</tr>
<tr>
<td><strong>M. prasina</strong></td>
<td>38.76</td>
<td>0.72</td>
<td>1.14</td>
<td>0.08</td>
<td>34.43</td>
<td>2.30</td>
<td>55.92</td>
<td>1.17</td>
<td>24.56</td>
<td>1.44</td>
<td>6.28</td>
<td>0.96</td>
<td>13.25</td>
<td>0.36</td>
</tr>
<tr>
<td>Mixed</td>
<td>45.93</td>
<td>2.18</td>
<td>0.91</td>
<td>0.09</td>
<td>50.95</td>
<td>3.41</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
<td>-----</td>
</tr>
<tr>
<td>Frass</td>
<td>37.89</td>
<td>0.08</td>
<td>2.43</td>
<td>0.04</td>
<td>15.60</td>
<td>0.25</td>
<td>61.60</td>
<td>1.60</td>
<td>8.65</td>
<td>1.03</td>
<td>11.98</td>
<td>0.44</td>
<td>17.76</td>
<td>0.66</td>
</tr>
</tbody>
</table>

There were significant differences between percent carbon, nitrogen and C: N between litter types. Fiber analysis was done only on single species litter and frass.
Total litter DNA concentration (i.e., the total amount of all DNA extracted from the litter) began low, peaked at 5 months, and declined at eight months ($F = 8.30$, $df = 2, 6, P = 0.02$). Adequate replication levels of fungal samples for TRFLP analysis were only acquired for the first time period (2 months). At this time, fungal richness or abundance were not different between canopy cover sites, litter types or herbivore treatments ($P > 0.05$). Adequate replication levels of bacterial samples for TRFLP analysis were only acquired for the second time period (5 months). Bacterial richness was about 3.5 times higher on *P. glabrescens* litter ($61 \pm 7.0$ OTUs) than *M. prasina* litter ($17.6 \pm 6.2$ OTUs). Although this same trend existed for bacterial abundance, it was not significant ($P > 0.05$).

4.4.2. Detritivore effects

Decomposition rates increased in the presence of detritivores, but this trend was not statistically significant (Table 4.2, Figure 4.2 B). There appears to be a positive non-significant interaction between the presence of detritivores and the large mesh litterbags. This same trend did not exist for small mesh litterbags, suggesting that litterbag mesh size affected how the detritivore interacts with the litter inside litterbags. Detritivores did not impact the total litter amount in enclosures (Table 4.3) but increased the ratio of fast: slow litter (Table 4.4).

4.4.3. Herbivore effects

Herbivores significantly reduced rates of leaf decomposition: litter in enclosures with herbivores decomposed over twice as slow as litter in enclosures without
TABLE 4.4

TOTAL LITTER (G/M² DRY WEIGHT) ANALYSIS RESULTS FROM FULLY CROSSED REPEATED-MEASURES ANOVA. ¹⁸

<table>
<thead>
<tr>
<th>Source</th>
<th>ss</th>
<th>Df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Within subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time</td>
<td>905.57</td>
<td>1</td>
<td>905.57</td>
<td>0.86</td>
<td>0.372</td>
</tr>
<tr>
<td>Time x Canopy</td>
<td>12659.59</td>
<td>1</td>
<td>12659.59</td>
<td>11.96</td>
<td>0.004</td>
</tr>
<tr>
<td>Error</td>
<td>13766.50</td>
<td>13</td>
<td>1058.96</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Between subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy</td>
<td>8782.21</td>
<td>1</td>
<td>8782.21</td>
<td>3.02</td>
<td>0.016</td>
</tr>
<tr>
<td>Herbivore</td>
<td>2065.31</td>
<td>1</td>
<td>2065.31</td>
<td>0.71</td>
<td>0.415</td>
</tr>
<tr>
<td>Detritivore</td>
<td>4291.41</td>
<td>1</td>
<td>4291.41</td>
<td>1.48</td>
<td>0.246</td>
</tr>
<tr>
<td>Error</td>
<td>37852.71</td>
<td>13</td>
<td>2911.75</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Herbivores (Table 4.2, Figure 4.2 C). Herbivores did not affect the total amount of litter in enclosures (Table 4.4). However, they impacted litter quality: without herbivores, the ratio of fast: slow litter was near 1 (1.07 ± 0.28), but fell well below 1 with herbivores (0.5 ± 0.16; see Table 4.4, Figure 4.5A). This group also reduced bacterial richness and abundance, with about twice as few OTUs when herbivores were present (Figure 4.4).

4.4.4. Herbivore + detritivore interactions

There were no significant herbivore + detritivore interactions on decomposition rates or the total litter quantity or quality.

¹⁸ Only main effects and interactions with $P < 0.2$ are reported.
4.4.5. Disturbance effects

Canopy cover did not affect litter decomposition rates (Table 4.2). The total amount of litter was greater in closed canopy sites (56.3 g/m² ± 7.78 g/m²) than light gap sites (34.4 g/m² ± 8.98 g/m²; Table 4.3). The ratio of fast: slow litter was lower in light gaps (0.26 ± 0.22; Table 4.4) than closed canopy sites (1.34 ± 0.21). There was no significant effect of canopy cover on litter DNA concentration or bacterial richness (at the 5 month time period; \( P < 0.7 \), Table 4.5).

### TABLE 4.5
RESULTS FROM REPEATED-MEASURES ANOVA ON FAST: SLOW LITTER. ¹⁹

<table>
<thead>
<tr>
<th>Source</th>
<th>ss</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Within subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time (T)</td>
<td>10.36</td>
<td>1</td>
<td>10.36</td>
<td>8.59</td>
<td>0.012</td>
</tr>
<tr>
<td>T x Canopy (C)</td>
<td>4.90</td>
<td>1</td>
<td>4.90</td>
<td>4.06</td>
<td>0.065</td>
</tr>
<tr>
<td>T x Detritivore (D)</td>
<td>2.79</td>
<td>1</td>
<td>2.79</td>
<td>2.32</td>
<td>0.152</td>
</tr>
<tr>
<td>T x C x D</td>
<td>4.15</td>
<td>1</td>
<td>4.15</td>
<td>3.44</td>
<td>0.086</td>
</tr>
<tr>
<td>T x Herbivore (H) x D</td>
<td>5.70</td>
<td>1</td>
<td>5.70</td>
<td>4.72</td>
<td>0.049</td>
</tr>
<tr>
<td>T x C x H x D</td>
<td>3.70</td>
<td>1</td>
<td>3.70</td>
<td>3.07</td>
<td>0.103</td>
</tr>
<tr>
<td>Error</td>
<td>15.70</td>
<td>13</td>
<td>1.21</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Between subjects</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C</td>
<td>12.20</td>
<td>1</td>
<td>12.20</td>
<td>13.10</td>
<td>0.003</td>
</tr>
<tr>
<td>H</td>
<td>3.289</td>
<td>1</td>
<td>3.289</td>
<td>3.53</td>
<td>0.037</td>
</tr>
<tr>
<td>D</td>
<td>5.01</td>
<td>1</td>
<td>5.01</td>
<td>5.38</td>
<td>0.083</td>
</tr>
<tr>
<td>C x H</td>
<td>2.82</td>
<td>1</td>
<td>2.82</td>
<td>3.03</td>
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</tr>
<tr>
<td>C x D</td>
<td>6.54</td>
<td>1</td>
<td>6.54</td>
<td>7.03</td>
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</tr>
<tr>
<td>H x D</td>
<td>8.13</td>
<td>1</td>
<td>8.13</td>
<td>8.74</td>
<td>0.011</td>
</tr>
<tr>
<td>Error</td>
<td>12.10</td>
<td>13</td>
<td>0.93</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹⁹ Only main effects and interactions with \( P < 0.2 \) are reported.
TABLE 4.6

RESULTS FROM A 3 X 2 ANOVA ON BACTERIAL TRFLP RICHNESS AND ABUNDANCE. 20

<table>
<thead>
<tr>
<th>Source</th>
<th>ss</th>
<th>df</th>
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</thead>
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<td></td>
<td></td>
</tr>
<tr>
<td>Canopy</td>
<td>16.07</td>
<td>1</td>
<td>16.07</td>
<td>0.04</td>
<td>0.761</td>
</tr>
<tr>
<td>Herbivore</td>
<td>4848.64</td>
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<td>4848.64</td>
<td>10.98</td>
<td>0.012</td>
</tr>
<tr>
<td>Litter</td>
<td>3180.07</td>
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<td>3180.07</td>
<td>7.20</td>
<td>0.039</td>
</tr>
<tr>
<td>Error</td>
<td>7507.29</td>
<td>17</td>
<td>441.61</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abundance</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Canopy</td>
<td>120128.14</td>
<td>1</td>
<td>120128.14</td>
<td>0.03</td>
<td>0.826</td>
</tr>
<tr>
<td>Herbivore</td>
<td>40481003.02</td>
<td>1</td>
<td>40481003.02</td>
<td>10.37</td>
<td>0.024</td>
</tr>
<tr>
<td>Litter</td>
<td>20980234.01</td>
<td>1</td>
<td>20980234.01</td>
<td>5.37</td>
<td>0.067</td>
</tr>
<tr>
<td>Error</td>
<td>66376497.92</td>
<td>17</td>
<td>3904499.88</td>
<td></td>
<td></td>
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</tbody>
</table>

20 There were no significant interactions.
Figure 4.3 Experimental results of ratios of fast (*P. glabrescens*) litter to slow (*M. prasina*) litter. Dashed lines represent a 1:1 ratio of fast:slow litter, and points represent the mean ratios (± 1 SE) of fast:slow litter biomass. A) Pooled herbivore effects. Consumer effects across: B) closed canopy sites, and C) light gaps.
Figure 4.4 Herbivore effects on bacterial richness and abundance across herbivore treatments. Bars represent mean ± 1 SE. Richness (top panels) was measured as the total number of significant TRFLP peaks (over 50 FU) in a given sample, and abundance (bottom panels) was measured as the total area underneath significant peaks of the electropherogram.
4.4.6. Enclosure effects

Enclosures did not affect decomposition rates \((F = 2.246, \text{df} = 1, 26, P > 0.05)\), and there were no significant interactions between mesh size, litter type or canopy cover and enclosure presence (for all these interactions, \(P > 0.1\)). Because enclosures excluded canopy inputs, there was almost 8 times more total litter in controls \((318.3 \text{ g/m}^2 \pm 41.62 \text{ g/m}^2)\) than enclosures \((39.8 \text{ g/m}^2 \pm 16.8 \text{ g/m}^2; F = 11.43, \text{df} = 1, 13, P < 0.01)\).

Consequently there was ~ 30% higher bacterial abundance in control plots \((8405 \pm 534 \text{ FU})\) than in enclosures \((6543 \pm 756 \text{ FU}; F = 123.43, \text{df} = 1, 13, P < 0.001)\). However, enclosures did not significantly affect litter quality \((F = 1.25, \text{df} = 1, 13, P > 0.05)\), DNA concentration or bacterial richness \((P > 0.10)\).

4.5. Discussion

Tropical forest production is thought to be mainly driven by nutrients derived from detrital food webs (Milton and Kaspari 2007). However, herbivores may alter the detrital food web through changes in the quality of resources reaching decomposers (Wardle and Bardgett 2005). This is the first study that demonstrates selective feeding by a tropical herbivore influences decomposition by altering the quality of resources available to the microbial community (Figure 4.5). Also, these results help to elucidate the pathway of herbivore influence on decomposition: herbivore preferential feeding on faster decomposing plants decreases the quantity of high quality litter, thereby reducing microbial activity and abundance, and rates of decomposition. Because detritivores did not impact decomposition rates, these results lend support to the hypothesis that snails act
as preferentially feeding microbivores, thereby altering N-cycling and primary production through this role.

Figure 4.5 Proposed graphical hypotheses for consumer alteration of decomposition. Arrows represent the movement of biomass from one component to another, and the circle represents the rate of decomposition, where the left panel is without herbivores and the right panel is with herbivores. Thick arrows represent the important pathways of material movement observed in this study.

4.5.1. Herbivore effects

Selective feeding by herbivores changes the resources available to the decomposer community: their consumption decreases quality of litter reaching the forest floor, leaving a detrital layer composed of the poorer quality, less nutritious *M. prasina* litter (which has higher C: N and percent hemicellulose). Microbes colonized this lower quality litter to a much lesser extent than higher quality litter, as shown by reduced bacterial richness and abundance on *M. prasina*. Since there was no significant interaction effect between herbivores and mesh size on litter decay, I do not think herbivores significantly alter the functionality of the litter micro-arthropod community, so the mechanism of the herbivores’ reduction of decomposition is due to changes in the
microbial community (Figure 4.5). Herbivores have been shown to alter litter microbial biomass, diversity and activity in other systems (Pastor et al. 1988, Holland 1995, Frost and Hunter 2004, Classen et al. 2007).

Even though this herbivore’s frass does provide higher quality material than plant litter (demonstrated by lower C: N ratios in frass than litter), *L. portoricensis*’s inputs to the slow cycle of decomposition (i.e., selective feeding) seem to overwhelm any stimulating impacts of their inputs to the fast cycle of decomposition (i.e., frass: Fonte and Schowalter 2005). In the Fonte and Schowalter study (2005) that showed *L. portoricensis* to be stimulating to decomposition rates, herbivores were given access to only one plant type (*P. glabrescens*), so only inputs to the fast cycle of decomposition were examined, not herbivore selective feeding.

In thinking about the whole forest’s functioning, canopy herbivores may also preferentially consume faster decomposing plants as indicated by the similar ratio of fast:slow litter between the enclosures and controls, which received overstory litter inputs. This preference for fast decomposing plants is a pattern that has been commonly shown (Grime et al. 1996, Wardle 2002). If both understory and overstory herbivores preferentially consume faster decomposing plants, then canopy herbivores in this forest could be impacting litter decomposition by mechanisms similar to the understory herbivores in this study.

4.5.2. Detritivore effects

I expected that the presence of *M. croceum* would increase the rate of litter decomposition because feeding on litter with their ratula would fragment the litter.
However, detritivores had no effect on $k$ values. Several different mechanisms may explain this result.

First, these snails are very slow growing (Prather, unpublished data). If the snails do not have significant metabolism needs, they may not consume enough litter to significantly impact decomposition. Secondly, they may exclusively feed on microbial biomass, which grows very quickly in the tropics. Lodge (1996) suggested that fungal biomass might be an important food source for many litter and soil invertebrates because fungi concentrate many nutrients that are essential to invertebrate physiology. This may be especially true for snails, because fungi concentrate calcium, which is essential for snail growth and abundance (Johannessen and Solhoy 2001, Hoptopp 2002). Detritivores in other systems have been shown to preferentially consume fungi (Moore et al. 1988) and decomposition rates in this experiment seem to be more sensitive to changes in bacterial communities. If $M. croceum$ does prefer fungi, then these detritivores may not alter decomposition rates. Lastly, if litterbags limited snail access to the litter, then the design of the bags themselves could inhibit detritivore feeding on litter. I found some indication that the design of the bags interfered with the interaction between snails and the litter inside the bags in my results. More research would be needed to determine whether one or more of these mechanisms may be causing these results.

4.5.3. Disturbance effects

Although I saw no significant herbivore + canopy cover interactions, the results of this experiment suggest that the influence of herbivores on decomposition may be amplified by disturbance. Because I controlled plant abundance and herbivore biomass
in this experiment, plant and herbivore populations could not respond to the release from light limitation in light gaps. However, in this forest *L. portoricensis* tends to aggregate on plants in light gaps (Willig et al. 1993) probably because of large numbers of highly palatable host plants, as seen in other systems (Coley and Barone 1996). Both disturbances and populations of these walking sticks tend to be patchily distributed in this forest (Willig et al. 1993). Therefore, herbivores’ impacts on decomposition could create spatial heterogeneity in decomposition rates, nutrient availability and plant biomass based on forest gap dynamics, as has been shown in other systems (Pastor et al. 1988).

4.5.4. Conclusions: Implications for decomposition in tropical forests

Because I sought to isolate the impacts that the consumers had on *understory* processes, the enclosure design excluded canopy litter inputs. Therefore, the enclosure reduced the total amount of litter reaching the forest floor, and consequently reduced the total abundance of litter bacteria, as indicated by TRFLP results. The enclosures did not affect decomposition rates, and thus I deem the enclosures an effective method of studying how consumer species affect decomposition rates.

Here, I demonstrate that organisms besides primary producers and microbes, like herbivores, can influence decomposition rates even in complex, highly productive ecosystems like rainforests. These patchily distributed herbivores may create spatial heterogeneity in decomposition rates in this forest. Also, because herbivore impacts to decomposition in this forest are influenced by herbivore inputs to the slow cycle of decomposition, I suggest that studies of tropical decomposition and rainforest ecosystem models explicitly consider consumer inputs to the slow cycle of decomposition, like those
proposed by DeAngelis (1992). More generally, since consumer organism effects on tropical decomposition are often considered negligible, these results highlight the need for more research to understand how common consumer impacts to tropical decomposition may be.

4.6. Acknowledgments

The past and current members of the Belovsky Lab provided much help with experimental design and statistics. Paul Klawinski, Jeanne Lodge and Todd Crowl provided crucial input and logistical support for this study. Erik Jansen, Rick and Donna Prather, Katie Hein, Jill Thompson, Kunal Mandal, Tim Hoellein and Cecelia Hennessey helped with field and lab work. The González lab, including Veronica Cruz, at the International Institute of Tropical Forestry prepared most of the mesh bags for both experiments. The microbial work was conducted in the microbiology lab of Universidad del Turabo, with much help from its lab members, including Jose Peréz Jiménez. A. Laws, D. Choate, E. Kistner, K. Mandal and C. Patrick provided comments on earlier drafts of this manuscript. C. Prather was supported on a University of Notre Dame Environmental Research Center fellowship for three summers and a Bayer Fellowship from CEST at the University of Notre Dame. This work is supported by NSF LTER DEB-0218039 and DEB-0620910 grants to Belovsky, Cantrell-Rodriguez and González.

4.7. Literature cited


5.1. Abstract

Most current models that predict primary production in tropical forests do not take trophic dynamics into account. Results from my previous studies have shown that trophic dynamics do indeed affect primary production and other ecosystem processes. I developed and parameterized a simplified trophic interaction model (TIM) to explore whether the proposed mechanisms behind trophic effects on rainforest ecosystems were supported. TIM models the distribution and flux of nutrients through different ecosystem components (plants, litter, soil, and herbivores) of a tropical forest in Puerto Rico. I verified the model with data from experimental enclosures that manipulated herbivore and detritivore presence. After verifying the model and exploring proposed mechanisms for trophic level effects, I used the model to make predictions about how changes in herbivore feeding preferences or the addition of a predator may affect understory primary production and nutrient dynamics. TIM successfully predicts an herbivore-induced temporary increase in primary production and a shift to a slow decomposing plant community that was observed in empirical studies. Additionally, with TIM results, I was

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21 I gratefully acknowledge my coauthors, Gary Belovsky and Todd Crowl.
able to make hypotheses about additional tropical complexity. For example, I hypothesize that if a predator of herbivores is added to my experimental systems, there would still be a temporary increase in primary production, but the predator maintain low levels of herbivore feeding, thus preventing a significant plant community shift. TIM was used successfully as a tool to examine the potentially important role of consumers to tropical forest functioning, suggesting that other tropical rainforest ecosystem models should incorporate these possibly important trophic interactions.

5.2. Introduction

Nutrients derived from the detrital food web are thought to support high levels of primary production in tropical forests (Vitousek 1984). There is growing awareness in non-tropical systems that the autotrophic food web (primary producers, herbivores and their associated carnivores) and detrital food web (detritus produced by the autotrophic food web, decomposers and their associated carnivores) mutually influence each other and affect ecosystem processes (DeAngelis 1992, Adams and Wall 2000, Wardle et al. 2002, Hooper et al. 2005). The effects of consumers are often overlooked in tropical systems, where it is commonly assumed that primary producers (that attain extremely high biomass) and microbial decomposers (where nutrient transformations occur) are the main groups that influence ecosystem processes. Additionally, the rich biodiversity in tropical forests has prevented descriptive studies of the autotrophic food web, further worsening the neglect of tropical trophic interactions. However, trophic interactions have commonly been shown to affect ecosystem processes in non-tropical systems (see Appendix A), and more recently in some tropical systems.
The combination of the autotrophic and detrital food webs into a single food web model has created a “new breed” of ecosystem model that explicitly incorporates the ecological interactions created by biodiversity (population and community ecology) into ecosystem functioning (decomposition, nutrient pools and fluxes, and primary production). This type of model has provided exciting new insights into how consumers accelerate or decelerate ecosystem processes (Pastor et al. 1988, Pastor and Naiman 1992, Belovsky and Slade 2000, 2002, Crowl et al. 2001, Wardle et al. 2002). This type of model could be very useful in tropical rainforest systems, which have particularly striking levels of biodiversity.

Several of these models that combine the autotrophic and detrital food webs have begun to incorporate a small degree of biodiversity. For example, several models divide the plant community into two types: fast and slow decomposing primary producer species (e.g., Belovsky 2000). Models using fast and slow decomposing plants (henceforth, fast and slow plants) have revealed a general pattern of ecosystem functioning. First, differential consumption of fast versus slow plants by herbivores in the terrestrial ecosystem can change the resource quantity and quality available to the detrital food webs. The direction of change in resource quality and quantity depends on which type of plant the herbivores prefer. Additionally, depending on whether the relative abundance of fast or slow decomposing detritus is increased, the rate of nutrient release from litter and primary production, which is nutrient dependent, will either increase or decrease. Lastly, changes to detrital resources and decomposer communities can be accentuated if
one plant has a competitive advantage over another. The competitive advantage emerges because fast plants tend to be relatively superior when decomposers release matter at a rapid rate, and slow plants tend to be relatively superior when decomposers release nutrients from detritus slowly.

Figure 5.1 Graphical depiction of concepts used in the Trophic Interaction Model. Solid arrows indicate biomass being built, and dashed lines represent biomass being lost by plants via litterfall, or decomposition. Detritivores are not explicitly built into the model, as they had no significant impacts on decomposition rates.

To examine the proposed mechanisms underlying demonstrated consumer effects on the functioning of a tropical rainforest in Puerto Rico, I developed a model combining consumers with primary producers and decomposers. This model, TIM (Trophic Interaction Model—see Figure 5.1 for graphical depiction), is a food web model that explicitly incorporates the effects of trophic levels empirically demonstrated as important to ecosystem functioning.
5.3. Methods

5.3.1. Modeling

TIM was reduced to *four main ecosystem components* (Table 5.1): (1) living plants, (2) plant litter, (3) available nutrients for plant growth, and (4) herbivores. Plants were separated into two categories: those producing litter that decomposes rapidly (fast plants), and those producing litter that decomposes slowly (slow plants; as determined by Prather, Chapter 4, this volume). The two plant categories are allowed to compete for resources (nutrients). Litter was split into three categories—litter produced by (1) fast and (2) slow plants, and litter that was added to the experimental enclosures at the onset of the experiment to ensure initial litter was similar among experimental treatments (other litter). Detritivores were not directly modeled because they had no observed significant effects on litter decomposition rates. However, since detritivores were shown to decrease soil N (Chapter 3), detritivores impacts were modeled by using available nutrients measured at the end of the experimental study as initial available nutrients.

Each main ecosystem component is represented as a nutrient pool and fluxes between all components are modeled using linear kinetics (e.g., Type I functional responses). Model fluxes were developed using a monthly time frame, a time span that is sufficient to track important ecosystem functions (e.g., decomposition, production, herbivore biomass, etc.), and with a small spatial scale (m$^2$). Because the model followed the flow of *nutrients* in the ecosystem, all parameters were in units of g N and fluxes were in units of g N / m$^2$ / mo. TIM was constructed using EXCEL, because EXCEL
enabled quick manipulation of the models and allowed me to obtain graphical output rapidly. To examine how consumers impact primary production and nutrient cycling, TIM was parameterized using data from experiments that manipulated consumers (Prather, this volume, Chapters 2, 3, and 4).

First, the model was solved for 25 years (300 monthly time periods) with the average initial conditions for experimental enclosures. Assuming that the forest is at steady state, the model contains the main ecosystem components, and the parameters are reasonably accurate, then the model should equilibrate relatively quickly and remain at equilibrium for the duration of the simulation.

Next, the model was solved for initial conditions in each experimental enclosure, and differences between predicted and observed values were determined with a series of paired t-tests (observed vs. model predicted values). If the model contains the main ecosystem elements and fluxes, the parameters are reasonably accurate, and the trophic effects are accurately modeled, then the model predicted values and the observed values for all of the main components should not be significantly different from one another. Subsequently, each parameter was perturbed by ± 20% to ascertain the sensitivity of the model to each component. Any major changes in unperturbed ecosystem components over time, particularly plants, were noted. These perturbations allowed me to determine which parameters may particularly affect ecosystem functioning in this model. For example, does herbivory modify the relative abundance of fast versus slow plants?

Lastly, to further hypothesize about the impacts of additional trophic complexity, I first changed the feeding preference of the herbivores from fast plants to slow plants by switching the values for herbivore consumption of fast and slow plants. This allowed me
to look at how selective feeding by herbivores impacts the main components in the ecosystem. Next, I added in a predation component to the model, where predators consumed herbivores. This component included the addition of the following predator parameters: initial biomass, consumption of herbivores (Type 1 functional response), death rate, and assimilation rate. Because I did not experimentally manipulate predators, these parameters were calculated using the literature average values for the understory of the forest. Using this additional component, I looked at how predation on herbivores altered the main components in the ecosystem.

5.3.2. Model Parameterization

Collection of empirical data

Study site and species characteristics

The data for this model was collected at the Luquillo Long Term Ecological Research site (LUQ LTER; described in Odum and Pigeon 1970). LUQ is located in the Northeastern corner of Puerto Rico (18° 19' N, 65° 45' W), and, as an insular forest, has a relatively low floral and faunal richness compared with mainland tropical sites (Waide and Reagan 1996). Consequently, the food web of this forest is one of the only tropical rainforest food webs to be well described, making easier to model and manipulate food web components in a meaningful fashion. This forest is driven by tropical storms, which create large light gaps, and consequently the forest is in a constant state of secondary succession (Waide and Lugo 1992).
Miconia prasina and Piper glabrescens were chosen as fast and slow decomposing representatives of the understory plant community for this experiment and model (Prather, Chapter 4, this volume), because these genera are abundant across the Neotropics (Molina and Alemany 1997). M. prasina is a small shrub-like tree (Liogier 1995), and is an important early colonizer at LUQ (Aide et al. 1996). P. glabrescens is a common understory shrub found only in Puerto Rico. The invertebrate consumers used in this experiment were M. croceum, the most abundant detritivorous litter snail at LUQ (Prather, unpublished) and L. portoricensis, the most abundant generalist herbivore in the forest (Willig et al. 1986). These plants and consumers were chosen because they are abundant, commonly studied, easy to transport and manipulate.

Enclosure study

To parameterize TIM, I used data from an enclosure experiment that manipulated herbivore, detritivore and canopy cover presence. A PVC frame supported these mesh enclosures. I removed all litter and visible organisms from enclosures and added 1050 (± 50 g) of a common forest litter collected near study sites to each enclosure (other litter). Treatments consisted of natural abundances of detritivores (≈ 5.7 g / m²), and herbivores (≈ 1.8 g / m²) and were constantly maintained over time.

Plants of each species were located in the forest, transplanted into seedling bags, and grown for at least 3 months under similar light conditions in common forest soil. Five individuals of each plant species were randomly chosen and planted into PVC pipes in the ground in each enclosure, with 12-2cm holes to allow the exchange of nutrients and water with the soil. Plant survival was measured annually, and plant abundances were held constant (i.e., when a plant died, it was replaced). To estimate plant growth, plant
dimensions were measured at the beginning of the experiment (2005) and annually thereafter (2006-2008). Plants were harvested at the end of the experiment and dimensional analysis was performed to estimate biomass at each time period (Parameters A and C, Table 5.1; King 1991).

Leaves of each species, litter and soil were sampled in each enclosure annually (2005-2008). Stem and root were sampled at the end of the experiment. Frass was collected from feeding trials with *L. portoricensis* feeding on *P. glabrescens* and *M. prasina* (see below). All samples were dried at 60°C and ground through 60 micron mesh, and carbon: nitrogen (C: N) was determined on an Elemental Analyzer (Costech Elemental Analyzer 4010, Valencia, CA, U.S.A.) by C. Prather at the Center for Environmental Sciences and Technology (CEST) at the University of Notre Dame (Parameters B, D, F, K, P, and Q, Table 5.1).

A litterbag experiment used to determine consumer effects decomposition rates of *M. prasina* or *P. glabrescens* litter. Each litterbag set contained 4 bags picked up at 4 consecutive time intervals: time 0 (to account for handling losses), 2 months, 5 months and 8 months. Remaining litter was dried and weighed to determine leaf mass lost from each bag at each time period. \( k \) values for each litterbag set were determined using Olson’s \( k: X_t/X_0 = e^{-kt} \), where \( X_0 \) is the initial mass of litter, \( X_t \) is the mass of litter at time \( t \), and \( k \) is the decay rate constant (Olson 1963; Parameters G, L, and O, Table 5.1). To determine the relative abundance of different types of litter in each enclosure, all litter was carefully removed from the enclosures, sorted into *M. prasina*, *P. glabrescens* and other litter, weighed and put back into the experiment once annually (Parameters E, J, and N, Table 5.1).
Herbivore feeding trials

Feeding trials with individual *L. portoricensis* were used to determine herbivore consumption rates. A mixture of 30 individuals across different sexes and ages of *L. portoricensis* were collected from the field, and starved overnight until they were no longer producing frass. Fresh leaves *M. prasina* and *P. glabrescens* were collected from the field, and the petioles were kept in water. Individual herbivores were fed two leaves of either *P. glabrescens*, *M. prasina* or a choice of one leaf of both species in 7.6 L aerated plastic containers (10 replicates each). All feeding trials lasted for two days and were replicated on 3 different days to account for any variability between days. Any frass produced in each trial was collected. Herbivores and leaves were weighed at the beginning of trial, and again at the end of the trial, as was the frass. Leaves and frass were subsequently dried for 24 hours at 60 °C and weighed again. Twenty herbivores and leaves of each species were weighed wet, dried and reweighed to determine a wet: dry conversion rate. Herbivore consumption rates were determined by calculating the amount of leaves being eaten per day in relation to the amount of leaves offered and the weight of the herbivore (Parameters R and S, Table 5.1). Assimilation rates were determined by the N amount eaten and the g N egested in frass for each trial (Parameter U, Table 5.1).
5.4. Results

5.4.1. Model validation

Several general patterns emerge when comparing TIM predicted values to experimentally observed values (Figure 5.2). First, TIM consistently under-estimated the N in soil over time. Also, TIM consistently over-estimated the amount of N in fast plants over time, as well as N in slow plants (but only in closed canopy sites where herbivores are present). TIM predicted the N in slow plants in light gaps, and the amount of N in all different litter types over time reasonably well.

5.4.2. Model sensitivity

TIM components were particularly sensitive to changes in the initial amount of N in plants, soil, and herbivores and the concentration of N in each of these components (Table 5.1). Fast and slow decomposing plants also were sensitive to changes in herbivore consumption, death and assimilation rates. However, model components were not particularly sensitive to changes in any litter-related parameters: the initial amount of N in any types of litter, the concentration of N in litter, decomposition rates or litter production rates.
Figure 5.2 The observed and expected average values of each component within each experimental treatment. Gray lines are observed values and black lines are predicted values. "*" denotes significant differences between the observed and expected values, as determined by paired t-tests at each point.
### TABLE 5.1
MODEL PARAMETERS. 22

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Meaning</th>
<th>Type of value</th>
<th>Disproportionate outcome of changing parameter</th>
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</thead>
<tbody>
<tr>
<td>A. Initial fast plant (1)</td>
<td>total nutrient in fast plants (g/m2)</td>
<td>Enclosure</td>
<td>Yes</td>
</tr>
<tr>
<td>B. Fast plant nutrient content</td>
<td>fast plant nutrient content (g/g)</td>
<td>Enclosure</td>
<td>Yes</td>
</tr>
<tr>
<td>C. Initial slow plant (1)</td>
<td>total nutrient in slow plants (g/m2)</td>
<td>Enclosure</td>
<td>Yes</td>
</tr>
<tr>
<td>D. Slow plant nutrient content</td>
<td>slow nutrient content (g/g)</td>
<td>Enclosure</td>
<td>Yes</td>
</tr>
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<td>total nutrients in fast litter (g/m²)</td>
<td>Enclosure</td>
<td>No</td>
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<tr>
<td>F. Fast litter nutrient content</td>
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<td>Static based on site</td>
<td>No</td>
</tr>
<tr>
<td>G. Fast litter decomposition rate</td>
<td>proportion of total fast litter decomposing per month</td>
<td>Enclosure</td>
<td>No</td>
</tr>
<tr>
<td>H. Fast plant litter production</td>
<td>proportion of fast leaves falling</td>
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<td></td>
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<tr>
<td>J. Initial slow litter (2)</td>
<td>total nutrients in slow litter (g/m²)</td>
<td>Enclosure</td>
<td>No</td>
</tr>
<tr>
<td>K. Slow litter nutrient content</td>
<td>slow litter nutrient content</td>
<td>Static based on site</td>
<td>No</td>
</tr>
<tr>
<td>L. Slow litter decomposition rate</td>
<td>proportion of total slow litter decomposing per month</td>
<td>Enclosure</td>
<td>No</td>
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<tr>
<td>M. Slow plant litter production</td>
<td>proportion of slow leaves falling</td>
<td>Static</td>
<td></td>
</tr>
<tr>
<td>N. Initial other litter (1)</td>
<td>total nutrients in slow litter (g/m²)</td>
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<td>No</td>
</tr>
<tr>
<td>O. Other litter decomposition rate</td>
<td>proportion of total slow litter decomposing per month</td>
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<td>P. Initial nutrients (3)</td>
<td>total nutrient pool (g/m2)</td>
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22 Bold parameters are ecosystem components.
TABLE 5.1 (CONTINUED)

<table>
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<td><strong>Q. Initial herbivore (4)</strong></td>
<td>total nutrient in herbivores (g/m²)</td>
<td>Static, based on treatment</td>
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<tr>
<td>R. Herbivore consumption of fast</td>
<td>proportion of fast plants being eaten per month</td>
<td>Static based on treatment</td>
<td>Yes</td>
</tr>
<tr>
<td>S. Herbivore consumption of slow</td>
<td>proportion of slow plants being eaten per month</td>
<td>Static based on treatment</td>
<td>Yes</td>
</tr>
<tr>
<td>T. Herbivore death rate</td>
<td>proportion of herbivores dying</td>
<td>Static based on treatment</td>
<td>Yes</td>
</tr>
<tr>
<td>U. Herbivore assimilation rate</td>
<td>proportion of plants digested</td>
<td>Static based on treatment</td>
<td>Yes</td>
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Figure 5.3 Main ecosystem components for average enclosures when no consumers (top panel), herbivores (middle panel), and predators (bottom panel) are present.
5.4.3. Response to trophic dynamics

With no macro-consumers built into the model, after 4 years fast plants are much more abundant than slow plants, and reached an asymptote at around 20 years, while slow plants gradually decline over time, reaching stable low levels at around 20 years (Figure 5.3). When herbivores that prefer fast plants are added to the system, slow plants increase rapidly, reaching their maximum at around 8 years. Also, when these herbivores are present, there is a short two year time period when total plant N is elevated compared to exclusion treatments. However, when herbivores prefer to consume slow plants, fast plants and their litter persists, while slow plants and their litter initially increase but remain at low levels after 20 years (Figure 5.4). Lastly, when predators that consume herbivores are added to the system, slow plants gradually increase in biomass and eventually reach their maximum at around 10 years and thereafter slowly decline, while fast plants increase rapidly, and then slowly increase, reaching their maximum around 10 years (Figure 5.3).
5.5. Discussion

TIM can be used to formulate hypotheses about how the plant community responds to changes in trophic dynamics. For example, the second most common walking stick in this forest, *Agamemnon iphimedeia*, appears to feed on slow plants (Prather, personal observations). Thus, if *A. iphimedeia* would have been used as the herbivore in these enclosure experiments, I may have seen an opposite plant community response compared to what I observed in my field experiments (Prather, Chapter 2, this volume). Based on TIM, I would expect that the feeding preferences of *A. iphimedeia* would lead to more abundant fast plants, that would eventually outcompete slow decomposing plants (Figure 3).
Also, TIM allows me to make predictions about what would happen to the plant community if a predator that consumes herbivores was added to these experiments. Based on this model, I expect that if predators were added to herbivore treatments, their consumption of herbivores would keep herbivory at low levels, allowing the preferred fast plants to persist for much longer in the community (Figure 4). In this forest, common predators (like coqui frogs, *Eleutherodactylus coqui*) attain very high biomass, and are capable of eating *L. portoricensis* (especially juveniles). Therefore, adding a natural abundance of *E. coqui* to herbivore treatments could mitigate the impacts of herbivores on ecosystem processes. Also, these predators could have other important impacts through their high production of feces that has been noted in other studies (Beard et al. 2002, Beard et al. 2003).

TIM accurately predicts the outcome of herbivore and detritivore treatments on fast vs. slow plant biomass. Also, TIM accurately predicts the temporary increase in total primary production that was observed in my empirical study when focal herbivores are present. However, this model does not accurately predict the time scale of plant growth. In general, plants in experimental enclosures acquired nutrients more slowly from the soil and thus grew more slowly than TIM predicts. There could be several explanations for this result. Nutrients in the soil may be over-estimated by this model because, at any given time, a large percentage of nutrients in this forest may be sequestered in fungal and bacterial communities (Lodge 1996), which TIM does not specifically account for. In TIM, nutrients released from litter or frass immediately enter the soil and cannot be sequestered in microbial biomass. Also, plants in this experiment were grown in PVC pipe to attempt to quantify the effects of consumers on belowground production.
However, PVC pipe may have limited plant growth by limiting root access to nutrients in the soil. This could also be another reason why TIM consistently overestimates the amount of N in soil. Even though the model does not accurately predict the rates at which plants grow and nutrients are acquired, I believe that TIM is a useful tool for examining the effect of consumers on the functioning of the understory of this tropical rainforest because it accurately predicts plant community outcomes.

Current concepts about tropical ecosystem dynamics assume that tropical plant communities are largely driven by detrital nutrient dynamics because tropical soils tend to be highly weathered and nutrient poor. However, this model was not very sensitive to changes in any litter-related parameters. Instead, model components were much more sensitive to changes in parameters relating to plants and herbivores. Model sensitivity to plant-related parameters was expected because plants sequester the majority of nutrients in these highly productive forests, but it is still not commonly accepted that tropical consumers impact rainforest functioning.

This model predicts that consumers do have important impacts, and this is supported by data from the experiment discussed in this paper. I find TIM to be a useful tool in examining the potentially important role of consumers to forest functioning. Subsequently, I suggest that ecosystem models utilized for tropical rainforests explicitly incorporate trophic interactions and biodiversity whenever appropriate and possible. This will allow for better understanding about how important trophic interactions and consumer effects are in tropical rainforest ecosystems.
5.6. Acknowledgments

Many members of the LUQ LTER program provided data and feedback on earlier, more complex versions of this model, especially Bob Waide and Jeanne Lodge. C. Prather was supported on a University of Notre Dame Environmental Research Center (UNDERC) Fellowship for three summers, a Pollard Fellowship from the Biology Department, and a Bayer Fellowship from CEST from University of Notre Dame. This work is supported by NSF LTER DEB-0218039 and DEB-0620910 grants to Belovsky and Crowl.

5.7. Literature cited


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CHAPTER 6:
CONCLUSIONS

“The truth is that we need invertebrates but they don’t need us. If human beings were to disappear tomorrow the world would go on with little change...life on Earth, would set about healing itself and return to the rich environmental states of a few thousand years ago. But if invertebrate species were to disappear, I doubt that the human species could last more than a few months.” E. O Wilson 1987

Even though prominent ecologists and conservationists make the claim that invertebrate consumers are more crucial to the functioning of the Earth’s ecosystems than large-bodied organisms (Wilson 1987, Attenborough 2005), their impacts to diverse and productive tropical forests remain understudied and not well understood (Prather, Chapter 1, this volume). The results of this dissertation provide evidence that consumer organisms have important impacts to primary production, nutrient cycling and litter decomposition in tropical rainforests, and these impacts are similar to those that their non-tropical counterparts have. In this conclusion, I summarize these findings and describe future research directions.

6.1. An unconventional view of rainforest functioning: the role of trophic interactions

Conventional views about rainforest ecosystem functioning claim that immense plant production is supported by nutrients derived from the detrital food web. These detritally-derived nutrients are quickly acquired by plants growing in the highly weathered, nutrient poor soils (Vitousek 1984, Feeley and Terborgh 2005, Milton and
The role of consumers has largely been ignored because highly productive plants sequester the majority of nutrients in these systems. Additionally, impacts of consumers within the autotrophic food web have been neglected because the vast biodiversity in tropical forests has precluded these food webs from being well described. However, for this dissertation, I was able to conduct research in one of the only rainforests whose food web and ecosystem structure has been clearly defined (Waide and Reagan 1996). Furthermore, because the ecosystem structure of tropical rainforests is largely driven by gap dynamics, it is important to understand how disturbance alters consumer impacts. Here I have shown that consumer effects were seen almost exclusively in light gaps, where plants grew rapidly, and thus consumer resources were high. Moreover, consumer feeding-ecology may regulate detrital dynamics and nutrient cycling. Consumers from the autotrophic food web had important effects on plant growth, nutrient cycling and litter decomposition rates.

6.1.1. Herbivore impacts to rainforest ecosystems

Herbivores increased plant growth (Chapter 2) and nutrient availability in light gaps (Chapter 3), but also decreased litter decomposition rates through alterations of the litter microbial community (Chapter 4). Additionally, walking sticks consumption of higher quality, more palatable plants shifted the plant community to slow decomposing plants. Nutrients that were then released from the decrease in N-rich plant tissue were quickly acquired by slowly decomposing, low N plants, which built more biomass per unit of N over time. Reduced decomposition rates were the result of an increase of slowly decomposing plants and their litter, that provided poor quality resources for
microbial decomposers, as exhibited by a less abundant and rich litter bacterial community.

The increase in plant growth observed in herbivore treatments is likely a temporary phenomenon. A shift to a more unpalatable plant community has been shown to decrease nutrient availability and reduce primary production in other systems (Pastor and Naiman 1992, de Mazancourt and Loreau 2000, Feeley and Terborgh 2005). This shift has been shown to decrease the quality of resources available to decomposers and decomposition rates, leading to reduced nutrients available to plants. However, I did not see a reduction in nutrient availability in my experiments, and thus I hypothesize that reduced nutrient availability must occur at longer time scale than my experiment ran. In order to see a reduction in primary production, the experiment would have needed to run until herbivore consumption decreased the biomass of preferred fast plants to very low levels. At this point, the negligible release of nutrients still sequestered in *P. glabrescens* tissues would have little impact on nutrients available to slower decomposing plants (*M. prasina*). Therefore, it is likely that if had I had measured plant biomass at year five, I would have seen the biomass of *M. prasina* level off due to a reduction in nutrient availability.

6.1.2. Detritivore impacts to rainforest ecosystems

Detritivores decreased plant growth over time, in combination with reductions in soil total N, and N availability. However, detritivores did not affect decomposition rates. Two concurrent mechanisms may be driving these results. First, these detritivores may have selectively fed on microbial groups that are important in N-cycling (e.g., nitrifiers or
mycorrhizal fungi), thus decreasing nutrients available for plant growth. There is little evidence of detritivores selectively feeding in terrestrial systems (but see Moore et al. 1988), although this phenomenon has been well studied in marine systems (e.g., Phillips 1984). Feeding trials that I conducted with *M. croceum* (unpublished) showed that they preferentially feed on litter colonized by microbes rather than litter without microbial communities present. This suggests that the *M. croceum* preferred to consume nutrient rich microbial tissue compared to relatively nutrient-poor plant litter. Additionally, the movement of snails in the litter layer and soil may have disturbed the physical structure of soil and litter, which could have resulted in leaching of nutrients from sediments, triggering the loss of nutrients in the system. This has been shown in other systems (Gardner et al. 1987, Meysman et al. 2006, Volkenborn et al. 2007, Richards 2009). Further research would be needed to decide if one or a combination of these mechanisms may be driving the detritivore effects on plants, nutrients and litter decomposition observed here.

6.1.3. Interaction of different consumer trophic levels

Members of the autotrophic food web of a tropical rainforest *can* impact the resources provided to the detrital food web. This counters the prevailing view that rainforest primary production is driven solely by nutrients derived from the detrital food web. Here, I observed that herbivore effects superseded detritivore effects on the rates of primary production (Chapter 2), and litter production as well as decomposition rates (Chapter 4). In both of these instances, the patterns observed when herbivores were found alone were similar to when both consumers were present in combination. These
results suggest that herbivore impacts to the plant community drive resources provided to the detrital food web, and thus affect how that food web functions.

6.1.4. Future research questions

Results from TIM hint at several interesting research questions regarding the role of consumers in rainforest ecosystems. These questions are described below.

(1) How do herbivore feeding preferences affect their impacts on rainforest ecosystem processes? Since the understory plant community in this forest is particularly sensitive to herbivore selective feeding, it would be important to examine how an herbivore with an opposite feeding preference (i.e., one that prefers to consume slower decomposing plants) affects the ecosystem processes examined in this study. The second most common walking stick (Agamemnon iphimedeia) at LUQ feeds on slowly decomposing plants (Prather, personal observations). If A. iphimedeia was used in the same experiments instead of L. portoricensis, I would expect to see the plant community shift to fast decomposing plants, as well as the acceleration of decomposition and primary production, which was opposite to what was seen in this study.

(2) Do predator-induced trophic cascades operate in rainforest systems? There has been little research conducted to understand if trophic cascades operate in tropical forests like they do in other ecosystems. Using TIM predictions, I hypothesize that the addition of a predator to the experimental system used in this dissertation would cause a trophic cascade: predators should mitigate the impacts of herbivores to the plant community. Predator consumption of herbivores would decrease herbivory rates, buffering the plant community against herbivores impacts. In this forest, predators (like coqui frogs, Eleutherodactylus coqui) attain very high biomass, and research has shown that coquis significantly affect the nitrogen cycle (Beard et al. 2002, Beard et al. 2003). Therefore, adding a natural abundance of E. coqui to herbivore treatments could induce a trophic cascade.

(3) How does increasing plant diversity (i.e., using a natural understory plant community) affect consumer impacts on rainforest ecosystems? I used an extremely simplified plant community (2 species) compared to the natural plant diversity of this forest understory, which may include dozens of plant species at the same spatial scale (Thompson et al. 2004). One way to start examining how consumers affect more realistic plant communities would be
to examine how these consumers affect a naturally occurring plant community. If the mesh were removed from these existing enclosures for a year, the natural plant community could reestablish. Mesh could be added to enclose these naturally developing plant communities, and the consumer treatments reestablished to see if these consumers have similar impacts to more complex plant communities compared to the 2-species communities used in this study.

(4) How does a natural consumer community affect rainforest succession? It remains important to understand how a natural community of rainforest consumers affects successional processes in light gaps. To do this, it may be possible to replicate herbivore and detritivore removals with a combination of pesticides and mesh fences surrounding the understory in multiple light gaps. With this type of experiment, we may be able to better understand how whole trophic levels impact plant succession in this tropical rainforest.

6.2. Final words

These results challenge a pervasive view about the functioning of tropical rainforest ecosystems: that trophic interactions are unimportant to the functioning of these complex, highly productive systems. This dissertation provides evidence that consumers are active components of the ecosystem structure in rainforest ecosystems, and that their feeding ecology likely determines the direction of consumer impacts on ecosystem processes. Consumers may be particularly important in light gaps of tropical forests whose structure is largely driven by gap dynamics, suggesting that consumers may also play an important role in how succession proceeds in the rainforest understory.

The results of this study add a more complex ecosystem to those that invertebrates are known to heavily influence. Wilson (1987) and Attenborough (2005) may indeed be correct in their suggestions that invertebrates run the world and that, without them, the Earth’s ecosystems would collapse.
6.3. Literature cited


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APPENDIX A:
REFERENCES USED IN TABLE 1 LITERATURE REVIEW


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