THESIS

SPATIAL AND TEMPORAL VARIATION OF DISTURBANCE: EFFECTS ON RIPARIAN AND AQUATIC COMMUNITIES ALONG TWO HEADWATER STREAMS IN PUERTO RICO

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER OUR SUPERVISION BY JULIE KAY HENRY ENTITLED SPATIAL AND TEMPORAL VARIATION OF DISTURBANCE: EFFECTS ON RIPARIAN AND AQUATIC COMMUNITIES ALONG TWO HEADWATER STREAMS IN PUERTO RICO BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT OF THESIS

SPATIAL AND TEMPORAL VARIATION OF DISTURBANCE: EFFECTS ON RIPARIAN AND AQUATIC COMMUNITIES ALONG TWO HEADWATER STREAMS IN PUERTO RICO.

The structure and composition of tropical ecosystems are often shaped by disturbance events, especially in areas that experience hurricanes and other severe storms. The structure of riparian forests along headwater streams in the Luquillo Long Term Ecological Research Site of Puerto Rico reflects the patchiness of periodic hurricane disturbance as well as the spatial pattern of past human land use. The result of these disturbance patterns is a clumped distribution of the dominant riparian tree species (the sierra palm, *Prestoea montana*) within and between riparian forests along two headwater streams, Quebrada Prieta and Quebrada Toronja. Fruit-fall and frond input from the sierra palm is an important source of food and refuge for stream consumers. Patchiness of palm fruit and frond availability may have important effects on the distribution patterns and relative abundance of consumers in headwater stream communities.

I studied the effects of disturbance from Hurricane Georges on a dominant riparian tree species in the Luquillo Forest Dynamics Plot of the Luquillo Long Term Ecological Research Site in northeastern Puerto Rico. I established 300 m by 10 m

riparian transects along the Prieta and Toronja, which were both dominated by the sierra palm (*Prestoea montana*). Following Hurricane Georges, I periodically surveyed sierra palm individuals for damage and subsequent recovery (measured by initial loss and subsequent regrowth of palm fronds), palm height, and reproductive status. I used Geographic Information System (GIS) data to determine variation in riparian topography (elevation, slope, and aspect) and tree densities within riparian transects. I analyzed logistic regression models to determine the influence of riparian topography, tree density, and palm height on spatial patterns of palm damage and recovery due to Hurricane Georges.

Palm height was the factor most related to initial hurricane damage to palms, with tall canopy palms receiving the most damage. Post-hurricane palm recovery was also related to wind exposure, measured by higher elevation of riparian transects and lower surrounding tree densities. A larger proportion of palms were damaged along the Toronja (33%) than the Prieta (25%), which may be a result of historical human disturbance in the Toronja basin which led to a shift in forest species composition. Large canopy palms constitute a greater proportion of the riparian forest along the Toronja than the Prieta, and so had a greater proportion of palms that were exposed to stronger hurricane winds. These spatial patterns of hurricane damage to riparian forests often affect detrital input to stream pools, which can influence distribution patterns and relative abundance of stream consumers.

Stream communities in the Luquillo Mountains of Puerto Rico support several species of omnivorous freshwater decapods. One of the most abundant predatory

decapods is the freshwater crab, *Epilobocera sinuatifrons*. I studied habitat selection of freshwater crabs in stream pools within the same 300 m riparian transects along the Prieta and the Toronja. Nine study pools were established along each stream transect, and were periodically sampled for juvenile crabs, mayfly nymphs, and physical and substrate characteristics. Juvenile crabs and mayfly nymphs were abundant in all pools, but both showed higher numbers along the Prieta. Because the land use history in the Toronja drainage has resulted in a less stable channel and increased abundance of fine sediment in Toronja pools, the more stable pools along the Prieta may retain more leaf litter and provide better pool habitats for juvenile crabs. Temporal variation and within-pool habitat variables (substrate composition, pool depth, flow velocity, and heterogeneity of pool width) were best at explaining variations in juvenile crab distributions.

To determine food web relationships of juvenile crabs within the stream community, I studied predation rates of juvenile crabs on mayfly nymphs, larval shrimp, and conditioned leaf disks collected from leaf packs within stream pools. Pools were apparently dominated by one mayfly species, *Farrodes taino (*Ephemeroptera: Leptophlebiidae). Feeding experiments demonstrated mayfly nymphs to be the preferred food source for juvenile crabs (8 mm to 18 mm carapace width), with feeding rates increasing with crab size. The observed predation rates were relatively high, ranging from 2 to 72 mayfly nymphs per crab per night. These feeding experiments suggest that aquatic insects may be an important source of protein for juvenile crab growth, and high aquatic insect predation rates by juvenile crabs may influence the low relative abundance of aquatic insects found in these two insular tropical streams.

In summary, detrital inputs are an important source of food, cover, and substrate for aquatic communities in tropical headwater streams. Spatial patterns of riparian palm damage influence the spatial distribution of detrital inputs across a watershed, in turn affecting distributions and relative abundance of stream consumers. The magnitude and frequency of disturbance, such as hurricanes or high rainfall events, influence the standing stock of detritus in stream pools, the availability of refuge, and the stability of the stream environment.

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PREFACE

This thesis has been prepared as two chapters. Each chapter will be submitted to a peer reviewed journal for publication. The first chapter will be submitted to *Journal of Tropical Ecology*, and the second chapter to *Freshwater Biology*. Chapters have been formatted as appropriate for the intended journal.

DEDICATION

This thesis is dedicated to my family: Diane Henry, Nancy and Ken Petersen, and Kevin, Geni, Daesoliel, and Sage Peterson Henry. You have all supported and encouraged my interest in ecology over the years, as well as enabling my exploration of the tropics. I also dedicate this to Guthrie Zimmerman, who not only provided emotional support throughout my graduate experience, but also taught me quite a bit about biology. Thank you all for everything.

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CHAPTER 2

Title - Landscape-level responses of riparian palms to Hurricane Georges

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Running title - Response of riparian palms to Hurricane Georges

Abstract

The structure and composition of tropical forest ecosystems are often shaped by disturbance events, especially in areas that experience hurricanes and other severe storms. We studied the effects of disturbance from Hurricane Georges on a dominant riparian tree species in the Luquillo Forest Dynamics Plot of the Luquillo Long Term Ecological Research Site in northeastern Puerto Rico. Three hundred meter by 10 m riparian transects were established along two headwater streams, the Prieta and the Toronja, and were dominated by the sierra palm (*Prestoea montana*). Following Hurricane Georges, sierra palm individuals were surveyed periodically for damage and recovery (measured by initial loss and subsequent regrowth of palm fronds), palm height, and reproduction. Geographic Information System (GIS) data were used to determine variation in riparian topography (elevation, slope, and aspect) and tree density within riparian transects.

We analyzed logistic regression models to determine the influence of riparian topography, tree density, and palm height on spatial patterns of palm damage and recovery due to Hurricane Georges. Palm height was the factor most related to initial palm damage (tall canopy palms received the most damage), whereas palm recovery was negatively correlated with wind exposure (measured by higher elevation and lower tree densities). A larger proportion of palms were damaged along the Toronja (33%) than the Prieta (25%), which may be a result of historical human disturbance in the Toronja basin which led to a shift in forest species composition. Spatial patterns of hurricane damage to riparian forests often affect detrital input to stream pools, which can influence distribution patterns and relative abundance of stream consumers.

Introduction

Disturbance is a crucial factor in determining the structure and dynamics of tropical forest ecosystems. In regions where hurricanes dominate the disturbance regime, ecosystem processes are often driven by spatial and temporal patterns of hurricane damage. The frequency and intensity of these storms influence spatial patterns of the biotic and physical landscape, which in turn affect biotic interactions within the ecosystem. The intensity of hurricane damage to tropical forests is often patchy; damage patterns are associated with topography, tree size, distance from the storm's center, storm duration, wind speed and direction, forest density, soils, and tree species characteristics (Foster and Boose 1992, Boose et al. 1994, Zimmerman et al. 1994, Walker 1995).

Canopy damage from hurricane winds usually results in a large pulse of leaf litter, woody debris, and fruit fall across the disturbed area (Frangi and Lugo 1991, Vogt et al. 1996, Harrington et al. 1997). This pulse of organic debris provides nutrients to the forest floor (Frangi and Lugo 1991), and is also an important input of detritus into stream food webs (Covich et al. 1991, Johnson and Covich 1997, Wallace et al. 1999). Leaf litter pulses vary temporally with disturbance events, and spatially with topography and patchiness of storm damage (Vogt et al. 1996). Terrestrially produced leaf litter, small twigs, and fruits constitute a relatively continuous input of detritus-based energy to small tropical headwater streams, such as those found in the Luquillo Experimental Forest of Puerto Rico (Covich 1988, Covich and McDowell 1996). Spatial patterns of hurricane damage may influence the distribution of leaf litter and fruit fall input to stream ecosystems. By analyzing spatial patterns of sierra palm disturbance from Hurricane

Georges, this study focuses on hurricane effects on a tropical riparian food web. Spatial and temporal patchiness of food or structural habitat inputs across a watershed could result in instream variation of biological diversity and habitat quality for stream detritivores. By studying the spatial pattern of hurricane damage for a common, dominant riparian tree species, the sierra palm *(Prestoea montana)*, we focus on the influence of hurricane disturbance on detrital inputs to stream food webs and the terrestrial-aquatic linkage in tropical forest ecosystems.

On 21 September 1998, Hurricane Georges passed through the Luquillo Experimental Forest, and high winds caused extensive damage to the forest canopy. Our objectives were to explore spatial and temporal patterns of sierra palm damage as a result of this hurricane disturbance, and to document how damage relates to topography of the riparian zone, palm height, and tree density. Most studies investigating the effects of hurricanes have focused on patterns of damage and recovery among species across forest stands. In contrast, we were interested in the patterns of hurricane damage and recovery for the dominant riparian tree species along two headwater stream reaches. Our analysis of palm damage, as it relates to palm height, riparian forest density, and various topographical characteristics of the watershed, focuses on spatial analysis of the effects of disturbance on terrestrial-aquatic linkages.

Study Site

The Luquillo Experimental Forest (LEF) is located in northeastern Puerto Rico (Fig.1), and is the only tropical ecosystem in a network of sites in the National Science

Foundation's Long-Term Ecological Research (LTER) Program. The Luquillo Forest Dynamics Plot (LFDP) (Fig. 1) is a 16 ha permanent study plot in the subtropical wet forest life zone (Zimmerman et al. 1994), and was established in 1989 in order to record changes in forest ecology as a result of severe disturbance. All trees >5 cm diameter breast height (DBH) within the LFDP are tagged and georeferenced on a grid of surveyed 20 m x 20 m plots with 5 m x 5 m subplots. Sierra palms are the most abundant species with more than 4,400 trees (Reed 1998). Other dominant species include *Dacryodes excelsa*, *Manilkara bidentata*, and *Sloanea berteriana*. Soils are mainly Zarzal clay of volcanic origin, and rainfall averages 350 cm/year (Zimmerman et al. 1994).

The LEF, like many areas in the Caribbean, has an aseasonal climate and experiences periodic severe storms. Hurricanes significantly affect the canopy structure and dramatically increase light gap areas (Zimmerman et al. 1994, Frangi and Lugo 1998, Sabat and Fetcher 1999). Two riparian transects were established along sections of Quebrada Prieta (first-order and second-order) and Quebrada Toronja (first-order) tributaries of the Rio Sonadora located within the LFDP near the El Verde Field Station ($18^{0}20'$N, $65^{0}49'$W, 350 m above sea level) in the northwest section of the LEF (Fig. 1). The Prieta and the Toronja are similar in size and location, but differ in riparian tree species composition and land-use history. In contrast to the Prieta, the Toronja drainage has been intensively disturbed by humans, with historical accounts of charcoal production, cattle grazing, coffee growing, and some hardwood timber harvest occurring within the Toronja riparian zone apparently prior to 1940 (Garcia-Montiel and Scatena 1994, Reed 1998). This disturbance regime has resulted in a riparian forest composed

mainly of palms and other early-successional tree species along the Toronja, whereas a relatively less disturbed, mixed forest exists along the Prieta (Reed 1998) (Fig. 2).

Methods

Palm Population Surveys

Riparian plots were established on the Prieta and the Toronja in July 1998. Each plot extended 200 m along the length of each stream with 5 m on either side to delineate the riparian zone, and were divided into 10 m x 5 m subplots along each side of the stream. The riparian zone was set at 5 m with the intention of only including palms that were likely to drop fruit into the stream channel. In January 1999 we extended the plots to include another 100 m (300 m total length) along each stream to increase the sample size of hurricane damaged palms. All sierra palms (>1.5 m in height) located within each 10 m x 5 m subplot were surveyed in November 1998, January 1999, and June 1999 to record canopy height and number of live fronds. Flowering and fruiting structures per palm were recorded in July 1998, November 1998, January 1999, and June 1999 to determine the effect of Hurricane Georges on palm reproductive patterns. This palm population (N=234) constituted the basis for our analysis.

We divided palms into small (1.5-5 m), subcanopy (5-7 m), and canopy (>7 m) size classes based on tree height from the top of the root mass to the bottom of the oldest frond scar (i.e. the length of the woody stem). The cut-off of 1.5 m for small palms was 0.5 m shorter than the height of the smallest observed reproductive palm. This height

classification was based on average subcanopy and canopy tree heights for the riparian forest.

Hurricane Damage to Palms

In November 1998, two months after Hurricane Georges, the original 200 m plots were surveyed for palm mortality and damage. We recorded mortality from landslides, tree falls, and wind damage, as well as the number of live fronds on each palm. We classified damage by determining major damage to a palm had occurred when only three or fewer fronds remained undamaged. This classification system was based on field observations of between six and 12 fronds on undamaged palms, and on the average annual sierra palm frond production of four fronds (Lugo and Rivera Batille 1987). In January 1999 we again surveyed the number of live fronds for each tree, noting any new mortality of trees. A third damage/mortality survey was repeated in June 1999.

Geographic Information Systems Analyses

We performed GIS analyses to explore the effects of natural disturbance on spatial patterns of damage and subsequent recovery of sierra palms as a result of Hurricane Georges, with respect to slope, aspect, and elevation of the riparian corridor, palm height, and riparian forest density. We used ArcView (Version 3.1, ESRI 1998) to perform GIS analyses.

Subplots (5 m x 10 m) on either side of the two study streams were used as the experimental unit in our GIS and statistical analyses. We used existing stream coverages of the Prieta and the Toronja (digital maps in ArcView format), and added a 5 m buffer representing the riparian zone along each stream. We created our own subplot cover from

this riparian zone map by digitizing subplot boundary locations using Global Positioning System (GPS) coordinates obtained in the field. We combined the palm height, palm damage and recovery (information gathered during the three field surveys), and forest density data (gathered from an existing coverage of all trees > 10 cm DBH in the LFDP) with the subplot grid for both streams at each survey date. These maps allowed us to assign subplot information to each palm surveyed. Therefore, we were able to observe palm distributions, as well as the distribution of damage along the two streams, and patterns of subsequent palm recovery. We calculated the number of palms, non-palms, and total tree density (palms and non-palms) for each subplot to use in statistical analysis.

We also examined palm damage as it related to slope, aspect and elevation along each riparian zone. We used an existing digital elevation model (DEM) of the LFDP, created from elevation data collected at 20 x 20 m resolution. In ArcView, the DEM was used to construct maps of mean aspect, slope, and elevation for each of the 5 m x 10 m subplots. We joined all subplot information (aspect, slope, elevation, palm, non-palm, and total tree density) with individual palm information (damage for each survey and palm height) for each stream to use in our statistical analyses.

Statistical Analyses

We used a logistic regression to model palm damage (damaged = 1, not damaged = 0) with aspect, slope, elevation, palm density, non-palm density, total tree density, and palm height as predictive variables (Fig. 3). We included interactions between aspect and slope, aspect and palm height, and slope and palm height. Data collected in November 1998 were analyzed for factors relating to hurricane damage. Only palms that were

damaged in November 1998 were analyzed for damage in January 1999 and June 1999. Palms still found to be damaged in January 1999 were analyzed for damage in June 1999 to examine factors related to palm recovery during those time periods. All four data sets were checked and corrected for overdispersion. Over-dispersed data show more variation than is explained by the binomial distribution, and can be corrected by scaling the covariance matrix by the estimate of the dispersion parameter (SAS 1998). The dispersion parameter for each data set was estimated from the deviance divided by its degrees of freedom from a global model (SAS 1998).

We used the modeling approach recommended by Burnham and Anderson (1998), and formulated *a priori* hypotheses (Appendix I) to determine factors most associated with hurricane damage and subsequent recovery patterns of riparian palms. Our *a priori* hypotheses were based on information gathered from our literature review, as well as field observations. However, we used some preliminary analyses to select the aspect to include in our models because we had little prior knowledge about how aspect may correlate with palm damage or recovery. For each data set (November 98 damage, November 98-January 99 recovery, November 98-June 99 recovery, and January 99-June 99 recovery) we used four initial models, each containing only one aspect as a predictor variable. We compared Akaike's information criterion (AIC) scores for each model, as well as p values for each aspect, to determine which aspect would be best to use in models explaining palm damage and recovery patterns.

AIC is an objective model selection procedure that ranks a set of competing models in their ability to explain the data (Burnham and Anderson 1998). The best of the

competing models has the lowest AIC score. AIC adjusts the log-likelihood from maximum likelihood estimates with a correction factor that penalizes for additional model parameters (Burnham and Anderson 1998). Thus, AIC balances bias and variance when ranking competing models. AIC indicates how well a model fits the data relative to the competing models rather than providing an absolute measure of how well the models explain the data. As such, it is important to develop *a priori* model hypotheses based on sound biological information. We determined which models best fit our data by comparing AIC scores and AIC weights (the proportion of times that a particular model will be selected as the AIC best model: Burnham and Anderson 1998). The AIC best model is the most parsimonious model explaining variation in the data. For palm recovery analyses, we improved the fit of our models by constructing *post hoc* models (Appendix I) that incorporated significant variables from our *a priori* models.

Results

Mean slope, aspect and elevation were calculated for each 5 m x 10 m subplot along the Toronja and Prieta (Figs. 4-6). The topography of both streams varied substantially over the two 300 m x 10 m study plots. Although the Toronja had slightly steeper gradients than the Prieta, both streams varied between 1° and 50° for the subplot mean slope (Fig. 5). Mean aspect varied along the banks of both streams with subplots on opposite sides of the stream exhibiting opposite aspects where slopes were steeper, and the same mean aspect in areas with gradual slopes (Fig. 6). Mean elevations for Toronja subplots ranged from 410 m to 360 m, whereas mean subplot elevations along

the Prieta ranged from 410 m to 370 m, with both streams flowing from the southeast (Fig. 4).

Palms were more abundant on the Toronja (Fig. 8) than the Prieta (Fig. 7), although palm distributions were patchy among subplots along both streams. Non-palm tree density was higher along the Prieta than the Toronja; however, total tree density along both streams was similar. Total tree density was also patchy among subplots.

The overall amount of sierra palm damage incurred from Hurricane Georges was slightly higher along the Toronja (Fig. 8) than the Prieta (Fig. 7). Thirty-three percent and 25% of palms on the Toronja and Prieta respectively were damaged in November 1998, two months after the hurricane (Table 1). Palm damage was patchy within each stream transect, with trees in some subplots exhibiting more damage than trees in other subplots. Palm recovery (i.e. growth of new fronds) was rapid, with only 16% and 13% of palms still damaged in January 1999, and only 9% and 7% of palms on each stream remaining damaged during the June 1999 survey. Overall palm mortality immediately following Hurricane Georges was less than 1%.

Hurricane Georges did have an effect on the reproductive patterns of riparian sierra palms for all post-hurricane surveys. Flower production was near zero in November 1998, and no inflorescences were found in January 1999 (Fig. 9). Fruiting structures were still abundant in November 1998 and January 1999 (Fig. 9). However, fruiting and flowering structures were both extremely low in June 1999, ten months after Hurricane Georges (Fig. 9).

A logistic regression on palm damage indicated that the top two AIC-selected models for palm damage in November 1998 included palm height and stream (Prieta and Toronja) as the variables most associated with palm damage patterns, with large-canopy palms and palms along the Toronja exhibiting the most damage (Tables 2, 4). The top AIC-selected model included only the canopy palm height class as the parameter most associated with palm damage. The canopy-height class parameter estimate was significant ($p=0.047$) and positive, indicating that this variable was positively associated with palm damage (Table 4, Fig. 10). This data set was shown to be over-dispersed and so the covariance matrix was scaled by 1.4 as a correction to allow for increased variation.

The top two AIC selected *a priori* models for palm recovery between November 1998 and January 1999 included west aspect (positively associated with palm recovery) and palm-canopy height (negatively associated with palm recovery) as the variables most associated with palm recovery patterns during this time period (Tables 2, 4; Figs. 10, 11). After examining significant parameters contained in other *a priori* models, we constructed *post hoc* models that provided a better fit to the palm recovery data. The top two AIC selected *post hoc* models included total tree density (positively associated with palm recovery) and slope (negatively associated with palm recovery) (Tables 3, 5). The top two *post hoc* models had higher AIC weights than the top *a priori* model (Table 3). Thus, the strongest relationships were a positive association of higher total tree density with palm recovery, whereas steeper slopes had a negative effect on palm frond regrowth. The overdispersion correction for this data set was 1.57.

The top two minimum-AIC *a priori* models for palm recovery between November 1998 and June 1999 included east aspect (positively associated with palm recovery), small palm height (negatively associated with palm recovery), and stream (more recovery was seen on the Toronja than the Prieta) (Tables 2, 4; Figs. 10, 11). *Post hoc* models were also constructed for this time period, and two models were calculated to have relatively similar AIC weights (Table 3). The variables included in the top *post hoc* AIC models included elevation (increases in elevation negatively associated with palm recovery) and total tree density (positively associated with palm recovery) (Tables 3, 5). Elevation was the only marginally significant parameter estimate ($p=0.06$), and the top two *post hoc* models all had higher AIC weights than the top *a priori* model (Table 3). Thus, the strongest relationships during this period were higher palm recovery rates at lower elevations and in subplots with higher total tree density. The covariance matrix of this data set was scaled by 1.26 to correct for overdispersion.

The top two AIC selected *a priori* models for palm recovery between January 1999 and June 1999 included east aspect (positively associated with palm recovery) and canopy palm height (positively associated with palm recovery) (Tables 2, 4; Figs. 10, 11). *Post hoc* models were constructed and the two top AIC selected *post hoc* models included elevation (increases in elevation negatively associated with palm recovery) and total tree density (positively associated with palm recovery (Tables 3, 5). The top two *post hoc* models all had higher AIC weights than the top *a priori* model (Table 3). Thus, the main relationships for January to June 1999 were the same as between November 1998 and June 1999, with increased palm frond regrowth at lower elevations and in subplots with

higher total tree density. These data were shown to be over-dispersed and were scaled by 1.57.

Discussion

Overall, we found low mortality of riparian palms caused by damage from Hurricane Georges. Palm mortality in our riparian transects was less than 1%, the same amount reported for palms by Zimmerman et al. (1994) after Hurricane Hugo in 1989. Hurricane damage studies throughout the LEF showed that palms experienced less overall mortality than the 9% average mortality calculated for all forest species (Zimmerman et al. 1994, Frangi and Lugo 1998). Palms also exhibited high recovery rates between our first and third damage surveys. Thirty-three percent of palms were damaged along the Toronja in November 1998, two months after Hurricane Georges, while 25% of palms were damaged along the Prieta. In June 1999, only 9% of the Toronja palms and 7% of the Prieta palms remained damaged. Because of low mortality rates and high recovery rates after hurricanes, sierra palms appear to be well adapted to the disturbance regime that characterizes this tropical forest ecosystem (Sabat and Fetcher 1999). Palms typically exhibit low mortality after hurricanes because wind damage to fronds often does not damage the palm's terminal meristem (Zimmerman et al. 1994). The palm mortality was mainly due to localized landslides, bank erosion, or fallen neighboring trees, whereas direct mortality from hurricane winds was rare.

Palm damage was patchy both within and among riparian plots for each survey date. Previous studies on damage associated with hurricanes have demonstrated this

patchiness to be associated with various topographical features, as well as initial canopy height of individual trees, species characteristics, tree density, individual storm characteristics, and soil composition (Foster and Boose 1992, Boose et al. 1994, Zimmerman et al. 1994, Walker 1995). Because our study is on a single dominant species over a relatively small spatial extent, we considered topography, palm height, and forest density to be the most relevant factors that could potentially influence the degree of hurricane damage.

Palm height was the most significant factor associated with riparian palm damage patterns due to Hurricane Georges. Large canopy trees are more exposed to hurricane winds, whereas small trees mostly suffer from overstory limbfall. Our results reveal that large canopy palms were damaged significantly more often than subcanopy or small trees, which is most likely explained by increased wind exposure to canopy palms. Other studies (Frangi and Lugo 1991, Harrington et al. 1997) concluded that tree height was an important factor relating to hurricane damage, with large canopy and small understory trees receiving more hurricane damage than subcanopy trees.

We observed that damage was greater along the Toronja riparian zone than along the Prieta, perhaps because of differences in species composition between the two streams. Palms are more abundant on the Toronja and comprise a greater percent of the forest canopy, which could result in higher wind exposure to a greater proportion of the palm population than along the Prieta. The riparian forest along the Prieta is more diverse (Reed 1998), which has resulted in a smaller proportion of the Prieta's riparian palm population to be classified as canopy trees. Differences in species composition and

forest structure between these sites may be caused by contrasting historical land use patterns (Garcia-Montiel and Scatena 1994, Zimmerman et al. 1995, Reed 1998, Foster et al. 1999).

The differences in species composition between our study streams was likely caused by persistent effects of historical land-use patterns in the Luquillo Mountains (Reed 1998). Forest-gap data from 1936 showed greater human impacts in the Toronja drainage, such as cattle grazing, charcoal production, hardwood timber removal, and coffee growing, whereas the Prieta has remained much less influenced by human disturbance (Garcia-Montiel and Scatena 1994, Zimmerman et al. 1995, Reed 1998). Historical human effects in tropical forests may not be immediately evident because of rapid vegetative regrowth. However, persistent effects of prior land-use patterns are a legacy of altered forest composition and structure that may affect ecosystem processes.

Zimmerman et al. (1994) found topography to be insignificant in hurricane damage for 26 common species in the LEF. However, other studies (Foster and Boose 1992 [Massachusetts], Boose et al. 1994 [LEF]) reported topography, especially aspect, to significantly affect hurricane exposure and damage patterns. Likewise, Frangi and Lugo (1991), and Walker (1995) observed that damage resulting from Hurricane Hugo was greater on aspects facing the prevailing storm winds (north-northwest). Our analysis did not detect topography to be greatly associated with riparian palm damage immediately after Hurricane Georges. However, topography and forest density seem to be the factors most associated with patterns of post-hurricane palm recovery.

Although our AIC-selected *a priori* models explained patterns correlated with palm damage immediately after Hurricane Georges, minimum-AIC *post hoc* models suggest that other factors may be more important to post-hurricane riparian palm recovery. Our top *a priori* models for all recovery periods suggested that aspect is the variable most correlated with palm recovery; however, *post hoc* models indicate that slope, elevation, and forest density are more relevant to palm recovery patterns. The top AIC-selected models for palm recovery between November 1998 and January 1999 indicated that steeper slopes were associated with lack of palm frond regrowth whereas increasing forest density was associated with palm recovery. These patterns suggest that post-hurricane riparian palm recovery is influenced by shelter from wind in months after the initial storm event.

The best AIC-selected models for palm recovery between November 1998 and June 1999, as well as models of recovery between January 1999 and June 1999, implied that higher elevation was correlated with lack of palm recovery, whereas forest density continued to be associated with palm regrowth. These models also suggest the importance of decreased wind exposure to riparian palm recovery patterns which may be due to the potential for increased wind exposure in sites with higher elevation. Our results indicate a positive correlation of increased forest density with palm recovery which suggests that light may not have been limiting to palm growth in the 10 months following Hurricane Georges, possibly due to defoliation of much of the forest canopy in those plots with numerous non-palm trees. Previous long-term studies on growth rates of the sierra palm have shown that palms grow more rapidly in forest gaps and high light

conditions (Lugo and Batille 1987, Sabat and Fetcher 1999). The positive correlation of increased forest density with palm recovery, combined with the negative association of steep slopes and higher elevation with palm recovery, suggest that riparian areas with less wind exposure may have been more important than light gaps for initial post-hurricane growth of fronds in the riparian forest.

Spatial patterns of hurricane damage in riparian forests result in patchiness of detrital-based energy inputs to stream food webs. Zimmerman et al. (1994) reported a pulse of leaf litter, woody debris, and fruit fall initially after hurricane disturbance, followed by a lack of detrital input, disrupting the normally continuous flow of energy through the forest ecosystem. The patchy distribution of palm damage after a hurricane is reflected in the riparian ecosystem through variations in detrital abundance and energy input to stream pools. Total leaf litter and fruitfall input to streams is usually high during and immediately after the initial storm event, but is low during post-hurricane recovery. Because the sierra palm is one of the most abundant trees of montane forests in the Caribbean (Reed 1998, Sabat and Fetcher 1999), it is an important food resource for many species of birds and other consumers. Sierra palm fruits have been reported as the principal food source for the endangered Puerto Rican parrot (*Amazona vittata*), and are also fed upon by red-necked pigeons (*Columba sqamosa*), ruddy quail doves (*Geotrygon montana*), black rats (*Rattus rattus*), and a scolytid beetle (*Cocotrypes carpophagus*) (Bannister 1970, Janzen 1972, Lugo and Frangi 1993, Wunderle 1999). Palms produce large quantities of fruit and some of this fruit falls into streams. Sierra palms are particularly abundant in riparian zones of lower montane forests (Bannister 1970), and so

palm fruit and leaf fall are important sources of food, substrate, and cover for stream consumers, including the freshwater crab (*Epilobocera sinuatifrons*) and several species of freshwater shrimp (Covich and McDowell 1996, Reed 1998). Palm fruitfall patterns may be especially affected by hurricane disturbance, with a substantial time lag needed for palms to return to pre-hurricane fruit production levels (Wunderle 1999). Our data also demonstrated a change in palm fruitfall patterns as a result of hurricane disturbance. Residual riparian palm fruitfall remained available for several months after the hurricane; however, new flower and fruit production remained extremely low for at least 10 months after the storm event. Stream consumers may be adapted to these detrital pulses and time lags, although pulses may cause population abundance and spatial distributions to fluctuate (Covich et al. 1996).

Population models predict that without hurricanes large palm populations would not exist in mature stands of lower elevation montane forests in the Caribbean (Brokaw 1999, Sabat and Fetcher, 1999). Dominance of palm populations is maintained in the montane forest by periodic opening and subsequent closure of the canopy, through hurricanes and other disturbances. Hurricanes are major drivers of tropical forest ecosystems. As such, they are important in determining tree species composition and energy flow in riparian communities. Patchiness of hurricane damage and recovery by riparian palms is influenced by factors such as topography, palm height, forest density, and time since the last storm, but species composition of the riparian forest may also play an important role. Historical land use patterns apparently produce long-term changes in

species composition, in turn affecting spatial patterns of hurricane damage and patchiness of nutrient inputs through changes in detrital composition.

Acknowledgments

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Table 1: Riparian palm damage over time as a result of Hurricane Georges. Percent of the riparian palm population along each stream that was classified as damaged during each survey date in the Luquillo Forest Dynamics Plot, Puerto Rico.

	November 1998	January 1999	June 1999
Quebrada Prieta	25%	13%	7%
Quebrada Toronja	33%	16%	9%

Table 2: The top competing *a priori* models by time period, for riparian palm damage due to Hurricane Georges measured in November 1998, and subsequent recovery through late June 1999.

Time period	Model Number[a]	Parameters	AIC	Weight	Correct Classification[b]	Sensitivity[c]	Specificity[d]
Nov.98 damage	11	canopy	159.87	0.35	65	40.7	76.6
	7	canopy, stream	161.05	0.19	65	40.7	76.6
Nov.98 - Jan.99 recovery	12	west aspect	56.06	0.27	54.2	53.3	55.2
	11	canopy	56.08	0.27	54.2	63.3	44.8
Nov.98 - June 99 recovery	12	east aspect	58.24	0.27	42.4	94.1	21.4
	2	small, stream	59.01	0.18	71.2	41.2	83.3
Jan.99 - June 99 recovery	12	east aspect	40.99	0.27	51.2	89.5	20.8
	11	canopy	41.38	0.22	51.2	73.7	33.3

[a]See appendix A for complete list of models
[b] rate of correct classification of an observation when that observation is removed from the data set and recalculated by the model
[c] ability of the model to predict a damaged palm correctly
[d] ability of the model to predict a non-damaged palm correctly

Table 3: The top competing *post hoc* models by time period, shown with top *a priori* models, for riparian palm recovery from Hurricane Georges. Hurricane Georges hit Puerto Rico in September 1998, and recovery was measured through late June 1999.

Time period	Model Number[a]	Parameters	AIC	Weight	Correct Classification[b]	Sensitivity[c]	Specificity[d]
Nov.98 - Jan.99 recovery	B	total tree density	54.56	0.23	57.6	53.3	62.1
	A	slope, total tree density	55.23	0.16	55.9	56.7	55.2
	12	west aspect	56.06	0.11	54.2	53.3	55.2
Nov.98 - June 99 recovery	E	elevation	56.62	0.17	76.3	52.9	85.7
	F	elevation, total tree density	56.77	0.16	71.2	35.3	85.7
	12	east aspect	58.24	0.07	42.4	94.1	21.4
Jan.99 - June 99 recovery	E	elevation	38.98	0.20	67.4	63.2	70.8
	F	elevation, total tree density	39.43	0.16	65.1	57.9	70.8
	12	east aspect	40.99	0.07	51.2	89.5	20.8

[a] See appendix A for complete list of models
[b] rate of correct classification of an observation when that observation is removed from the data set and recalculated by the model
[c] ability of the model to predict a damaged palm correctly
[d] ability of the model to predict a non-damaged palm correctly

Table 4: Estimated logistic regression equations for *a priori* AIC selected damage and recovery models for riparian palms surveyed from November 1998 through June 1999. Palm damage and recovery is measured in response to Hurricane Georges, which hit the Luquillo Experimental Forest of Puerto Rico in September 1998. Positive parameter estimates are positively associated with damaged palms for all models.

Time Period	Model Number	Regression equation parameters (Wald 95% confidence intervals) for AIC selected models
Nov.98 damage	11	-1.00(-1.46,-0.53)+0.81(0.01,1.61)canopy
Nov.98 - Jan.99 recovery[a]	12	0.21(-0.71,1.12)-0.34(-1.62,0.94)west aspect
	11	0.17(-0.66,1.00)-0.34(-1.64,0.96)canopy
Nov.98 - June 99 recovery	12	-0.72(-1.39,-0.03)-1.47(-3.89,0.94)east aspect
Jan.99 - June 99 recovery	12	-0.11(-0.93,0.71)-0.81(-3.02,1.41)east aspect

[a]AIC scores were nearly identical for two models during this time period.

Table 5: Estimated logistic regression equations for *post hoc* AIC selected recovery models for riparian palms surveyed from November 1998 through June 1999. Palm recovery is measured in response to Hurricane Georges, which hit the Luquillo Experimental Forest of Puerto Rico in September 1998. Positive parameter estimates are positively associated with damaged palms for all models.

Time Period	Model Number	Regression equation parameters (Wald 95% confidence intervals) for AIC selected models
Nov.98 - Jan.99 recovery	B	1.25(-0.69,3.19)-0.20(-0.50,0.10)total tree density
Nov.98 - June 99 recovery	E	-23.13(-46.66,0.41)+0.06(0.00,0.12)elevation
Jan.99 - June 99 recovery	E	-21.51(-48.60,5.58)+0.06(-0.02,0.13)elevation

Figure Legends

Fig. 1 Map of Puerto Rico, map of 50 m elevation contours in the Luquillo Experimental Forest (LEF), and 5 m elevation contours in the Luquillo Forest Dynamics Plot (LFDP) with the locations of the two study streams, Quebrada Prieta and Quebrada Toronja.

Fig. 2 Differences in canopy structure between riparian forests along Quebrada Prieta and Quebrada Toronja within the Luquillo Forest Dynamics Plot, Puerto Rico. The riparian zone along the Prieta is comprised of relatively mixed forest, with the canopy dominated by large non-palm trees, whereas the riparian canopy along the Toronja is dominated by the sierra palm, *Prestoea montana*. Canopy height in the Luquillo Forest Dynamics Plot averages approximately 20 m, although canopy height in areas dominated by the sierra palm may be lower.

Fig. 3 Flow chart of analysis procedures resulting in models describing patterns of riparian palm damage and regrowth after Hurricane Georges.

Fig. 4 Mean elevation of riparian subplots along the Prieta and the Toronja transects, located within the Luquillo Forest Dynamics Plot, Puerto Rico.

Fig. 5 Mean slope of riparian subplots along the Prieta and the Toronja transects, located within the Luquillo Forest Dynamics Plot, Puerto Rico.

Fig. 6 Mean aspect of riparian subplots along the Prieta and the Toronja transects, located within the Luquillo Forest Dynamics Plot, Puerto Rico.

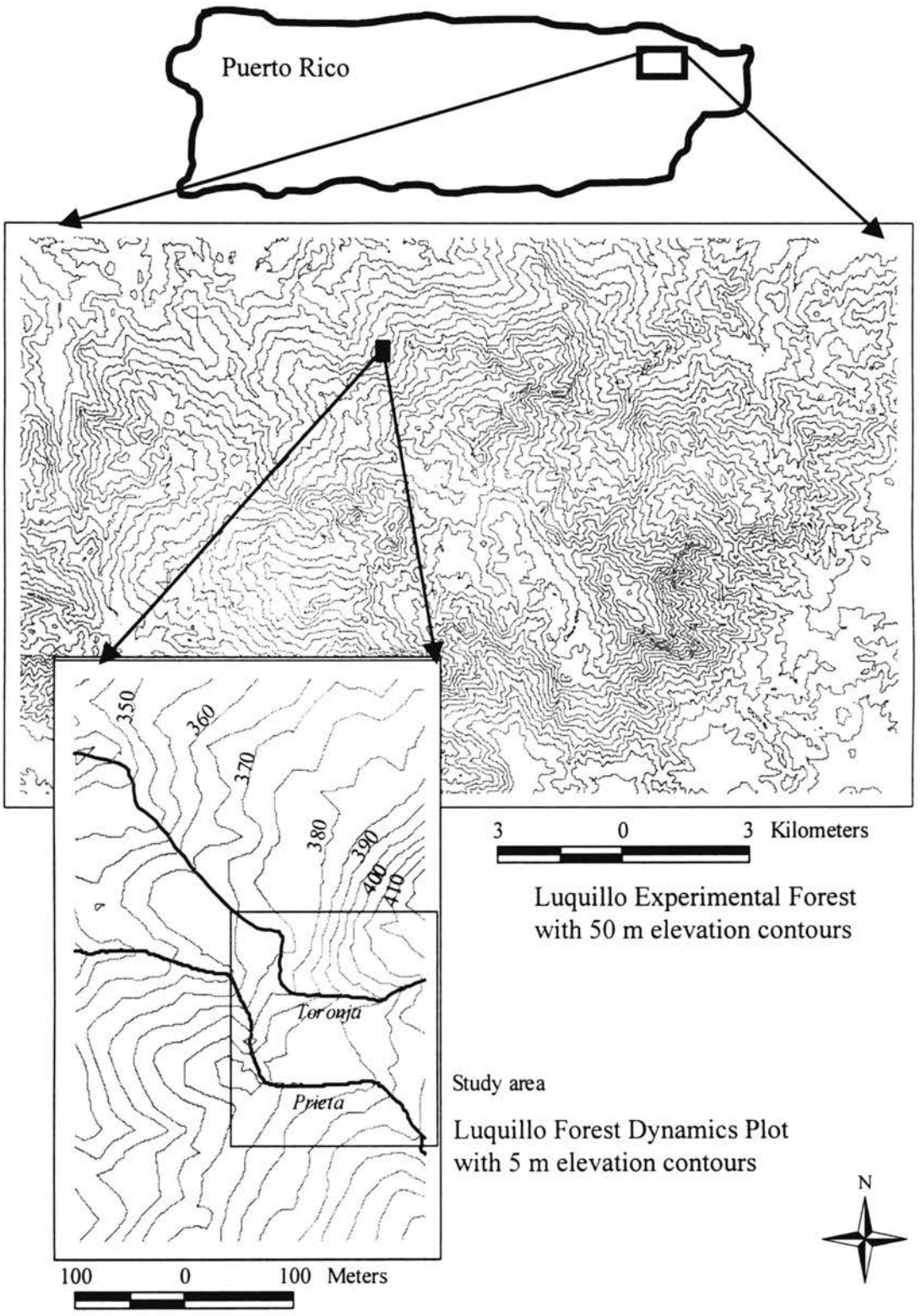
Fig. 7 Location of damaged and non-damaged palms within riparian subplots along the Prieta, located within the Luquillo Forest Dynamics Plot, Puerto Rico. Damaged and non-damaged palms are shown for our initial damage survey in November 1998 (two months after Hurricane Georges), as well as subsequent surveys in January 1999 and June 1999.

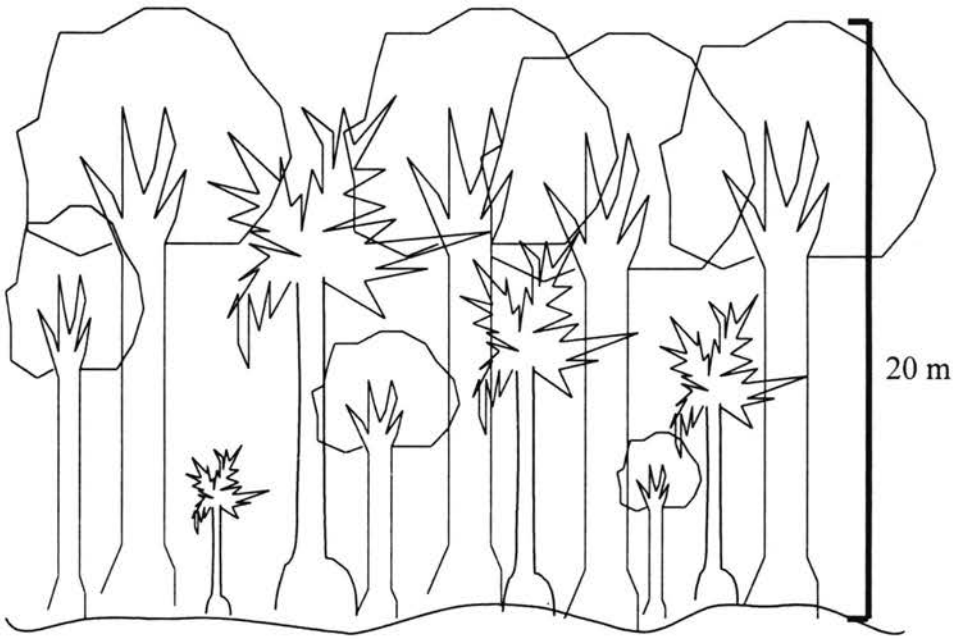
Fig. 8 Location of damaged and non-damaged palms within riparian subplots along the Toronja, located within the Luquillo Forest Dynamics Plot, Puerto Rico. Damaged and non-damaged palms are shown for our initial damage survey in November 1998 (two months after Hurricane Georges), as well as subsequent surveys in January 1999 and June 1999.

Fig. 9 Graph of mean flowering and fruiting structures per palm surveyed in riparian subplots along the Prieta and the Toronja, located within the Luquillo Forest Dynamics Plot, Puerto Rico. The initial survey was conducted in July 1998. Subsequent surveys were conducted in November 1998 (two months after Hurricane Georges), January 1999, and June 1999.

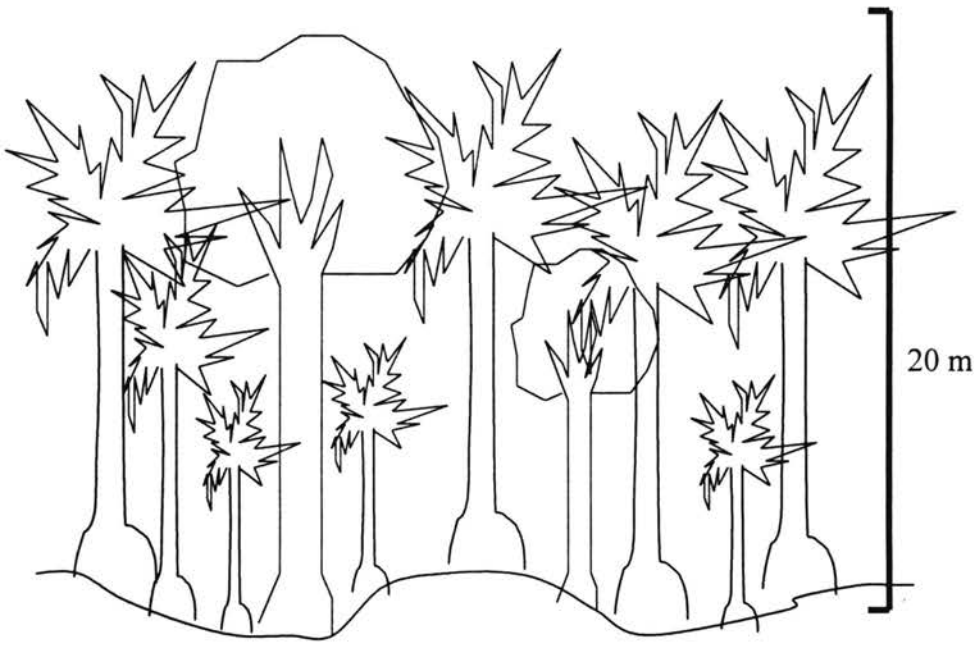
Fig. 10 Graph of percent of total damaged palms for each tree height class by survey date. Total damaged palms represents all palms with 3 or fewer fronds per tree per survey date, for both the Prieta and the Toronja, Luquillo Forest Dynamics Plot, Puerto Rico.

Fig. 11 Graph of percent of total damaged palms for each aspect by survey date. Total damaged palms represents all palms with 3 or fewer fronds per tree per survey date, for both the Prieta and the Toronja, Luquillo Forest Dynamics Plot, Puerto Rico.


Puerto Rico
3 0 3 Kilometers
Luquillo Experimental Forest
with 50 m elevation contours
350
360
370
380
390
400
410
Toronja
Prieta
Study area
Luquillo Forest Dynamics Plot
with 5 m elevation contours
N
100 0 100 Meters



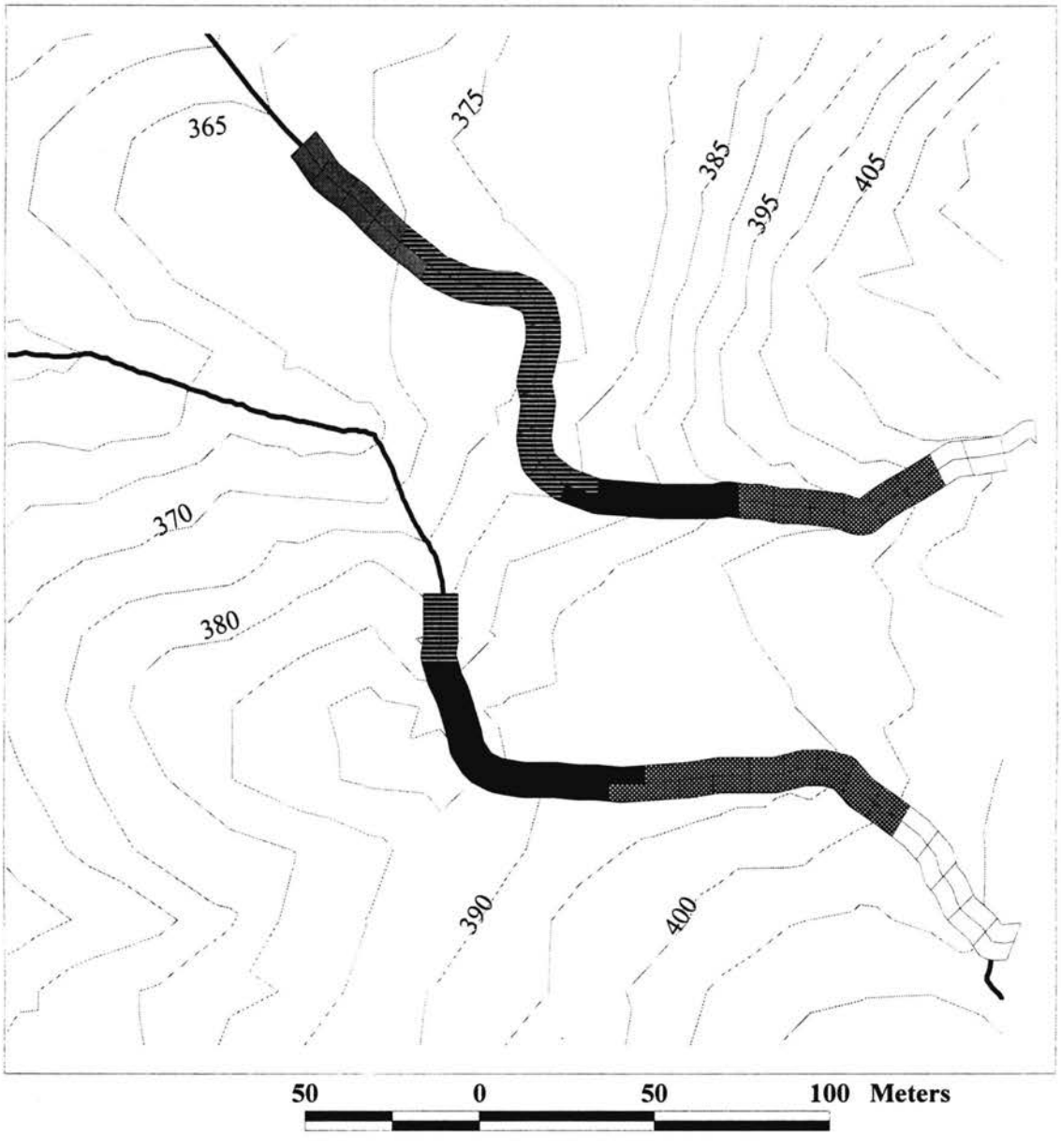
Quebrada Prieta



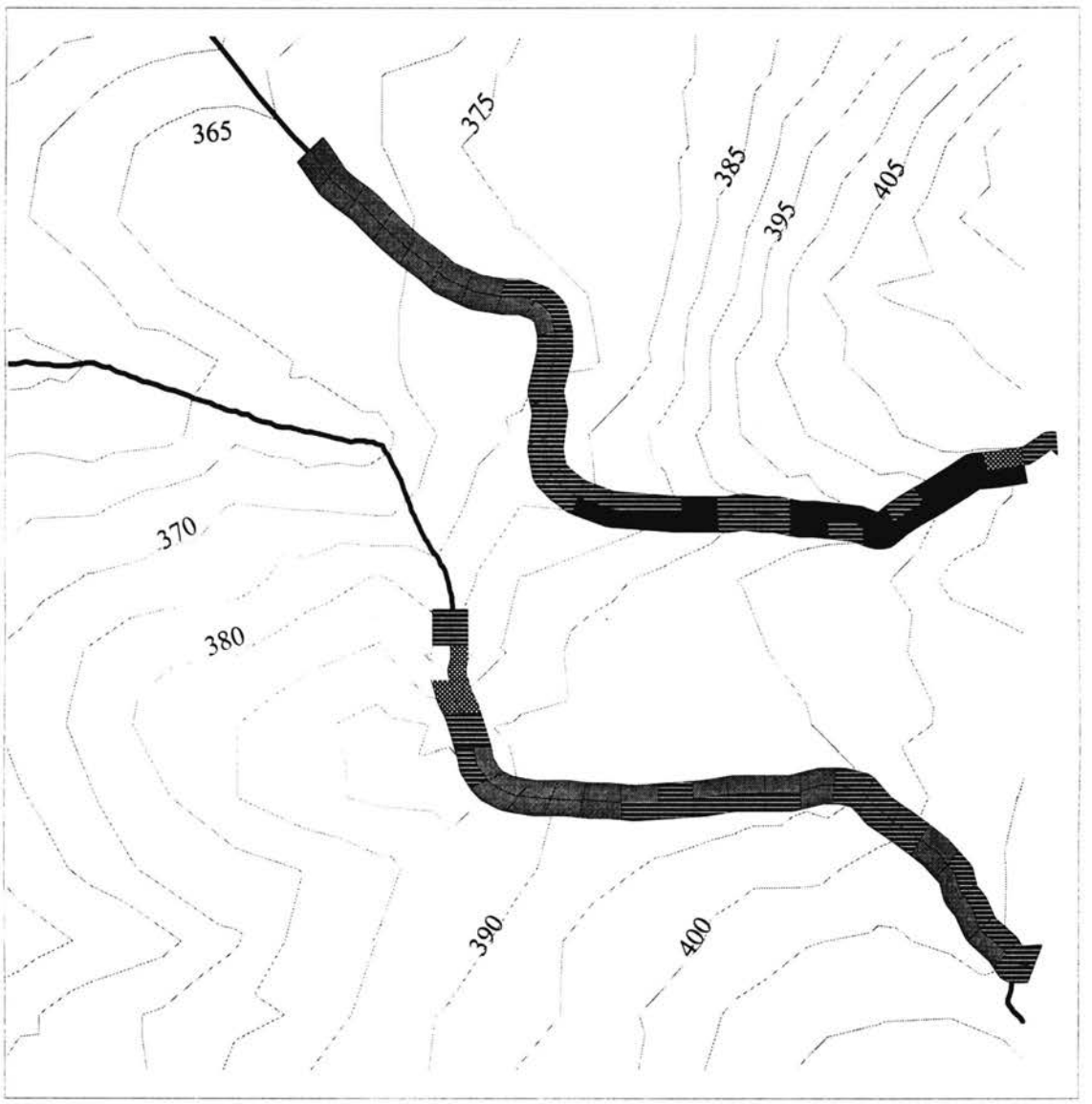
Quebrada Toronja

GIS Analysis
Riparian Topography
Tree Density
Field Observations
Palm Height
Palm Damage
Literature review
Logistic Regression (Palm damage as response variable)
A priori damage models
A priori recovery models
AIC model selection
Damage model
Recovery models
Post hoc recovery models
AIC model selection
Recovery models

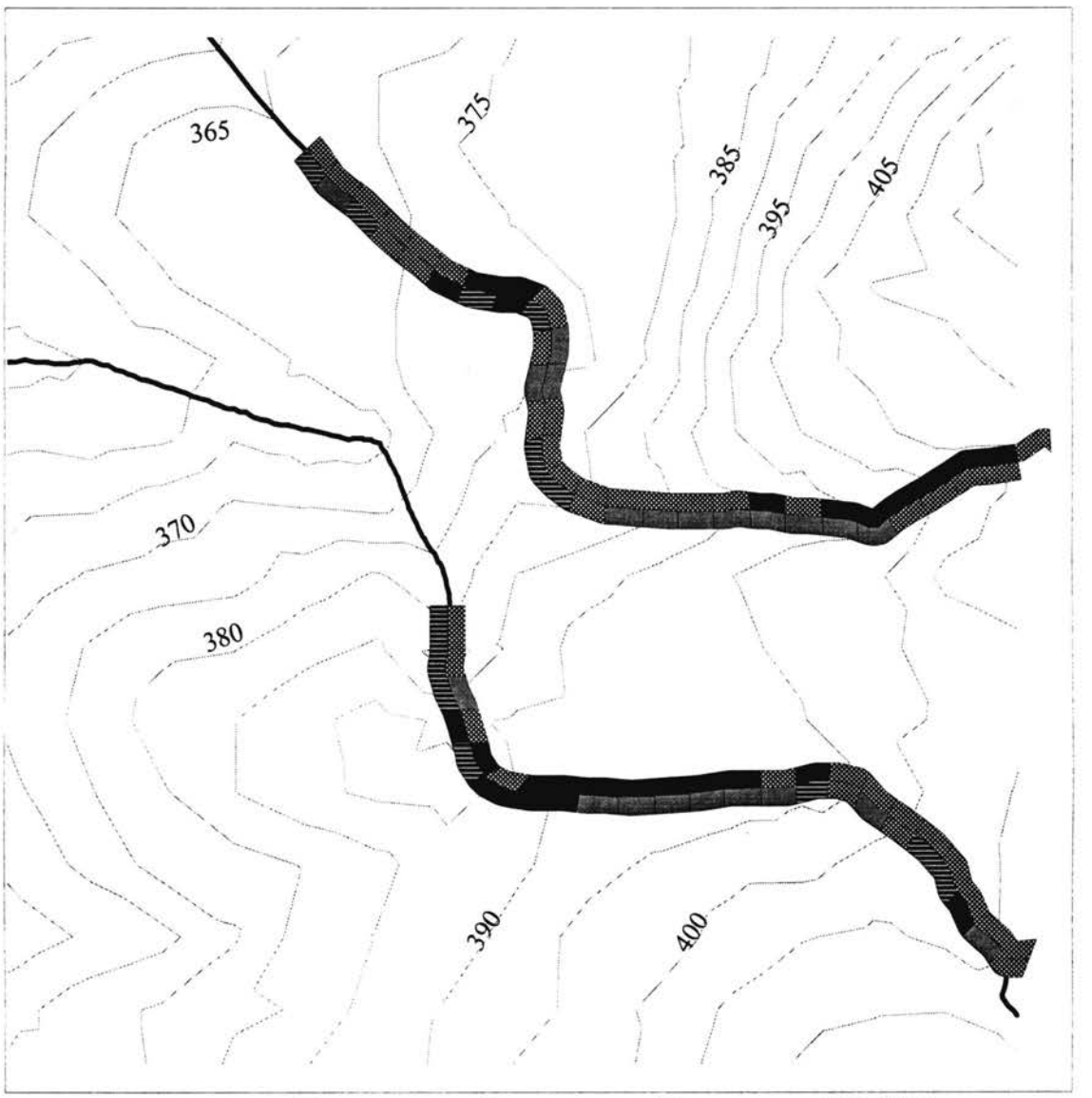
Elevation range of riparian subplots

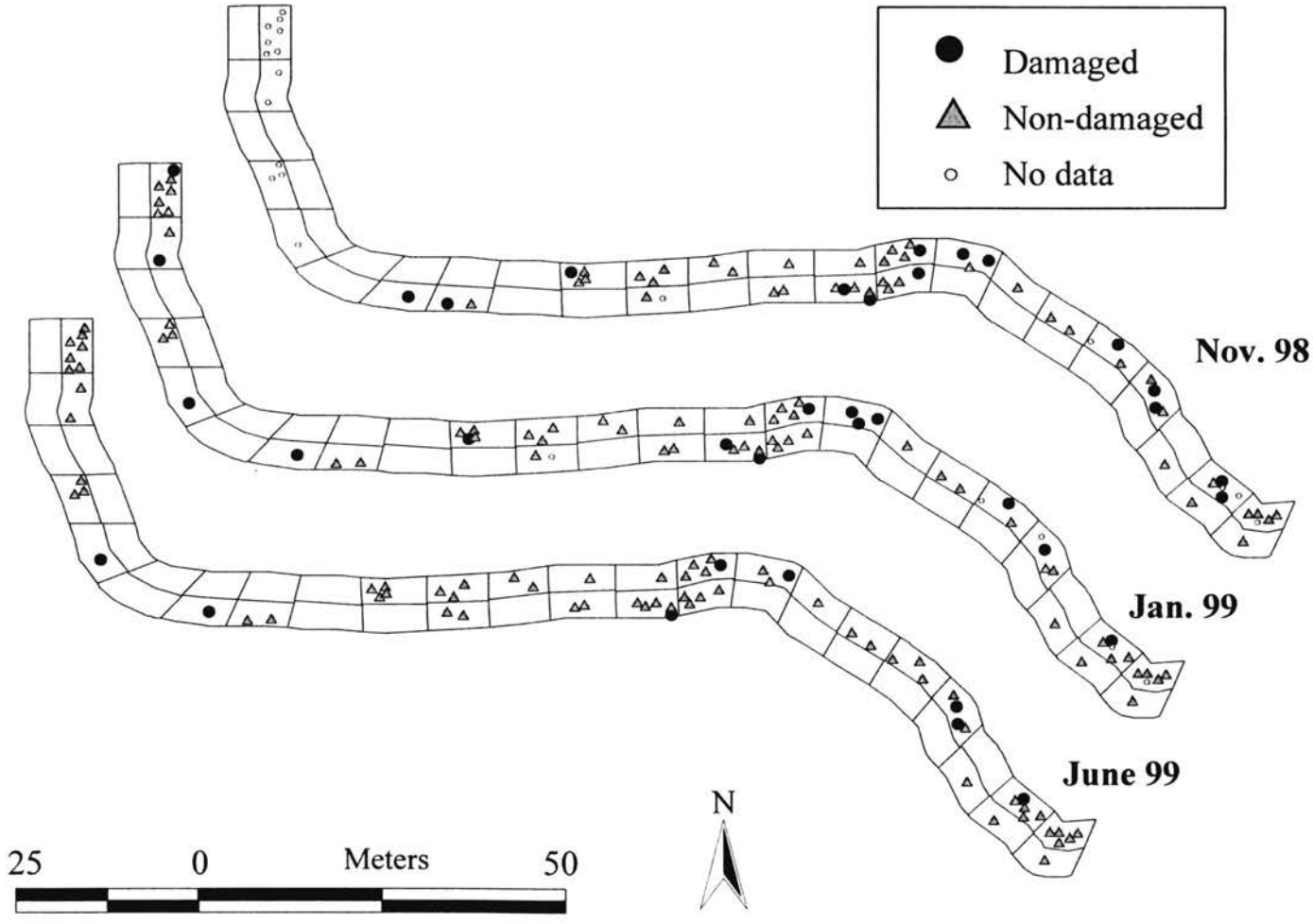


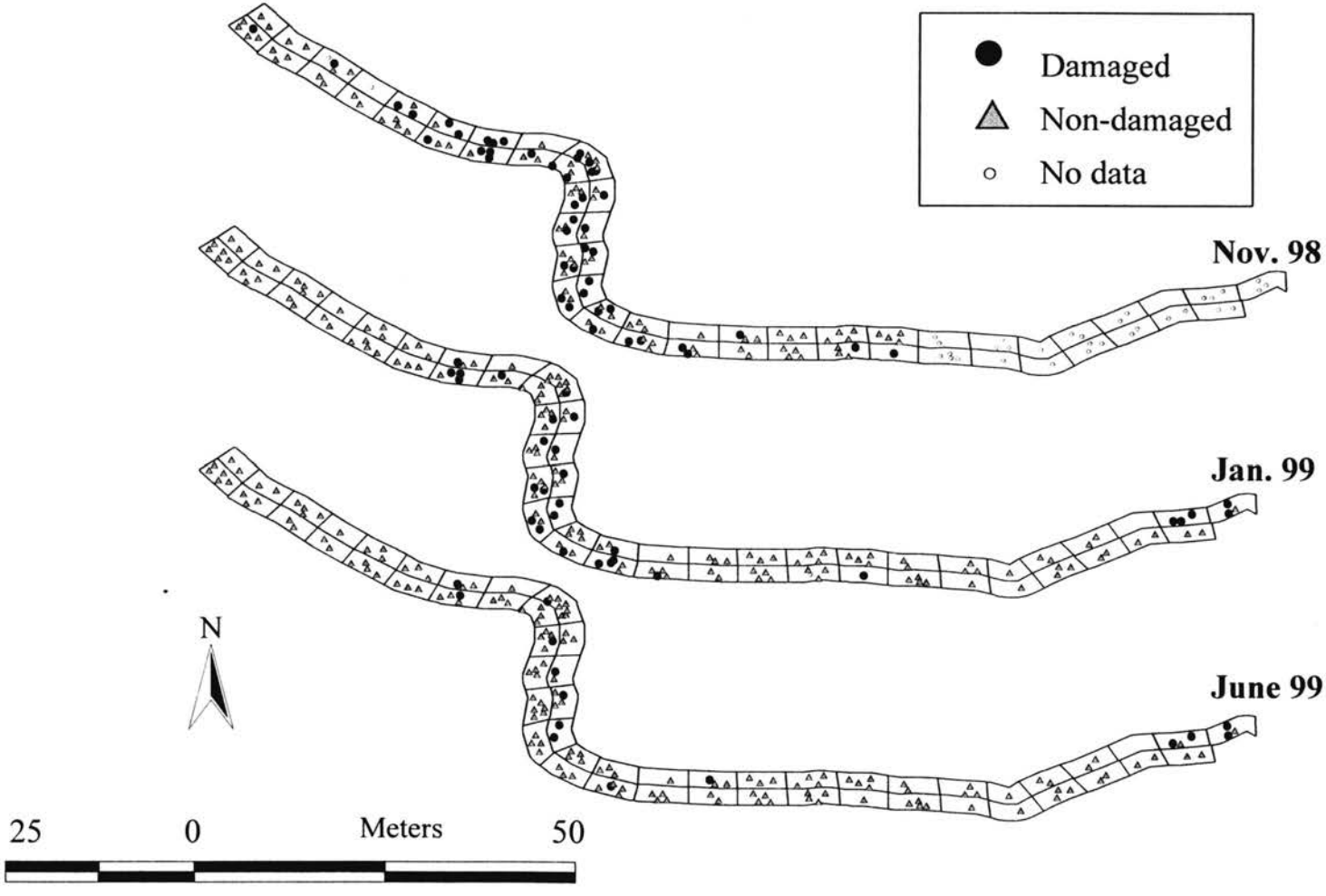
Mean slope of riparian subplots

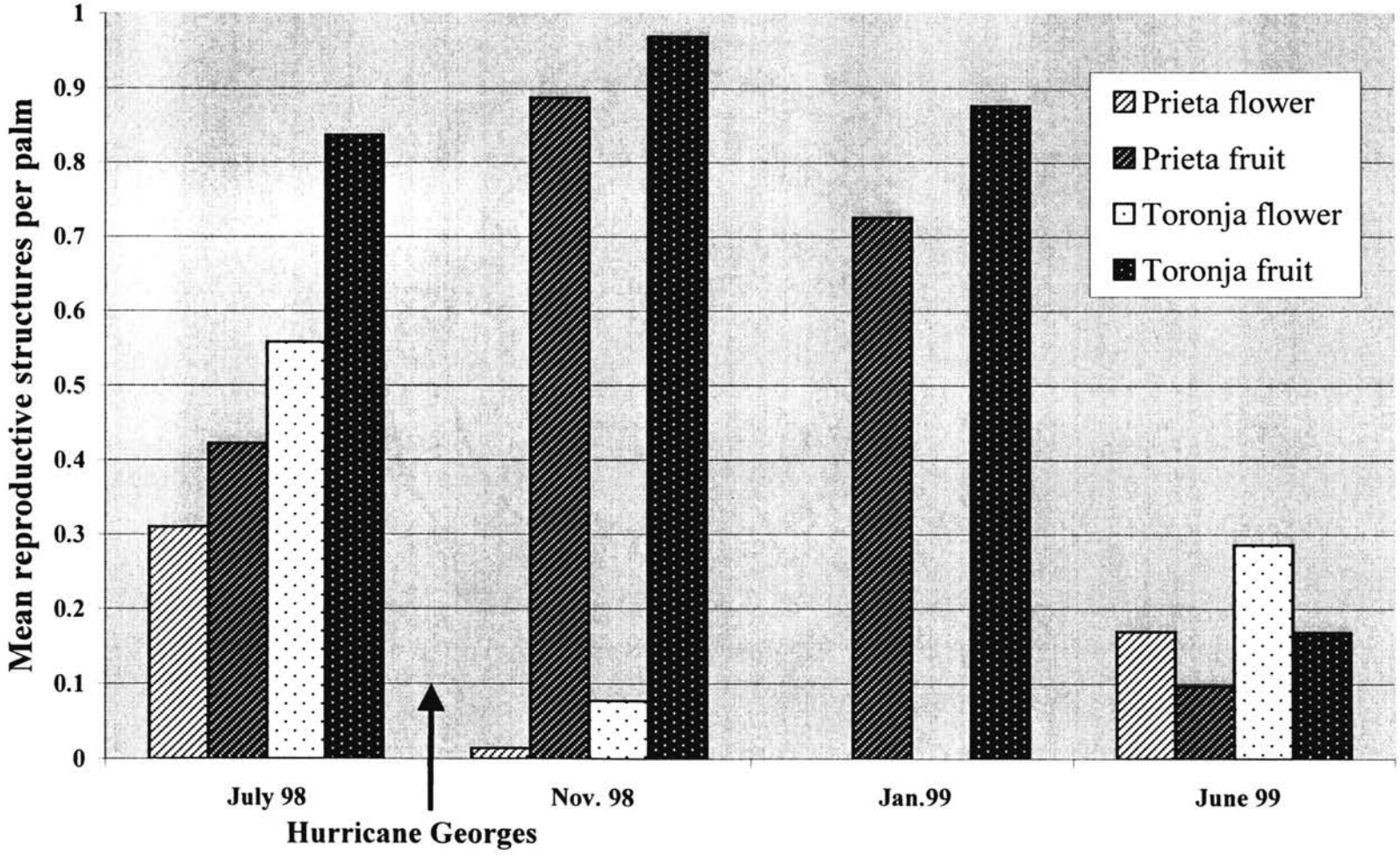


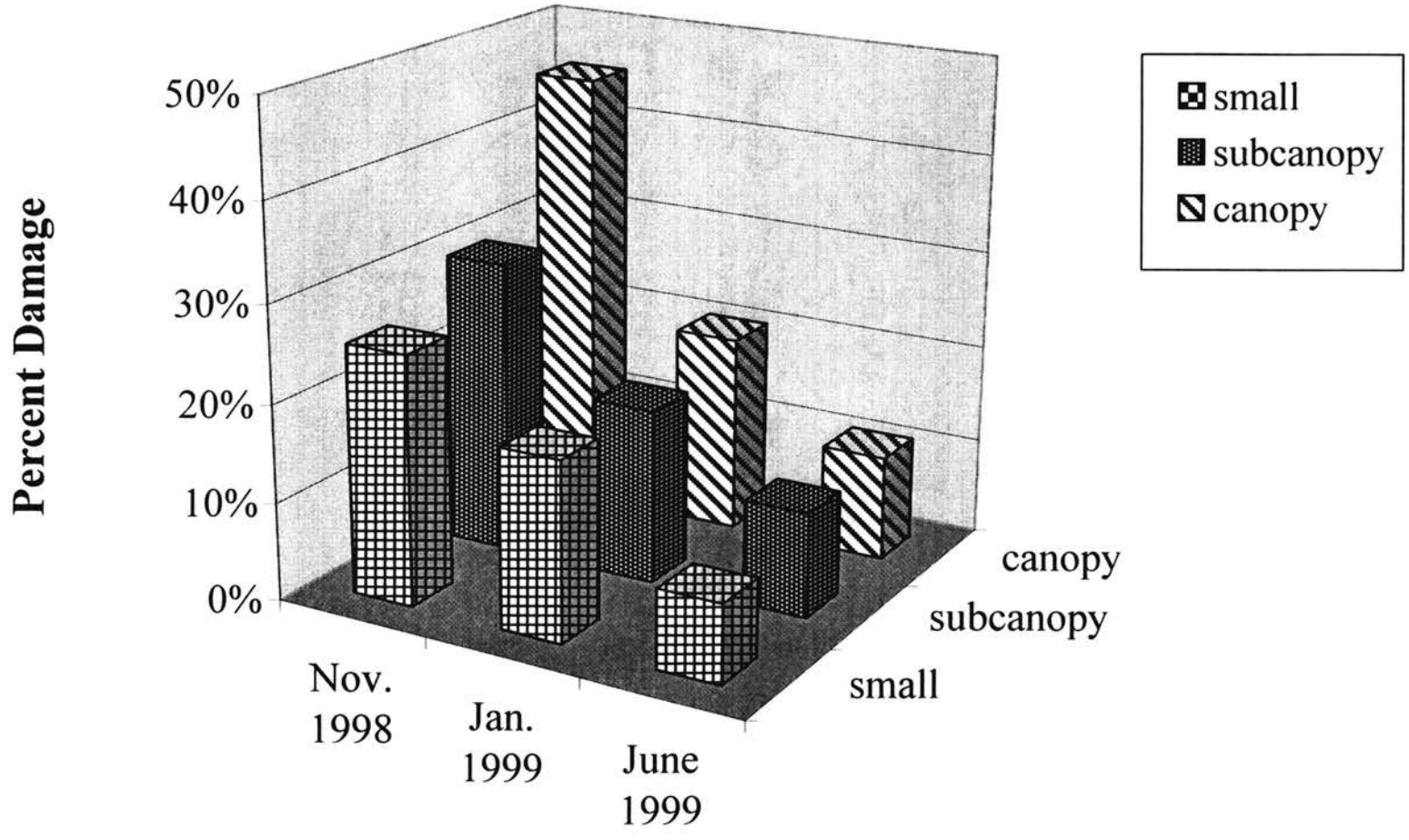
Aspect of riparian subplots

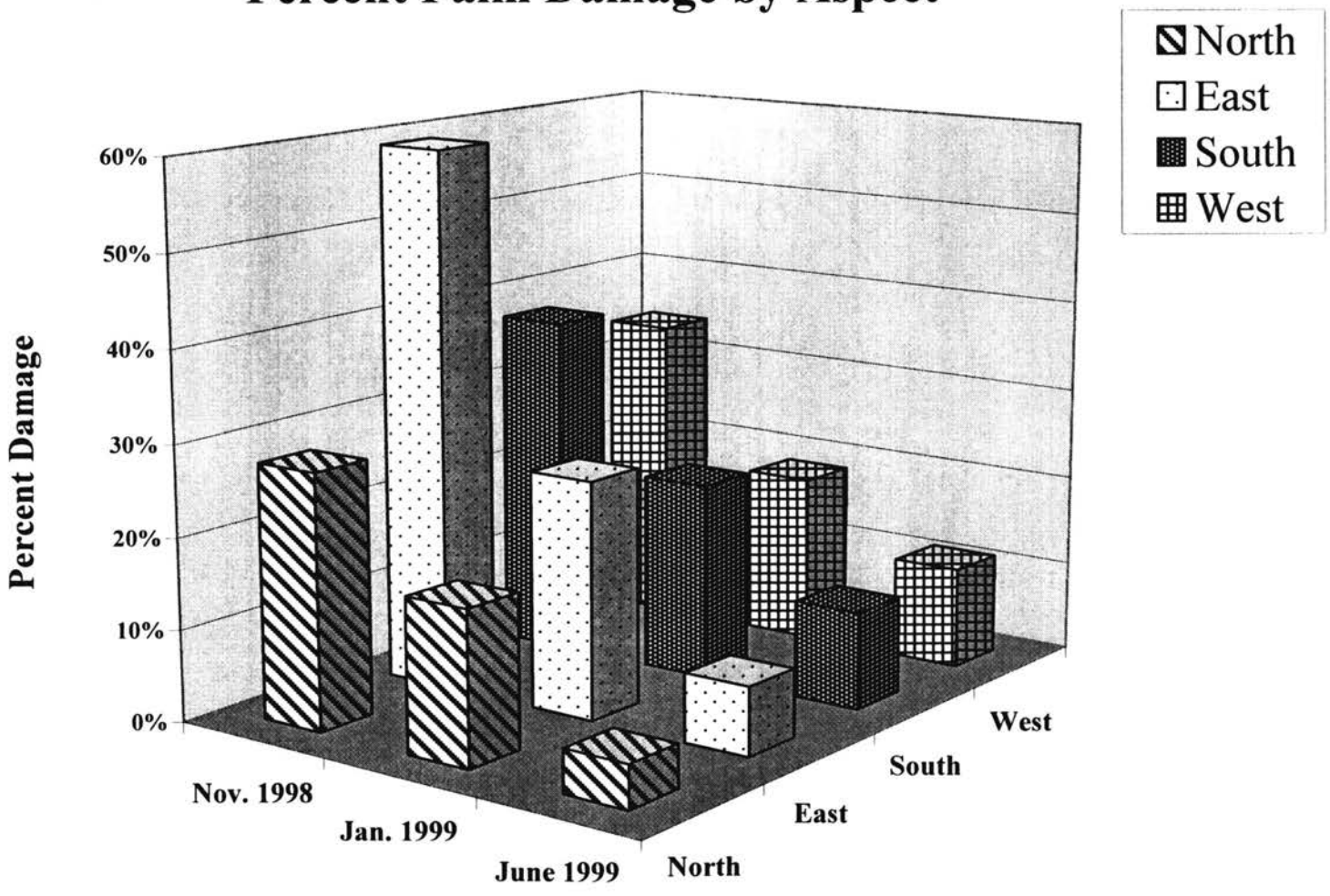



Damaged
Non-damaged
No data
Nov. 98
Jan. 99
June 99
N
25
0
Meters
50


Damaged
Non-damaged
No data
Nov. 98
Jan. 99
June 99
N
25
0
Meters
50


Riparian palm reproduction over time
Prieta and Toronja
Mean reproductive structures per palm
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
Prieta flower
Prieta fruit
Toronja flower
Toronja fruit
July 98
Nov. 98
Jan.99
June 99
Hurricane Georges


Percent Palm Damage by Height Class
Percent Damage
50%
40%
30%
20%
10%
0%
Nov. 1998
Jan. 1999
June 1999
canopy
subcanopy
small
small
subcanopy
canopy


Percent Palm Damage by Aspect
North
East
South
West
Percent Damage
60%
50%
40%
30%
20%
10%
0%
Nov. 1998
Jan. 1999
June 1999
North
East
South
West

Title: Mayfly predation by juvenile freshwater crabs: Implications for crab habitat selection

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Running title - Mayfly predation by juvenile freshwater crabs

Abstract

Streams in the Luquillo Mountains of Puerto Rico support several species of omnivorous freshwater decapods. One of the most abundant predatory decapods is the freshwater crab, *Epilobocera sinuatifrons*. We studied predation rates of juvenile crabs on mayfly nymphs collected from pools along headwater streams located in the Luquillo Forest Dynamics Plot of the Luquillo Long Term Ecological Research Site in northeastern Puerto Rico. Pools were apparently dominated by one mayfly species, *Farrodes taino (*Ephemeroptera: Leptophlebiidae). Nine study pools were established along 300 m of two headwater streams, Quebrada Prieta and Quebrada Toronja, and were periodically sampled for juvenile crabs, mayfly nymphs, and physical and substrate characteristics. Juvenile crabs and mayfly nymphs were abundant in all pools, but both showed higher numbers along the Prieta. However, temporal variation and pool habitat variables (substrate composition, pool depth, flow velocity, and heterogeneity of pool width) were best at explaining variations in juvenile crab distributions. Crab feeding experiments demonstrated mayfly nymphs to be an important food source for juvenile crabs (8 mm to 18 mm carapace width), with feeding rates increasing with crab size. The observed predation rates were relatively high, ranging from 2 to 72 mayfly nymphs per crab per night. This is the first report of mayfly predation and habitat selection by juvenile freshwater crabs.

Introduction

Tropical headwater streams often have an absence of predatory fish species, and aquatic insect diversity and abundance is low compared to similar streams in temperate latitudes (Covich 1988, de la Rosa 1995, Benstead 1996). Insular tropical stream food webs are usually dominated by omnivorous macro-consumers and often have a much higher decapod biomass than coastal or continental streams in the temperate zone (Covich 1988, Pringle et al. 1993, Covich and McDowell 1996, Pringle and Hamazaki 1998). These insular tropical streams are often dominated by omnivorous decapods, and the food webs have relatively few trophic levels (Covich and McDowell 1996), although linkages among species and between levels may be complex. To understand community structure and food-web dynamics in these tropical freshwater ecosystems, it is essential to observe habitat selection as it relates to feeding preferences of dominant decapod consumers in all life cycle stages and under different environmental conditions.

One dominant consumer in headwater streams in the Luquillo Experimental Forest of Puerto Rico is the freshwater crab (*Epilobocera sinuatifrons*). These decapods are omnivorous, and are semi-aquatic in later life stages, roaming stream banks and feeding on fruits and seeds (such as those of the sierra palm, *Prestoea montana*) and terrestrial snails (Covich and McDowell 1996). Crabs are among the largest predators in intermediate to high-elevation streams, especially above waterfalls where most fish species are absent. The genus is widespread in the Greater Antilles, and the species is endemic to Puerto Rico and Saint Croix (Chace and Hobbs 1969, Villalobos-Figueroa 1982, Covich and McDowell 1996). However, few investigators have studied freshwater

crabs in the Carribean. *E. sinuatifrons* are abundant in the streams where they occur and unlike the other species of decapods in these streams they complete their life cycle entirely in freshwater (Chace and Hobbs 1969, Covich and McDowell 1996). As such, studies of the distribution and relative abundance of *E. sinuatifrons*, as well as studies on feeding preferences in various stages of their life cycle, are important in determining their role in controlling the abundance of stream macroinvertebrates, detrital processing, and the effect of terrestrial feeding by adults on terrestrial-aquatic linkages in the stream food web (Hill and O'Keefe 1992).

Female freshwater crabs carry their eggs and larvae under their carapace and release free-roaming young into suitable pool habitats (Gherardi and Vannini 1988, Covich and McDowell 1996). Younger age classes of freshwater crabs are confined to the stream and take refuge under rocks or in crevices or leaf packs (Gherardi et al. 1985, Gherardi and Vannini 1989). Juvenile crabs are rarely caught in baited traps, often because dominance hierarchy among crabs excludes smaller individuals from high-quality sources of food (Vannini and Gherardi 1981, Hill and O'Keefe 1992, Somers and Nel 1998). Where food availability is not limiting, size distributions and localized differences in crab densities may be determined by environmental factors such as turbidity, water temperature, current speed, water level, or the availability of refuges, characterized by the abundance and size of substrate particles (Gherardi et al. 1985, Somers and Nel 1998).

The objectives of this study were to determine food preferences of juvenile freshwater crabs (4 mm to 18 mm carapace width) and to observe environmental factors influencing juvenile crab distributions and relative abundance within and between two

headwater streams in Puerto Rico. This study is the first to examine food preferences and habitat selection by juvenile freshwater crabs in the Carribean. These juvenile crabs may be important in determining food web structure in these tropical headwater streams, especially as they consume a wide range of food resources.

Study Site

The Luquillo Experimental Forest (LEF) is located in northeastern Puerto Rico (Fig.1), and is the only tropical ecosystem in a network of sites in the National Science Foundation's Long-Term Ecological Research (LTER) Program. The Luquillo Forest Dynamics Plot (LFDP) (Fig. 1) is a 16 ha permanent study plot in the subtropical wet forest life zone (Zimmerman et al. 1994), and was established in 1989 to record changes in forest ecology as a result of severe disturbance following Hurricane Hugo. Sierra palms are the most abundant species in the LFDP (Reed 1998, Henry 2000); other dominant species include *Dacryodes excelsa*, *Manilkara bidentata*, and *Sloanea berteriana*. Soils are mainly Zarzal clay of volcanic origin, and rainfall averages 350 cm/year (Zimmerman et al. 1994).

The LEF, like many areas in the Caribbean, has an aseasonal climate and experiences infrequent but severe wind storms. Hurricanes significantly affect the forest canopy structure and detrital input patterns into stream food webs (Covich 1988, Zimmerman et al. 1994, Frangi and Lugo 1998, Sabat and Fetcher 1999). Two riparian transects were established along sections of Quebrada Prieta (first-order and second-order) and Quebrada Toronja (first-order) tributaries of the Rio Sonadora located within

the LFDP near the El Verde Field Station (18^{0}20'N, 65^{0}49'W, 350 m above sea level) in the northwest section of the LEF (Fig. 1). The Prieta and Toronja are similar in size, location, and water temperature (21° - 24°), but differ in riparian tree species composition, current velocity, stream substrata, and land-use history. In contrast to the Prieta, the Toronja drainage was intensively disturbed by humans, with historical accounts of charcoal production, cattle grazing, coffee growing, and some hardwood timber harvest occurring within the Toronja riparian zone apparently prior to 1940 (Garcia-Montiel and Scatena 1994, Reed 1998). This disturbance regime has resulted in a riparian forest composed mainly of palms and other early-successional tree species along the Toronja, whereas a relatively less disturbed, mixed forest exists along the Prieta (Reed 1998). These palms produce abundant fruit that is consumed by a wide range of terrestrial species (Wunderle 1999) as well as by adult crabs. Tabonuco (*Dacryodes excelsa*) is a dominant riparian tree species along the study streams, and is often co-dominant with the sierra palm. Tabonuco provides a relatively continuous source of leaf-litter input to stream pools.

Methods

Spatial Distribution of Juvenile Crab Consumers

We sampled juvenile crab population distributions along 300 m reaches of both the Prieta and Toronja to determine if crab populations were evenly distributed or clumped in specific stream pools. We selected nine pools along each stream; three pools were within the first 100 m of the stream transect, three pools along the second 100 m,

and three pools along the last 100 m. Using this design we could observe changes in crab densities along the elevational gradient from 350 m to 410 m. We defined suitable pools as those having at least 20 cm maximum depth during base flow, no surface turbulence, and at least enough volume and surface area to allow submersion of three leaf packs without overlap. We used every suitable pool along the 300 m transect of the Toronja in this study. We selected pools along the Prieta to provide a variety of pool morphology and flow velocity conditions for comparison and contrast with the pools along the Toronja.

Crab populations were sampled using leaf packs consisting of rolled plastic mesh containing tabonuco leaves as leaf-litter microhabitat for juvenile crabs (4mm to 18mm carapace width). Tabonuco is a dominant riparian tree species along the study streams (co-dominant with the sierra palm), and provides a continuous source of leaf-litter input to stream pools. To create the leaf packs we rolled pieces of Tensor plastic multi-use hardware utility net (45 cm x 65 cm pieces, mesh size 1.27 cm x 1.91 cm) into cylinders of double thickness secured around the middle and at each end with fishing line. This tube shape allowed openings at the ends for entry of crabs larger than 19 mm carapace width. These cylinders were loosely packed with approximately 70 g (+/- 10 g) of dead, undecomposed tabonuco leaves that were collected from fallen branches. We placed three individually tagged leaf packs on the bottom of each of the 18 study pools. A few rocks were placed in each leaf pack to keep them from moving and washing out of the pools. Each leaf pack was secured with 45 kg test fishing line. We sampled the 54 leaf packs every two weeks during January - March 1999 and June - August 1999. After

sampling each pack we replaced lost tabonuco leaves to keep the leaf mass constant, along with a high overall amount of conditioned leaves. The leaf packs were first colonized by mayflies, and then by juvenile crabs as tannins from the tabonuco leaves leached out and the leaves became conditioned.

On each sampling date individual leaves from each pack were rinsed into a bucket, and the water was strained through 5 mm, 2.5 mm, and 0.7 mm mesh size sieves. All crabs were caught in the two largest mesh sizes. We sorted all crabs into eight size classes (3 mm - 3.9 mm, 4 mm - 5.9mm, 6 mm - 7.9 mm, 8 mm - 9.9 mm, 10 mm - 11.9 mm, 12 mm - 13.9 mm, 14 mm - 15.9 mm, and 16 mm - 18 mm carapace width) and recorded total number of crabs and individual crab-size classes per trap. All crabs were immediately returned to the same pool after handling. Mayflies were caught in the smallest sieve, and were taken to the lab and counted for all surveys between June and August 1999.

Physical habitat of pools

Physical parameters of pools were measured for each sampling date to obtain mean values for describing pool morphology. Pool length, three values of pool width, five values of pool depth, maximum pool depth, individual trap depth, and current velocity were all measured in the field. From these data we calculated mean pool surface area, average and maximum depth, and average velocity as predictors of juvenile crab densities. We also calculated the coefficient of variation for pool width, length, and depth as indicators of pool habitat heterogeneity (Covich et al. 1996). Two of the nine pools along the Toronja were filled with sediment between March and June 1999.

Therefore, two new pools were chosen that met pool-selection criteria and elevation requirements, and had similar substrata and physical characteristics as the original pools.

We characterized differences in substrata among pools as an indicator of availability of refugia that may contribute to variations in juvenile crab densities. On each sampling date between June and August 1999 we classified each pool into percent of each type of substratum of the total pool area. Types of substrata included large boulders (>1 m diameter), small boulders (0.5 - 1 m diameter), rocks (10 - 50 cm diameter), cobble (2 - 10 cm diameter), gravel (2mm - 20 mm diameter), sand and silt (< 2 mm diameter), leaf litter, and woody debris.

Feeding experiments

We conducted feeding experiments with juvenile *E. sinuatifrons* (8 mm - 18 mm carapace width) to determine food preferences of juvenile freshwater crabs for mayflies, larval shrimp, and leaf litter. Crabs and mayflies (dominated by *Farrodes taino* Lugo-Ortiz and McCafferty, identified by M.L. Pescador, Lugo-Ortiz and McCafferty 1994) were caught in leaf packs in stream pools near the study streams. We also netted larval shrimp (*Atya lanipes* and *Xiphocaris elongata*) while they were migrating upstream along stream banks. Crabs were kept in plastic aquaria (36.5 cm x 24.8 cm x 31.1 cm) with tight-fitting lids. Water levels in aquaria were maintained at 4.5 liters per container, and a terra cotta tile was added to each aquarium as refuge for crabs. Aquaria were aerated and placed outside under shading to allow for ambient light and temperature conditions; water temperature ranged from 22°C to 26°C over each 24 hr. period.

Crabs were randomly placed in aquaria and randomly assigned a food type. Food types for crab feeding experiments (mayflies, larval shrimp and tabanuco leaf disks) were selected by observing organisms found in leaf packs in the study pools. Each crab was given either 50 mayfly nymphs, 10 larval shrimp (4 mm to 7 mm carapace length), or 5 conditioned leaf disks (20 mm x 20 mm squares) in the evening after the crab was captured. We left the crabs overnight (14 to 16 hours) and then counted all the remaining mayflies, larval shrimp, or leaf disks in each aquarium. Mayflies and larval shrimp were also added to two control aquaria to ensure the macroinvertebrates could not escape from the containers and were counted adequately. Two crabs ate all 50 mayflies in one feeding period. They were given 100 mayflies in a successive feeding trial to determine an estimate of maximal feeding rates. Each crab (N=47) was fed for two or three trials (one food type for each trial in random order) and then returned to stream pools.

Statistical analyses

Because our study included several measured pool-habitat variables, we analyzed these data for possible correlations between independent variables. We eliminated one variable of each correlated pair to avoid multicollinearity (Neter et al. 1996). Juvenile crabs caught per leaf pack were summed within each stream pool, and individual pools for each sampling date were used as the experimental unit in our analysis. We used a multiple linear regression to model juvenile crab distributions with pool area, average pool depth, flow velocity, coefficient of variation of pool length, width and depth, pool substrata composition, trap date, and mayfly density per pool as predictive variables. We began with all possible independent variables in the model and systematically eliminated

the variable with the largest p value, until all remaining variables were significant at the alpha = 0.10 level (Neter et al. 1996).

To determine if spatial variables explained juvenile crab distributions better than within-pool habitat variables, we used multiple linear regression analysis to compare models at different spatial scales (Fig. 2). Juvenile crab distributions were analyzed by individual pool (crabs summed for three leaf packs per pool per trap date), by elevation block (crab densities for low, medium, and high elevation for each trap date), by stream (crabs densities for each stream per trap date), and a stream by elevation interaction (crab densities for low, medium, and high elevation on each stream). We compared Akaike's Information Criterion (AIC) (the best of the competing models has the lowest AIC score) and AIC weights (i.e., the proportion of times that a particular model will be selected as the AIC best model: Burnham and Anderson 1998) of models to determine the spatial scale (stream, elevation, stream by elevation, pool, or within-pool habitat) that best explained juvenile crab distributions. AIC is an objective model selection procedure that ranks a set of competing models in their ability to explain the data and adjusts the log-likelihood from maximum likelihood estimates for additional model parameters (Burnham and Anderson 1998).

To test the hypothesis that feeding rates of juvenile crabs are dependent on crab size, we used a correlation procedure (SAS 1998) to test the strength of the linear relationship between crab size classes (8 mm - 9.9 mm carapace width, N=11; 10 mm - 11.9 mm, N=20; 12 mm - 13.9 mm, N=9; 14 mm - 15.9 mm, N=3; and 16 mm - 18 mm, N=4) and the number of mayflies eaten. We calculated the Pearson product-moment

correlation coefficient (SAS 1998) with alpha set at .05 to test the significance of this relationship.

Results

Pool-habitat heterogeneity

Pool-habitat differences between streams were characterized by differences in pool substrata composition. Pools along the Prieta were dominated by large boulders and cobble, whereas the Toronja pools were mainly comprised of fine sediments (sand and silt) and gravel. Pools along the Prieta were also generally larger and deeper than those along the Toronja, with higher average flow velocities. Leaf litter and woody debris accumulation were low in all pools during the study period. Pool size, average pool depth, and maximum pool depth generally decreased with increasing elevation along both stream transects, and this trend was especially evident along the Toronja.

Differences in riparian vegetation composition between and within stream reaches contributed to the variation in leaf litter and fruit fall input between stream pools. The Toronja riparian zone was dominated by the sierra palm, *Prestoea montana*, which drop large amounts of fruit and frond litter into the stream. The riparian forest along the Prieta was more mixed, with tabanuco and sierra palm both dominant species. However, the sierra palm increased in dominance with increasing elevation.

Juvenile crab distributions

Juvenile freshwater crabs were abundant in all pools sampled along both study streams, and mean size of sampled crabs was similar for both streams and among

sampling dates. Juvenile crabs caught in leaf packs ranged from 4 mm to 30 mm carapace width, with a mean carapace width of 6 mm. However, a greater proportion of smaller crab size classes were trapped in the June through August sampling periods than in the January through March trap dates (Figs. 3 and 4). Field observations suggested that leaf packs were first colonized by mayflies, then by juvenile *E. sinuatifrons* and some larval shrimp.

Juvenile crabs were found in all pools during each two-week sampling period (21 January 1999, 4 February 1999, 22 February 1999, 4 March 1999, 20 June 1999, 4 July 1999, 18 July 1999, and 1 August 1999: Table 1), suggesting that some adult crabs were reproducing throughout the study stream transects for all sampling dates. More juvenile crabs were trapped along the Prieta than the Toronja ($p = 0.004$) at the stream scale, and when analyzed by elevation most juvenile crabs were found in the high elevation pools of the Prieta ($p = 0.04$). There was also a high degree of variation in juvenile crab abundance among stream pools. Juvenile crab abundance in pool 7 (high elevation) of the Prieta was significantly higher ($p = 0.006$) than juvenile crab densities among other pools. However, model comparison among spatial scales (stream, elevation, stream by elevation, pool, and within-pool habitat) indicated that within-pool habitat variables were the most significant in explaining the variation in juvenile crab distributions (Table 2: AIC weight = 0.99).

Within-pool habitat was characterized by composition of pool substrata and pool morphology, and variables were included in the multiple regression analysis to account for the effect of pool heterogeneity on juvenile crab distributions. The proportion of

small boulders ($p = 0.0005$) and gravel ($p < 0.0001$) comprising individual pool substrata composition were negatively associated with juvenile crab densities (Table 3). Average pool depth ($p = 0.002$), flow velocity ($p = 0.0009$) and the coefficient of variation of pool width ($p = 0.007$) were positively associated with juvenile crabs (Table 3). The model explained 59% of the variation in juvenile crab distributions ($R^2 = 0.59$, Table 3) throughout our eight sampling periods. Sampling dates were also significant in explaining variation in juvenile crab density. The January 1999 ($p = 0.0002$) sampling period was negatively correlated with the number of juvenile crabs trapped per pool (Table 2). However, the late July ($p < 0.0001$) and August (0.02) sampling dates were positively correlated with overall juvenile crab densities (Table 2), indicating that the density of juvenile crabs increased from winter to summer.

Feeding experiments

Forty-six of 47 juvenile crabs ate mayfly nymphs, ranging from two to 72 nymphs eaten per night per crab. The total number of mayfly nymphs consumed per feeding trial was significantly correlated with crab size (correlation coefficient = 0.66, $p < 0.0001$, Fig. 5). Five crab size classes were used in feeding experiments, and the total number of crabs used per size class reflected the abundance of each size class in leaf packs. Juvenile crabs ate more mayfly nymphs than any other food type. Five crabs ate portions (25% to 75%) of one larval shrimp, two crabs ate one entire shrimp, and two crabs ate two shrimp each. Only two crabs ate small portions (approximately 10%) of one conditioned leaf disk.

Discussion

Although numerous studies have focused on marine crabs, as well as feeding ecology and movement patterns of land crabs (i.e. Wolcott and O'Connor 1992, Thacker 1996, Green et al. 1997, Green et al. 1999a, Green et al. 1999b), very few studies exist on the role of freshwater crabs in stream and riparian food webs. Several studies on a Mediterranean freshwater crab are mainly focused on dominance hierarchies and spatial movement of semi-aquatic adult crabs (Vannini and Gherardi 1981, Gherardi et al. 1985, Gherardi et al. 1988, Gherardi and Vannini 1989). Research on freshwater crabs in South Africa examined dominance hierarchies and crab population structure (Somers and Nel 1998) and feeding ecology and leaf litter processing of adult crabs (Hill and O'Keeffe 1992).

Because research on freshwater crabs is relatively rare, this study was designed as an exploratory analysis to examine juvenile crab abundances and habitat preferences, as well as feeding relationships and food web interactions. We found that juvenile crabs were abundant throughout the study area on all sampling dates, although crab densities varied both seasonally and spatially. The AIC model selection procedure determined that measured within-pool habitat variables were best at explaining crab distributions compared to unmeasured processes operating at the pool, elevation, stream, or elevation by stream spatial scales, and identified specific within-pool variables that correlated with juvenile crab density. However, crab distributions were spatially clumped, with more crabs found in the Prieta than in the Toronja, especially at higher elevations. These spatial patterns of juvenile crab distributions may be influenced by overall habitat

differences between streams, such as differences in substrata composition or riparian vegetation.

Differences in crab abundance by trap date were significant in explaining crab distributions. This temporal information suggests that seasonal variations in environmental factors are important controls on adult crab birth rates. Because water temperatures in the study streams remain fairly constant all year, variations in monthly rainfall amounts may influence birth rates of adult female crabs. Although Puerto Rico does not have distinct wet and dry seasons, January through April tend to be the driest months (Covich et al. 1996). Lowest numbers of juvenile crabs were found in the January through March samples, with January 21, 1999 crab densities significantly lower than any other sampling date. Samples in June, July, and August had higher crab densities, with the highest numbers of crabs trapped on July 18 and August 1, 1999. The summer samples also had higher proportions of younger crabs (i.e. smaller crab size classes) than samples in the winter months (Figs. 3, 4). However, some juvenile crabs were found in all study pools on all sampling dates, which suggests that some adult crabs were reproducing throughout the study period. Gherardi and Vannini (1989) found that reproductive patterns of Mediterranean freshwater crabs were seasonal, with most females reproducing in September. However, this previous study was in a more seasonal climate, and reproductive seasonality may have been temperature dependent. Somers and Nel (1998) did not find reproductive seasonality in populations of freshwater crabs in South African streams.

Differences in substrata among stream pools clearly influenced relative crab abundances, although the only significant relationships were negative correlations. Freshwater crabs were negatively associated with high proportions of gravel and small boulders in a stream pool. This pattern suggests that pools with high proportions of gravel and small boulders have a limited amount of crevice space and refugia available for juvenile crab size classes. The availability of crevice sizes that allow for tight-fitting refugia for crabs is an essential habitat attribute for all crab size classes (Covich and McDowell 1996). Other studies (Gherardi et al. 1985, Gherardi and Vannini 1989) have shown that younger crab age classes are usually found hiding under stones and rocks, in burrows or crevices, or in leaf litter, and the size of crevices and refugia available often determines the size class and abundance of crabs found in a pool (Somers and Nel 1998). Pools with high proportions of gravel and small boulders may also be less structurally suited to retain standing stocks of leaf litter and other debris, which is important microhabitat for aquatic insect prey (Benstead 1996) and juvenile crabs. Low amounts of leaf litter and debris accumulation in stream pools during the study was probably due to periodic high flows that washed debris out of both streams.

Measurements of variations in pool morphology also had predictive value in explaining differences in juvenile crab abundance among stream pools. Juvenile crab densities have strong positive correlations with deeper pools, higher current velocities, and increased variation in pool width. Higher water levels and greater heterogeneity of pool width may provide more crab habitat in a pool, including refugia and crevice space for both juvenile and adult crabs. Higher flow velocities, deeper pools, and greater pool

heterogeneity may also provide better habitat for reproductive adult female crabs, which must live in the water while their young are developing (Gherardi et al. 1988). Deep, heterogeneous pools may also retain greater amounts of leaf litter (Covich et al. 1996), providing food and cover for juveniles and adults.

Results from the AIC model selection procedure indicate that the selected model of within-pool habitat variables provided more explanatory power than unmeasured variables operating on a larger spatial scale. Although this study identified several variables significant in explaining differences in freshwater crab abundance among stream pools, the pool habitat model explains 59% ($R^2 = .59$) of the variation in among-pool crab distributions. This moderate R^2 value suggests that other unmeasured variables are likely contributing to the variation in crab densities. Unmeasured processes occurring at spatial scales other than pool microhabitat may also influence variations in juvenile crab abundance.

Differences in pre-1940 land-use history between the Prieta and the Toronja has resulted in present-day differences in riparian forest composition and dominate pool substratum between the two streams (Garcia-Montiel and Scatena 1994, Reed 1998, Henry 2000). Large boulders dominate the Prieta substrata, whereas Toronja pools are primarily comprised of find sediments and gravel. These stream-scale substrata differences may affect overall pool quality between the streams, with Prieta pools retaining larger amounts of leaf litter and providing more suitable crab habitat. Fine sediments in Toronja may bury leaf litter or fill in crevices. These stream effects may also interact with differences in riparian vegetation along the stream transects. The sierra

palm is the dominant riparian tree species along both streams, but is particularly abundant along the high elevation section of the Prieta transect and in the entire Toronja transect. Fallen palm fronds provide excellent structural habitat for stream organisms (Reed 1998) and produce large amounts of fruit that are an important food source for adult crabs (Covich and McDowell 1996, Reed 1998, Henry 2000). High palm abundance along the Toronja suggests that higher crab densities should be found in the Toronja than the Prieta. However, differences in substrata composition and higher channel stability in the Prieta may override the effect of riparian palm inputs along the Toronja. As such, pools that are structurally suited to retain leaf litter and fruit fall, and are located in areas with high riparian palm densities, may provide the highest quality habitat for juveniles and adult females. Pools along the high elevation section of the Prieta meet this criteria, and had significantly higher densities of juvenile crabs than other pools in the study area.

Another factor that may be affecting juvenile crab distributions is the relative abundance of mayfly nymphs among stream pools. In this study the mayfly densities in leaf packs were only measured for the June through August samples, and so could not be added to the model without eliminating the January through March crab observations in the statistical analysis. However, feeding experiments demonstrated that mayflies were a preferred food source of juvenile crabs, and so may have an important effect on variations in crab densities. Continuous warm water in Puerto Rico allows for year-round growth and development of aquatic insects (Pescador et al. 1993). Mayfly nymphs then are a continuously available food source in these headwater streams. Feeding studies by Hill and O'Keeffe (1992) on freshwater crabs in South Africa found that smaller crabs ate

high amounts of aquatic insects and required high protein diets for growth. However, adults crabs were more omnivorous and were important processors of stream leaf litter and detritus, as well as feeding on other crabs, stream organisms, and terrestrial vegetation (Hill and O'Keeffe 1992).

Tropical stream food webs are usually characterized by high decapod biomass and low aquatic insect abundance and diversity. Decapods may contribute to low aquatic insect abundance through direct and indirect effects (Pringle et al. 1993, Covich et al. 1999). However, few studies have addressed the role shrimp and crabs may be playing in controlling aquatic insect abundance through direct predation in juvenile life stages. Small juvenile crabs have relatively high feeding rates on mayfly nymphs, and so it is possible that high crab densities in tropical streams may help keep aquatic insect abundance low. Streams dominated by omnivorous consumers, such as crabs, often have few trophic levels although the linkages between levels are usually complex (Covich and McDowell 1996). Adult freshwater crabs are important shredders, and are efficient leaf litter and detrital processors in stream food webs, mobilizing nutrients and energy for use by other stream organisms (Hill and O'Keeffe 1992). Omnivorous adults also help to link terrestrial and aquatic systems by feeding on terrestrial vegetation, fruitfall, seeds, snails, and other organisms (Hill and O'Keeffe 1992, Covich and McDowell 1996), whereas juveniles in these Puerto Rican streams are mainly predatory and prefer aquatic insects. Crabs are dominant stream consumers, but the complete role of their interactions in a food web of a tropical stream is not yet fully understood. Examining crab feeding ecology in all life stages, and analyzing environmental factors that relate to variations in

crab abundance in different pool and stream habitats are essential studies to understand the importance of this species to the stream ecosystem.

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Table 1: Total number of juvenile freshwater crabs (*E. sinuatifrons*) caught per trap date along 300 m reaches of Quebrada Prieta and Quebrada Toronja, Luquillo Experimental Forest, Puerto Rico.

Date	Q. Prieta	Q. Toronja
21 Jan. 1999	99	83
4 Feb. 1999	198	151
22 Feb. 1999	178	145
4 March 1999	190	121
20 June 1999	68[a]	186
4 July 1999	238	165
18 July 1999	350	340
1 August 1999	272	176

[a] High stream flow washed out several traps during this sampling period.

Table 2: Results from model selection procedure to determine spatial scale and variables that best explain juvenile freshwater crab distributions. The model with the lowest AIC score has the best explanatory power.

Scale of model parameters	AIC	ΔAIC	AIC weight
Within-pool habitat	955.06	0	0.99
Pool	964.18	9.12	0.1
Stream * elevation interaction	965.96	10.9	0
Stream	979.42	24.36	0
Elevation	987.78	32.72	0

Table 3: Results from multiple regression analysis on juvenile crab distributions by variables measured within stream pools. The dependent variable was total crabs trapped per pool on each trap date. Independent variables included sampling date (Jan 21, Feb 4, Feb 22, March 4, June 20, July 4, July 18, Aug 1), pool substrate composition (large boulders, small boulders, rocks, cobble, gravel, leaf material, and woody debris), and pool physical parameters (pool average depth, area, flow velocity, and coefficient of variation (CV) of length, width, and depth). Alpha was set at 0.10 for variable entry into the model.

Variable	Parameter estimate	t Value	P	Model R^2
Intercept	14.48	3.78	0.0002	0.59
Trap date				
Jan 21	-8.09	-3.82	0.0002	
July 18	15.54	7.04	<0.0001	
Aug 1	5.29	2.33	0.02	
Substrate				
small boulders	-0.22	-3.55	0.0005	
gravel	-0.82	-4.77	<0.0001	
Physical				
average depth	32.62	3.18	0.002	
flow velocity	47.6	3.41	0.0009	
CV width	0.19	2.72	0.007	

Figure Legends

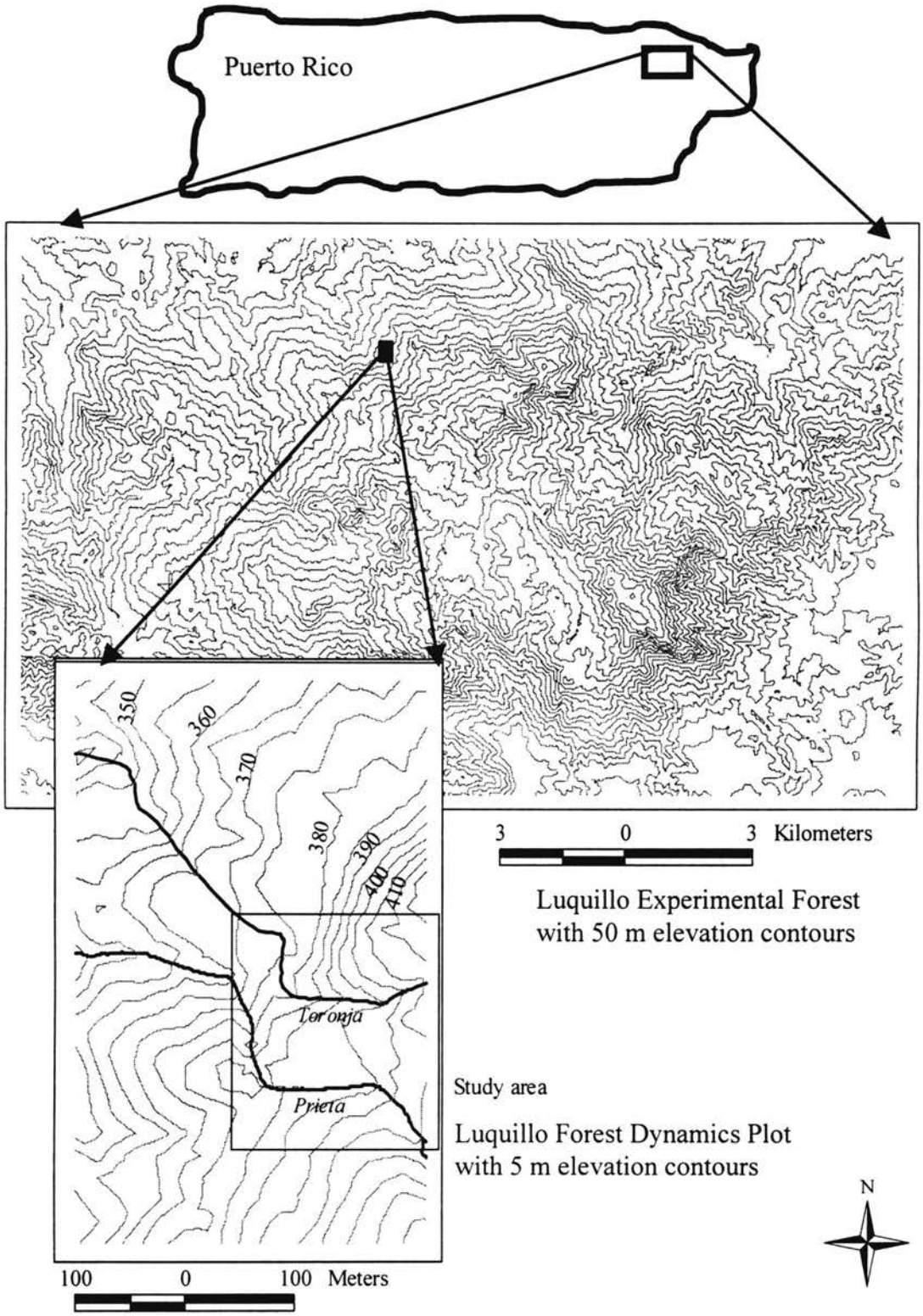
Fig. 1 Map of Puerto Rico, map of 50 m elevation contours in the Luquillo Experimental Forest (LEF), and 5 m elevation contours in the Luquillo Forest Dynamics Plot (LFDP) with the locations of the two study streams, Quebrada Prieta and Quebrada Toronja.

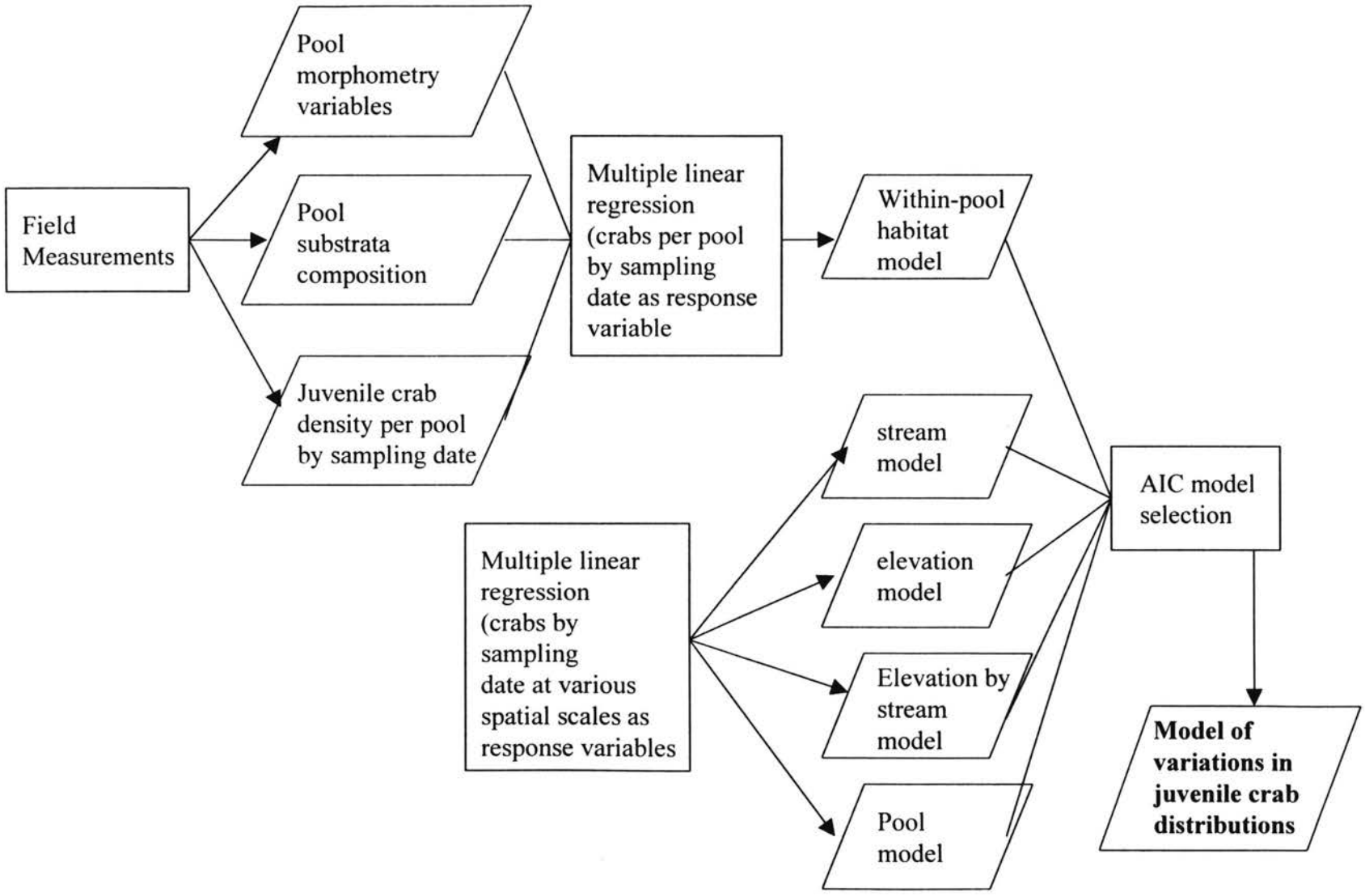
Fig. 2 Flow chart of analysis procedures resulting in a model describing variations in juvenile crab distributions.

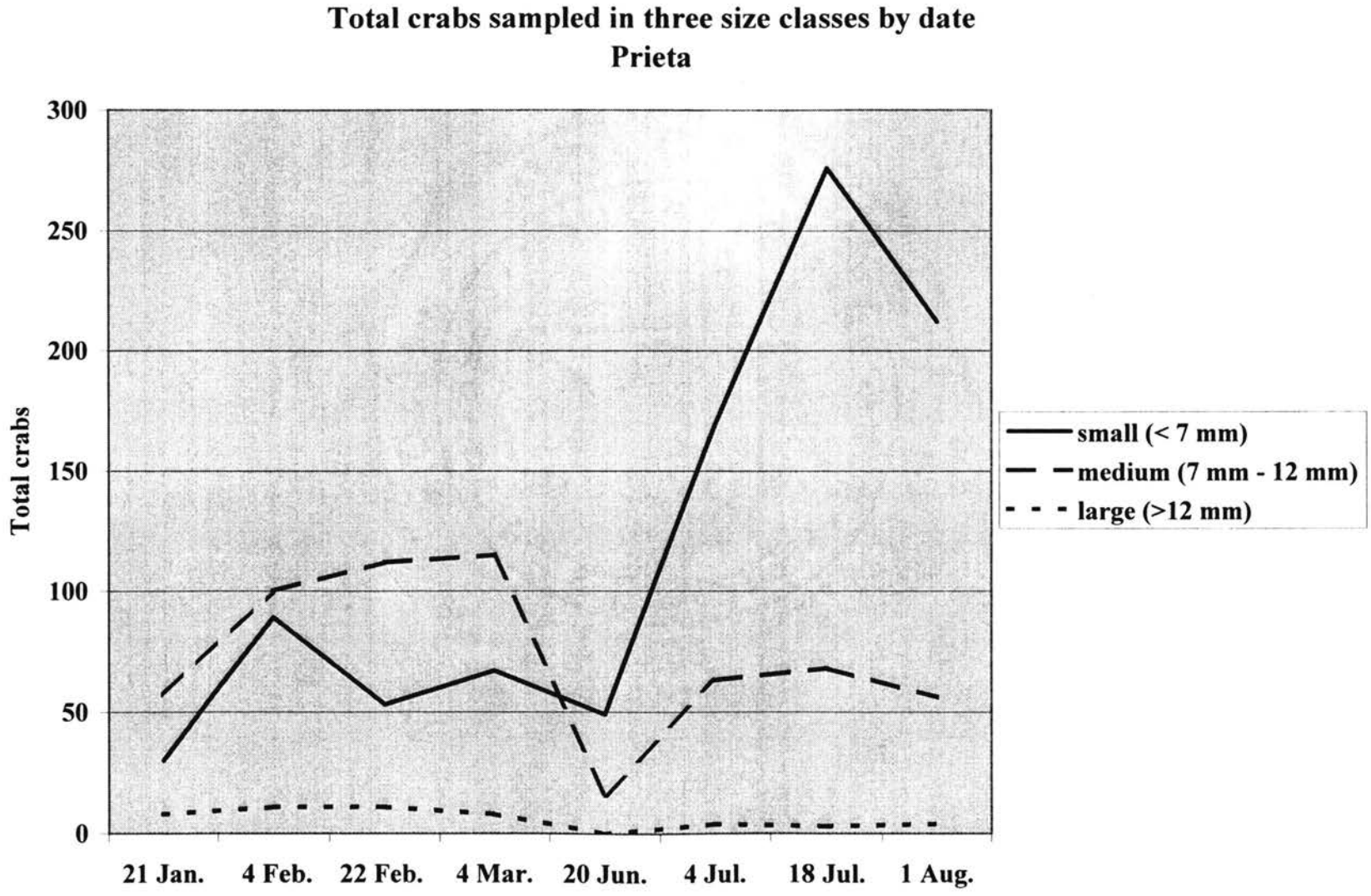
Fig. 3 Graph of size distributions of juvenile crabs trapped during each of eight sampling periods along Quebrada Prieta, Luquillo Experimental Forest, Puerto Rico. Y-axis represents frequency of crabs trapped for each sampling period. Note: Low crab numbers for June 20 were due to high storm flows that washed out traps for this sampling period.

Fig. 4 Graph of size distributions of juvenile crabs trapped during each of eight sampling periods along Quebrada Toronja, Luquillo Experimental Forest, Puerto Rico. Y-axis represents frequency of crabs trapped for each sampling period.

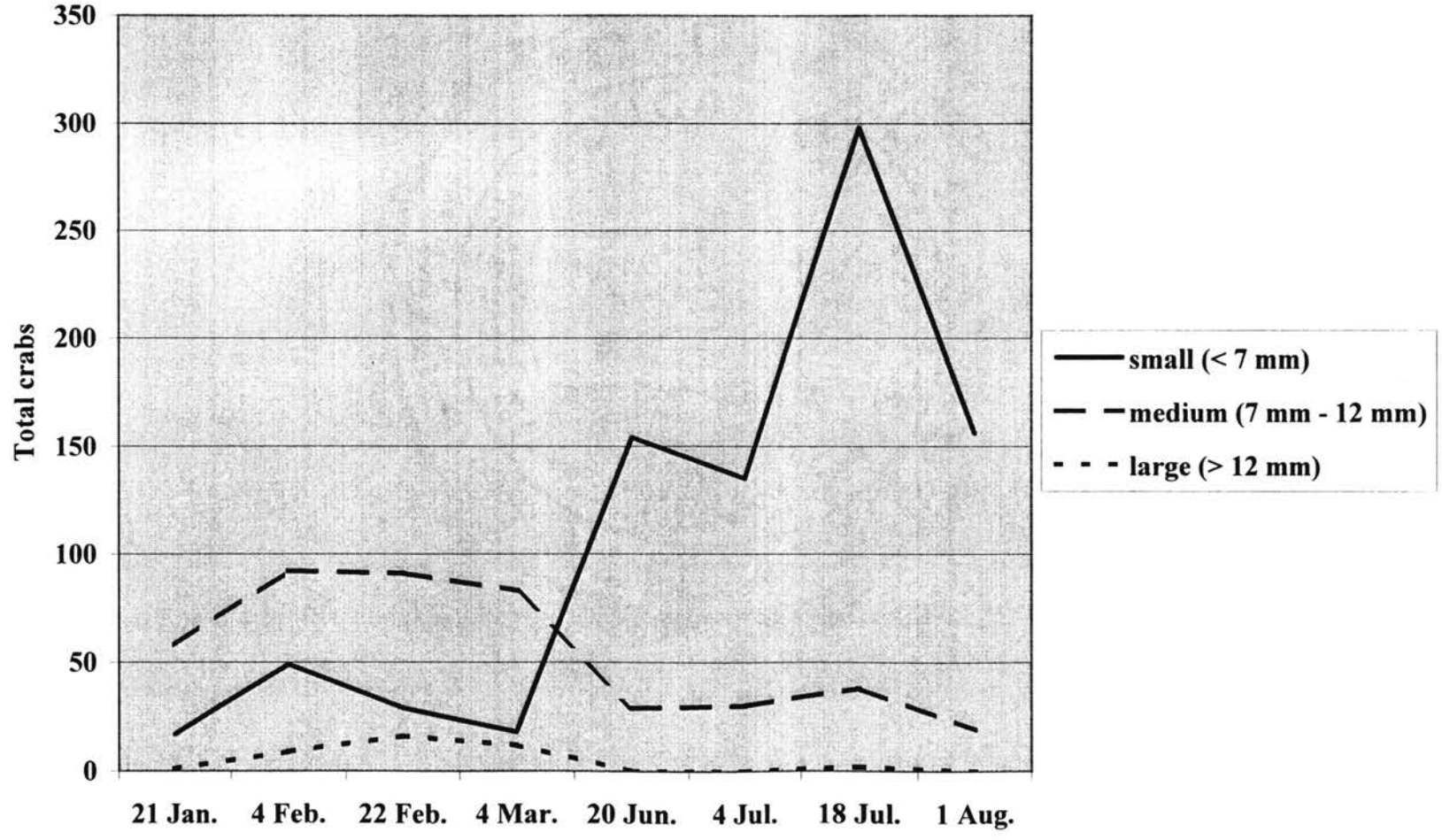
Fig. 5 Graph of mean number of mayflies eaten per night by individual crabs in each size class (8 mm to 18 mm carapace width). Error bars are one standard deviation.

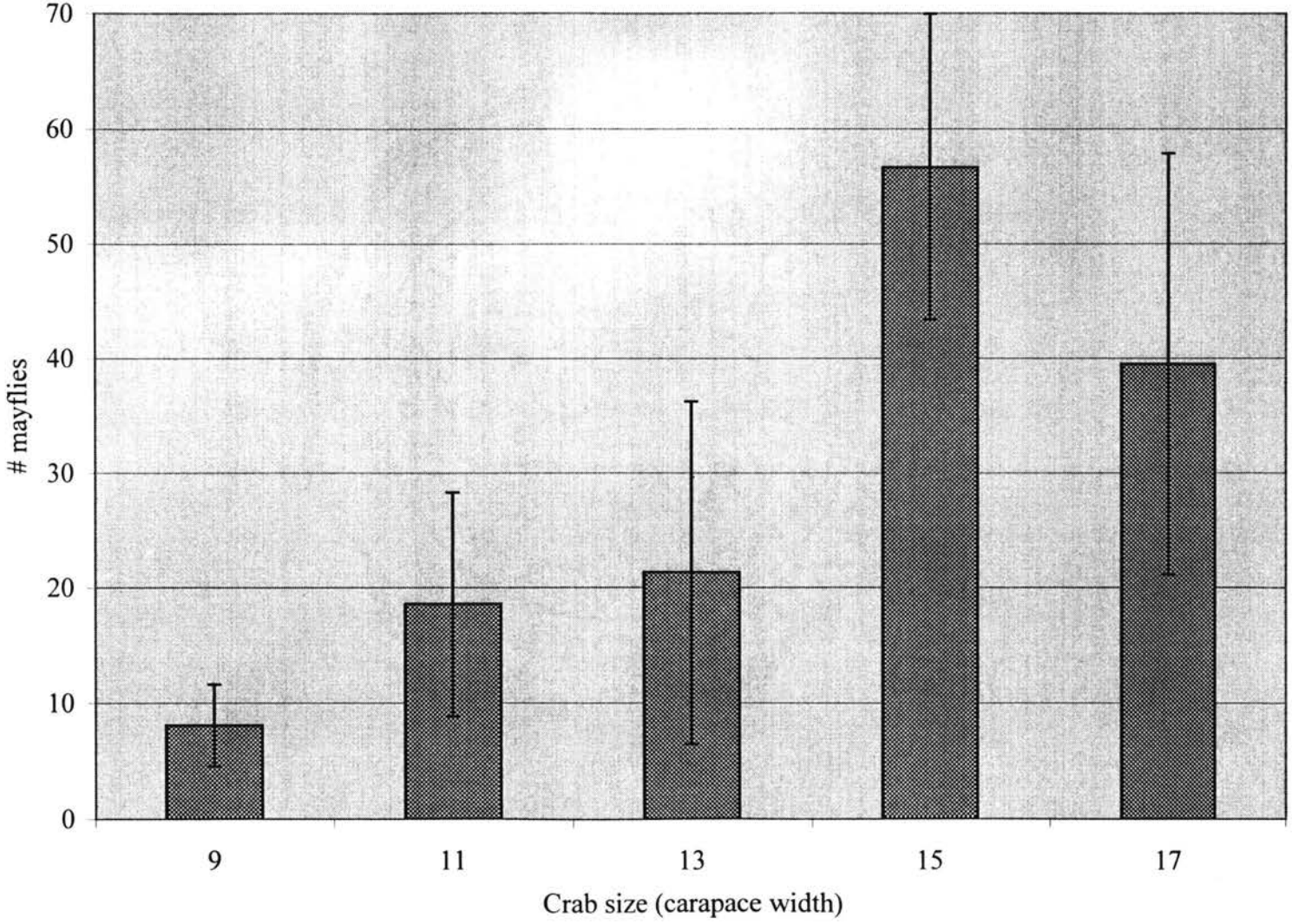

Puerto Rico
3 0 3 Kilometers
Luquillo Experimental Forest
with 50 m elevation contours
350
360
370
380
390
400
410
Lo ronja
Prieta
Study area
Luquillo Forest Dynamics Plot
with 5 m elevation contours
N
100 0 100 Meters


Field Measurements
Pool morphometry variables
Pool substrata composition
Juvenile crab density per pool by sampling date
Multiple linear regression (crabs per pool by sampling date as response variable
Within-pool habitat model
Multiple linear regression (crabs by sampling date at various spatial scales as response variables
stream model
elevation model
Elevation by stream model
Pool model
AIC model selection
Model of variations in juvenile crab distributions


Total crabs sampled in three size classes by date
Prieta
Total crabs
300
250
200
150
100
50
0
21 Jan.
4 Feb.
22 Feb.
4 Mar.
20 Jun.
4 Jul.
18 Jul.
1 Aug.
small (< 7 mm)
medium (7 mm - 12 mm)
large (>12 mm)

Total crabs sampled in three size classes by date
Toronja




70
60
50
40
30
20
10
0
mayflies
9
11
13
15
17
Crab size (carapace width)

APPENDIX I:

Models analyzed in study of damage and subsequent recovery of riparian palms due to Hurricane Georges

Models analyzed in study of damage and subsequent recovery of riparian palms due to Hurricane Georges. Hurricane Georges hit in September 1998; palms were surveyed in November 1998, January 1999, and June 1999. Canopy, subcanopy, small = 3 tree height classifications, north, south, east, west = aspect directions, slope = slope calculated in degrees, elevation = elevation in meters, palm = palm density, non-palm = non-palm density, total tree density = palm + non-palm density, eastcan = east aspect*canopy, canslo = canopy*slope, eastsm = east aspect*small, eastslo = east aspect*slope, westcan = west aspect*canopy, westslo = west aspect*slope.

***A priori* models**

Time period	**Model Number**	**Variables in model**
November damage	1	canopy, east, slope, eastcan, canslo, eastslo
	2	stream, small
	3	canopy, east, eastcan
	4	canopy, east, elevation, slope, total tree density, eastcan
	5	canopy, small, east, slope, non-palm, eastcan
	6	canopy, small, east, slope, palm, eastcan
	7	canopy, stream
	8	canopy, east, eastcan, total tree density
	9	canopy, east, eastcan, palm
	10	canopy, east
	11	canopy
	12	east
Nov.98-Jan.99 Recovery	1	canopy, west, slope, westcan, canslo, westslo
	2	stream, small
	3	canopy, west, westcan
	4	canopy, west, elevation, slope, total tree density, westcan
	5	canopy, small, west, slope, non-palm, westcan
	6	canopy, small, west, slope, palm, westcan
	7	canopy, stream
	8	canopy, west, westcan, total tree density
	9	canopy, west, westcan, palm
	10	canopy, west
	11	canopy
	12	west
Nov.98-Jan.99 Recovery	1	canopy, east, slope, eastcan, canslo, eastslo
	2	stream, small
	3	canopy, east, eastcan
	4	canopy, east, elevation, slope, total tree density, eastcan

	5	canopy, small, east, slope, non-palm, eastcan
	6	canopy, small, east, slope, palm, eastcan
	7	canopy, stream
	8	canopy, east, eastcan, total tree density
	9	canopy, east, eastcan, palm
	10	canopy, east
	11	canopy
	12	east
Jan.99-June 99	1	canopy, east, slope, eastcan, canslo, eastslo
Recovery	2	stream, small
	3	canopy, east, eastcan
	4	canopy, east, elevation, slope, total tree density, eastcan
	5	canopy, small, east, slope, non-palm, eastcan
	6	canopy, small, east, slope, palm, eastcan
	7	canopy, stream
	8	canopy, east, eastcan, total tree density
	9	canopy, east, eastcan, palm
	10	canopy, east
	11	canopy
	12	east

***post hoc* models**

Time period	**Model Number**	**Variables in model**
Nov.98-Jan.99	A	slope, total tree density
Recovery	B	total tree density
	C	west, total tree density
	D	canopy, total tree density
Nov.98-June 99	E	elevation
Recovery	F	elevation, total tree density
	G	elevation, non-palm
	H	elevation, palm
	I	elevation
	J	elevation, east, total tree density
Jan.99-June99	E	elevation
Recovery	F	elevation, total tree density
	G	elevation, non-palm
	H	elevation, palm
	I	elevation
	J	elevation, east, total tree density

APPENDIX II:

Data Dictionary for GIS coverages

Layer: DEM FOR FOREST RECOVERY PLOT

Description: Digital Elevation Model (DEM) in grid format. Elevation is for the Long-Term Ecological Research (LTER) Luquillo Forest Dynamics Plot (LFDP) within the Luquillo Experimental Forest (LEF), near the El Verde Field Station (18^0 10'N, 65^0 30'W), Puerto Rico. The elevation grid was also transformed into an aspect grid and a slope grid using ArcView software.

Class: Grid

Source: The elevation grid was surveyed by a company called GeoDatum, which appears to be no longer in business. Elevation and x,y coordinates were recorded on a 20 m x 20 m grid and digitized into ArcInfo, then transformed to a TIN, and then to a lattice, which was incorporated into the Luquillo LTER database. Contact: John Thomlinson at the Institute for Tropical Ecosystem Studies, University of Puerto Rico, Rio Piedras.

Format: PC ArcView

Date: The original grid was created in 1990.

Scale: Meters recorded to 3 decimal places. The Luquillo Forest Dynamics Plot was recorded in its own coordinate system, but the corner points were surveyed in Puerto Rico state plane meters.

Layer: TORONJA

Description: Location of Quebrada Toronja, a headwater stream that runs through the Long-Term Ecological Research (LTER) Luquillo Forest Dynamics Plot (LFDP) within the Luquillo Experimental Forest (LEF), near the El Verde Field Station (18^0 10'N, 65^0 30'W), Puerto Rico.

Class: Line

Source: The stream points were surveyed by a company called GeoDatum that appears to no longer be in business. The ArcInfo stream points were created from the survey points, and incorporated into the Luquillo LTER database. The ArcInfo coverage was then transformed into an ArcView shapefile. Contact: John Thomlinson at the Institute for Tropical Ecosystem Studies, University of Puerto Rico, Rio Piedras.

Format: PC ArcView

Date: Stream points were surveyed in 1990.

Scale: Meters recorded to 3 decimal places - point location data were taken directly from the field survey. A total of 894.958 m of the Quebrada Toronja was surveyed, using 37 survey points, averaging 24.188 m/pt. The stream points were surveyed in Puerto Rico state plane meters and converted to the Luquillo Forest Dynamics Plot coordinate system. Metadata source: Reed 1998.

Layer: PRIETA

Description: Location of Quebrada Prieta, a headwater stream that runs through the Long-Term Ecological Research (LTER) Luquillo Forest Dynamics Plot (LFDP) within the Luquillo Experimental Forest (LEF), near the El Verde Field Station (18^0 10'N, 65^0 30'W), Puerto Rico.

Class: Line

Source: The stream points were surveyed by a company called GeoDatum that appears to no longer be in business. The ArcInfo stream points were created from the survey points, and incorporated into the Luquillo LTER database. The ArcInfo coverage was then converted into an ArcView shapefile. Contact: John Thomlinson at the Institute for Tropical Ecosystem Studies, University of Puerto Rico, Rio Piedras.

Format: PC ArcView

Date: Stream points were surveyed in 1990.

Scale: Meters recorded to 3 decimal places - point location data were taken directly from the field survey. A total of 469.961 m of the Quebrada Prieta was surveyed, using 17 survey points, averaging 27.645 m/pt. The stream points were surveyed in Puerto Rico state plane meters and then converted to the Luquillo Forest Dynamics Plot coordinate system. Metadata source: Reed 1998.

Layer: STREAM SUBPLOTS AND TOPOGRAPHY

Description: Location and mean slope, aspect, and elevation of study subplots (5 m x 10 m) within 300 m riparian transects along Quebrada Prieta and Quebrada Toronja within the Long-Term Ecological Research (LTER) Luquillo Forest Dynamics Plot (LFDP) within the Luquillo Experimental Forest (LEF), near the El Verde Field Station (18^0 10'N, 65^0 30'W), Puerto Rico.

Class: Point

Attributes:

NAME	DESCRIPTION	TYPE	EXAMPLE
stream	location - Prieta (QP) or Toronja (TOR)	string	QP
meter_side	subplot location for each stream	string	190L
area	area of subplot (m^2)	numeric	49
elev_mean	mean elevation (m) per subplot	numeric	397
elev_std	standard deviation of mean elevation per subplot	numeric	0.28
slope_mean	mean slope (degrees) per subplot	numeric	15
slope_std	standard deviation of mean slope per subplot	numeric	1.77
aspect_mean	mean aspect per subplot	string	west
aspect_mean2	mean aspect (degrees) per subplot	numeric	266
aspect_std	standard deviation of mean aspect per subplot	numeric	6.45

Source: The subplot layer was created by adding a 5 m riparian buffer to the Q. Prieta and Q. Toronja coverages and digitizing in subplot boundaries using GPS locations taken in the field in July 1999. Topography information was calculated using the elevation, slope, and aspect grids and calculating the mean value of each for each subplot. Contact: Julie Henry, Dept. of Fishery and Wildlife Biology, Colorado State University, Ft. Collins.

Format: PC ArcView

Date: Coverage was created in 1999 from GPS points taken in July 1999 and stream maps created in 1990.

Scale: Meters - point location data were taken directly from the field survey and entered into the GIS data layer. Stream coordinates and GPS points were surveyed in Puerto Rico state plane meters and then converted to the Luquillo Forest Dynamics Plot coordinate system.

Layer: TREEMAP

Description: Location of surveyed trees greater than 10cm DBH for the Long-Term Ecological Research (LTER) Luquillo Forest Dynamics Plot (LFDP) within the Luquillo Experimental Forest (LEF), near the El Verde Field Station (18^0 10'N, 65^0 30'W), Puerto Rico. The treemap layer was used to calculate the number of non-palms per subplot for this study, by selecting all trees that were not *Prestoea montana*, and clipping the layer with the stream subplots coverage.

Class: Point

Attributes:

NAME	DESCRIPTION	TYPE	EXAMPLE
tag	individual tag number for each surveyed tree	numeric	10
x-coord	grid x-coordinate of each surveyed tree	numeric	0.596
y-coord	grid y-coordinate of each surveyed tree	numeric	2.234
spcode	species name for each tree	string	PREMON

Source: The trees were surveyed by a field crew working for University of Puerto Rico under Jill Thompson. The locations were digitized into an ArcInfo data layer and incorporated into the Luquillo LTER database. The ArcInfo coverage was then converted into an ArcView coverage. Contact: John Thomlinson at the Institute for Tropical Ecosystem Studies, University of Puerto Rico, Rio Piedras.

Format: PC ArcView

Date: Points were surveyed in 1990.

Scale: Meters recorded to 3 decimal places - point location data were taken directly from the field survey and entered into the GIS data layer. The tree coordinates were surveyed in Puerto Rico state plane meters and transformed into the Luquillo Forest Dynamics Plot coordinate system. Metadata source: Reed 1998.

Layer: PALMMAP

Description: Location of surveyed Sierra palms (*Prestoea montana*) greater than 1.5 m in height for stream subplots within the Long-Term Ecological Research (LTER) Luquillo Forest Dynamics Plot (LFDP) within the Luquillo Experimental Forest (LEF), near the El Verde Field Station (18^0 10'N, 65^0 30'W), Puerto Rico.

Class: Point

Attributes:

NAME	DESCRIPTION	TYPE	EXAMPLE
stream	location - Q. Prieta (QP) or Q. Toronja (TOR)	string	TOR
tag	individual tag number for each surveyed tree	numeric	11
meters	subplot location for each stream	string	10
side	side of stream	string	R
height	palm height class	string	subcanopy
July_98_light	light class for July 1998 survey	numeric	2
July_98_flower	number of inflorescences In July survey	numeric	1
July_98_fruit	number of fruiting structures for July survey	numeric	2
Nov_98_light	light class for November 1998 survey	numeric	1
Nov_98_flower	number of inflorescences in Nov. survey	numeric	1
Nov_98_fruit	number of fruiting structures in Nov. survey	numeric	3
Nov_98_damage	damage status after Hurricane Georges	string	damaged

*light, flower, fruit, and damage attributes also present for January 1999 and June 1999 surveys

Source: The palms were surveyed by Julie Henry, Dept. of Fishery and Wildlife Biology, Colorado State University, Ft. Collins. All palms greater than 1.5 m in height were surveyed within 5 m x 10 m riparian subplots along 300 m of Quebrada Prieta and Quebrada Toronja and digitized into ArcView. Contact: Julie Henry, Dept. of Fishery and Wildlife Biology, CSU.

Format: PC ArcView

Date: Points were surveyed in 1998.

Scale: Meters - point location data were taken directly from the field survey and entered into the GIS data layer. The tree coordinates were surveyed in Puerto Rico state plane meters and transformed into the Luquillo Forest Dynamics Plot coordinate system.