Stream community structure and the role of allochthonous inputs in Quebrada Moquina at Monteverde

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Abstract: Allochthonous inputs may be important in structuring stream invertebrate communities, particularly in streams with low primary productivity. This study examined the invertebrate community in Quebrada Moquina, a densely shaded headwater stream in Monteverde, Costa Rica. I hypothesized that (1) the stream had low primary production, and therefore low scraper abundances, and (2) a strong relationship existed between allochthonous inputs and invertebrate distribution, represented by collector abundances relative to localized sources of forest debris ("debris dams"). As predicted, the abundance of collectors was linked to the location of debris dams. However, scraper abundances were relatively high in all locations, suggesting surprisingly high primary productivity.

Key words: functional feeding groups, large woody debris, primary production

Introduction

Stream invertebrate communities can be structured by resource availability. Streams in tropical forests generally have very low primary productivity due to low light and low nutrients. Thus, allochthonous resources may be especially influential in structuring the invertebrate community. The Quebrada Moquina stream in the Monteverde biological station appears to have low in-stream primary productivity. The stream is covered by dense canopy which blocks almost all direct sunlight. Allochthonous inputs may be the main resource for stream invertebrates. Within the stream, large woody debris often blocks the passage of other coarse particulate organic matter (CPOM) like leaves and sticks. The majority of allochthonous material in the stream is localized in these "debris dams," making the distribution of resources spatially heterogeneous.

If there is low in-stream primary productivity and patchy allochthonous material this should be reflected in the structure of the stream invertebrate community, as defined by the relative abundance of different function feeding groups (FFGs). For example, scrapers, which utilize periphyton, should be in low abundance within most reaches. Shredders, which rely on CPOM, should be aggregated in the vicinity of debris dams. Collectors (both filterers and gatherers of fine particulate organic matter, or FPOM), should decrease in abundance with increasing downstream distance from debris dams. I tested these predictions by sampling the Quebrada Moquina invertebrate community.

Methods

I sampled two to three invertebrate communities downstream from each of five debris dams in the Quebrada Moquina, a cloud forest, first-order stream at Monteverde biological station, Costa Rica. I haphazardly chose runs or riffles and sampled invertebrates with a 20 cm-wide kick-net. I repeated sampling three times at each run or riffle. I measured the distance of each sample site from the nearest debris dam upstream.

I identified organisms using aquatic insect keys (Lehmkuhl 1979 and Merrit et al. 1996) and categorized them into functional feeding groups using information from Merrit at al.

(1996). I examined abundances of all FFGs and correlated collector abundances with distance of sample sites from debris dams. I evaluated patterns in collector abundance with a general linear model (ANCOVA) that included debris dams (categorical variable) and distance below the nearest debris dam (continuous variable).

RESULTS

I identified 16 invertebrate taxa, which included representatives from the five generally recognized functional feeding groups (Table 1). Scrapers and collectors were among the most abundant groups (Table 2). Abundance of collector-filterers, collector-gatherers, and all collectors decreased with increasing distance from debris dams (Fig. 1), significantly so for collector-filterers and collectors combined (Table 2). Surprisingly, the abundance of collectors associated with each debris dam seemed to be related to their position along the stream, with the highest abundance upstream and the lowest downstream. Shredders, although rare overall, also decreased with distance from debris dam (Table 3).

DISCUSSION

The high abundance of scrapers suggests that primary production was higher than I expected in the Quebrada Moquina. The overall structure of the invertebrate community in this cloud forest stream may therefore be less de-

Table 1. Invertebrate morphotypes, their mean abundance, and their functional feeding group (after Merrit et al. 1996).

Invertebrate morphotype		Mean # per sample ± SD	Functional feeding group
Tricoptera	Polycentropidae	1.82 ± 3.9	Collector-filterer
	Hydrocychidae	3.27 ± 3.1	Collector-filterer
	Odontoceridae	0.09 ± 0.3	Shredder
Plecoptera	Perlidae	2.82 ± 2.5	Predator
Ephemeroptera	Beatidae	8.64 ± 5.0	Collector-gatherer
	Heptageniidae	15.36 ± 10.7	Scraper
	Leptophlebeidae	0.36 ± 0.7	Collector-gatherer
Coleoptera	Psephenidae	0.36 ± 0.5	Scraper
	Dytiscidae	1.18 ± 2.2	Predator
	Elmidae	4.0 ± 0.4	Collector-gatherer
Diptera	Tipulidae	0.45 ± 0.5	Predator
	Chironomidae	1.45 ± 1.4	Collector-gatherer
	Simulidae	19.36 ± 22.3	Collector-filterer
Odonata		0.45 ± 1.2	Predator
Amphipoda		1.82 ± 1.7	Collector-gatherer
Crab		0.64 ± 0.5	Shredder

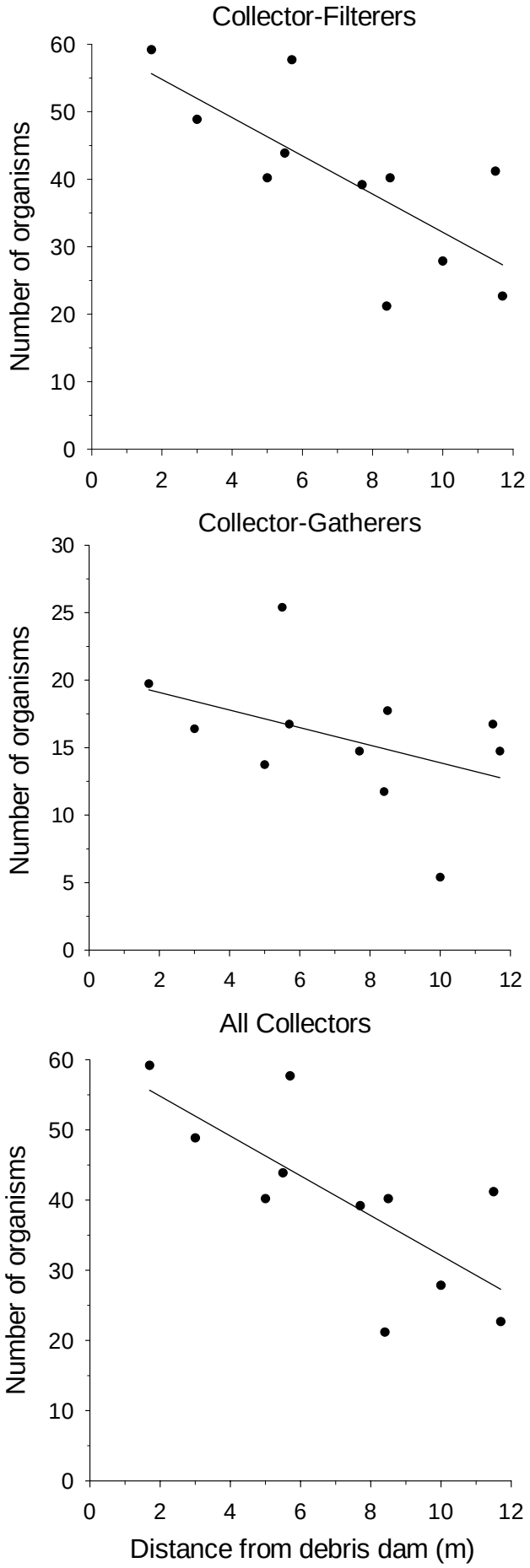

Table 2. Results of ANCOVAs testing for effects of debris dams (categorical variable) and distance from dams (continuous variable) on abundance and richness of different functional feeding groups.

	F-statistic		
Independent variable	Debris dams[a]	Distance from dam[b]	Mean ± SE
Collector-gatherers	1.30	1.71	16 ± 2
Collector-filterers	9.10*	8.69*	24 ± 7
All collectors	13.50**	15.02*	40 ± 8
Scrapers	0.91	1.24	16 ± 3
Predators	1.05	0.83	4 ± 1
Shredders	3.00	9.39*	1 ± 0.3
All organisms	22.29**	8.91*	60 ± 9
Family richness	2.68	1.37	10 ± 0.5

* $P < 0.05$, ** $P < 0.01$
[a] df = 4,10 [b] df = 1,10

Table 3. Mean collector abundance with respect to debris dam order, from upstream (1) to downstream (5). Least square means adjusted for variation in distances from debris dams.

Debris dam order	Least square mean	Standard error
1	69.85	6.29
2	23.47	5.22
3	53.48	6.46
4	42.51	6.73
5	10.43	6.62

Figure 1. Abundance of collector organisms as a function of distance downstream of debris dams. Numbers of organisms have been adjusted for the effects of overall stream position, relative to debris dam order. Collector-gatherers ($r^2 = 0.19$, $P = 0.19$); Collector-filterers ($r^2 = 0.55$, $P < 0.01$); All collectors ($r^2 = 0.46$, $P = 0.02$).

pendent on allochthonous inputs than postulated. Collector abundances, however, showed the predicted decline with distance from debris dams, supporting the hypothesis that consumer community structure was influenced by distance relative to debris dams. It appears that allochthonous inputs may play a key role in community structure, and debris dams represent the primary sites of this resource within the stream.

Because collector abundance depends on FPOM, the relationship between debris dam order and collector abundance suggests that FPOM concentrations may be higher upstream. There may be a relationship between elevation and the role of runoff inputs: if increased elevation and higher air moisture causes higher soil moisture, runoff carrying FPOM from soil may increase. The relationship between collector abundance and debris dam order may reflect a FPOM gradient as this effect diminishes downstream. This hypothesis could be tested by comparing FPOM concentrations, based on dry weights of filtered samples, along an elevational gradient in the stream.

Evidence of substantial in-stream primary production was unexpected, but allochthonous inputs still appear to strongly influence the invertebrate community. This negative correlation between collector abundance and distance downstream of debris dams highlights the role of large woody debris in resource retention in headwater streams.

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Female flower size and deceptive pollination in *Begonia involucrata*

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Abstract: Female flowers of *Begonia involucrata* offer no reward to pollinators, relying on mimicry of male flowers to attract bees. In this study we modeled possible strategies that female flowers may use to mimic the size of male flowers and then used our models to predict the size distribution of female flowers that would optimize their pollination success. We observed that the actual mean size of female flowers is slightly lower than the mean size of male flowers. Based on our model, this size distribution results in lower than predicted optimal pollination success, contrary to our hypothesis that the distribution of female flower sizes will correspond to the predicted optimal flower size distribution for female pollination success. We conclude that the size distribution of female flowers is either not optimal or that other biological factors or physiological constraints of female flowers not accounted for in our model may be important to reproductive success in this pollination system.

Key words: bee pollinators, deceit, monoecious, Monteverde, pollinator rewards, size mimicry

Introduction

Begonia involucrata is a 1 - 2 m tall perennial herb common in the understory of the tropical montane cloud forest at Monteverde, Costa Rica. This species is monoecious and pollinated by deceit. Female flowers offer no reward to pollinators, but attract bees by being mimics of male flowers, which do provide rewards (nectar and pollen). Female stigmas mimic the size and spectral properties of male anthers and male and female flowers contain identical petal structure (Ågren and Schemske 1991) (Fig. 1). Deception is maintained by a skewed sex ratio of approximately one female to three male flowers (Campbell et al. 2001).

Ågren and Schemske (2000) showed that bee pollinators are more attracted to large flowers. They proposed that selection for female resemblance to male flowers could take two different forms based on a tradeoff between deception by sex ratio and attractiveness based on size: mean female flower size could either equal the mean male flower size or it could equal the larger male flower size associated with a higher reward. In the first situation, the 1 : 3 sex ratio is maintained among all sizes, providing maximum pollination and reproductive success for females at mean male flower size (Figs. 2a and 2b). In the second, large female flowers may be pollinated more often and therefore have higher reproductive success because they are more attractive to bees (Fig. 3a). However, the 1 : 3 sex ratio would no longer be maintained, so their deceptive ability may be decreased (Fig. 3b).

We modeled the effects of each strategy to predict which should result in the greatest number of female flowers pollinated. We hypothesized that *B. involucrata* should utilize the

Figure 1. Female *B. involucrata* flowers. (Photo courtesy of Jill Harris)

mimicry strategy that results in the highest pollination index value as calculated by the model. To test this hypothesis, we examined the size distributions of male and female flowers in nature and compared them to predictions from our model.

METHODS

Field methods

From 0730 to 1100 on 22 January 2004, we sampled a population of *B. involucrata* along the Cariblancos trail near the Estación Biologica Monteverde in Monteverde, Costa Rica. We established 20 quadrats along 160 m of trail; quadrats were 3 m long, extending 2 m on either side of the trail and spaced 5 m apart.

We examined all the open flowers on the left branch of every inflorescence within each quadrat for a total of 492 flowers and 97 inflorescences. We noted the sex of each flower and measured both the widest point and total length of the flattened petals. Then we multiplied width and length to calculate a size index value for each flower and log transformed these values to establish normality.

Modeling

We constructed models based on the observed sex ratio and male flower size distribution that determined an index of total female flower pollination for three different female flower size distributions. Based on the observed data, we restricted possible female flower size distributions to lognormal distributions (Figs. 2a, 3a and 4a). We then calculated the proportion of females and males across sizes (Figs. 2b, 3b and 4b). We assumed pollinator reward per male flower to be a linear function of size, which, when multiplied by the proportion of males, yielded pollinator reward per flower as a function of size (Figs. 2c, 3c and 4c). Assuming that pollinators are behaving optimally, flower visitation rate should increase with pollinator reward. For our model, we assumed this to be a linear relationship. To determine the probability of pollination across flower sizes, we used the function $p(\text{pollination}) = 1 - (1 - k)^{\text{visitation rate}}$, where k is the proportion of visits that result in successful pollination (Figs. 2d, 3d and 4d). Thus, multiplying the female flower size distribution by the probability of pollination yields pollination frequency across size indices. The integral of the pollination frequency curve provides a pollination index, PI (Figs. 2e, 3e and 4e).

Model 1 evaluated the first proposed deceit strategy by calculating the PI of a female lognormal flower size distribution with mean and variance matching that of the observed male flower size distribution and complying with the observed 9 : 32 sex ratio (Fig. 2). Model 2 determined the optimal female lognormal flower size distribution, given the observed male size distribution, by using the mean and standard deviation as parameters to solve for the maximum possible PI. The optimal female flower size distribution had a mean higher than that of the male flower size distribution, and thus served to evaluate the second proposed deceit strategy (Fig. 3). Model 3 evaluated the observed female flower size distribution by determining the PI for comparison to the other two models (Fig. 4).

RESULTS

We found that the population consisted of 22.0% female flowers and 78.0% male flowers (n = 492), or a ratio of nine females to thirty-two males. Flowers from the same inflorescence were almost always of the same sex (94 of 97). The number of flowers per inflorescence branch ranged from one to fourteen, with a median of five. The mean size index of female flowers (1.83) was 10% smaller than that of male flowers

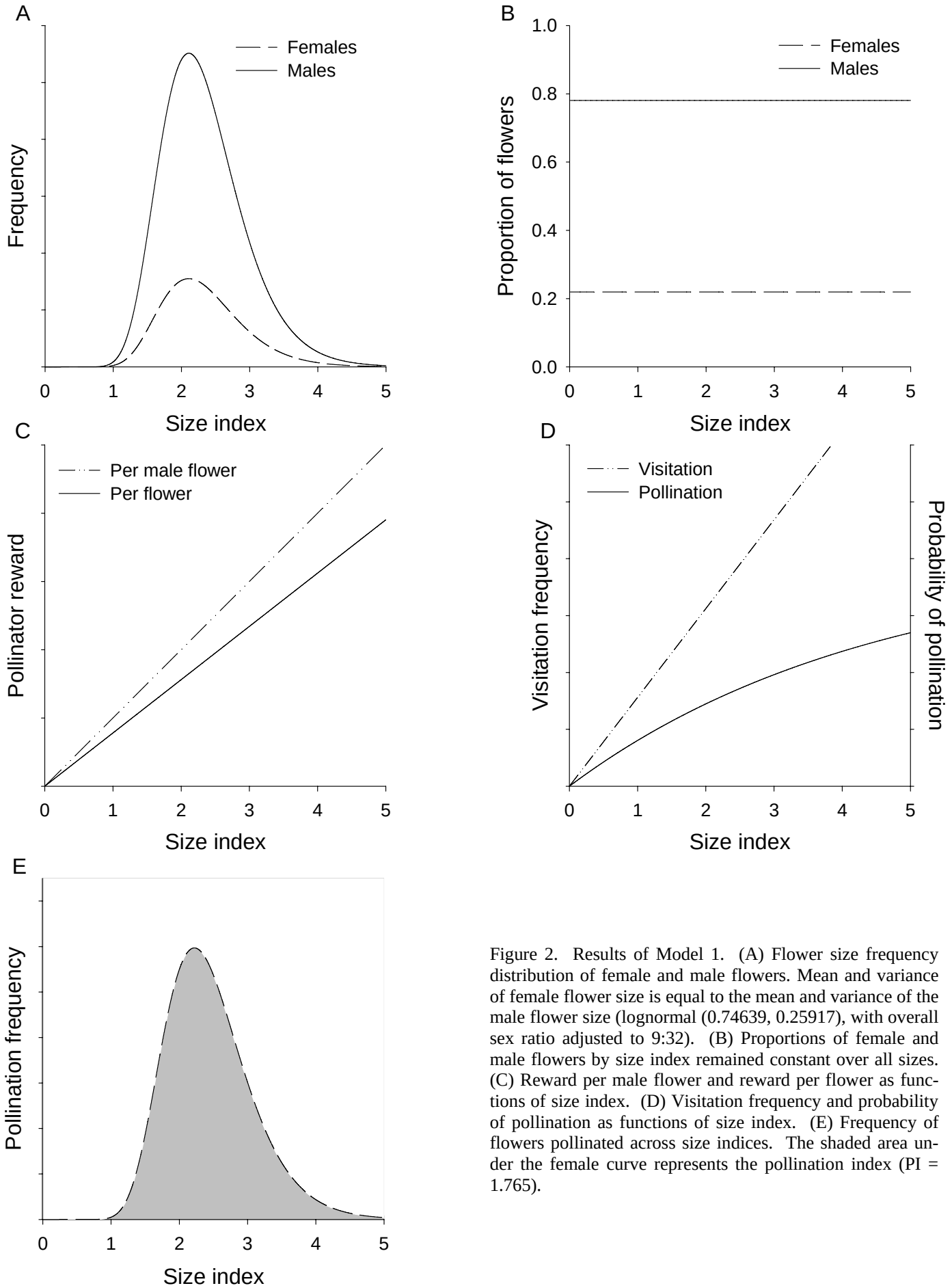

Figure 2. Results of Model 1. (A) Flower size frequency distribution of female and male flowers. Mean and variance of female flower size is equal to the mean and variance of the male flower size (lognormal (0.74639, 0.25917), with overall sex ratio adjusted to 9:32). (B) Proportions of female and male flowers by size index remained constant over all sizes. (C) Reward per male flower and reward per flower as functions of size index. (D) Visitation frequency and probability of pollination as functions of size index. (E) Frequency of flowers pollinated across size indices. The shaded area under the female curve represents the pollination index (PI = 1.765).

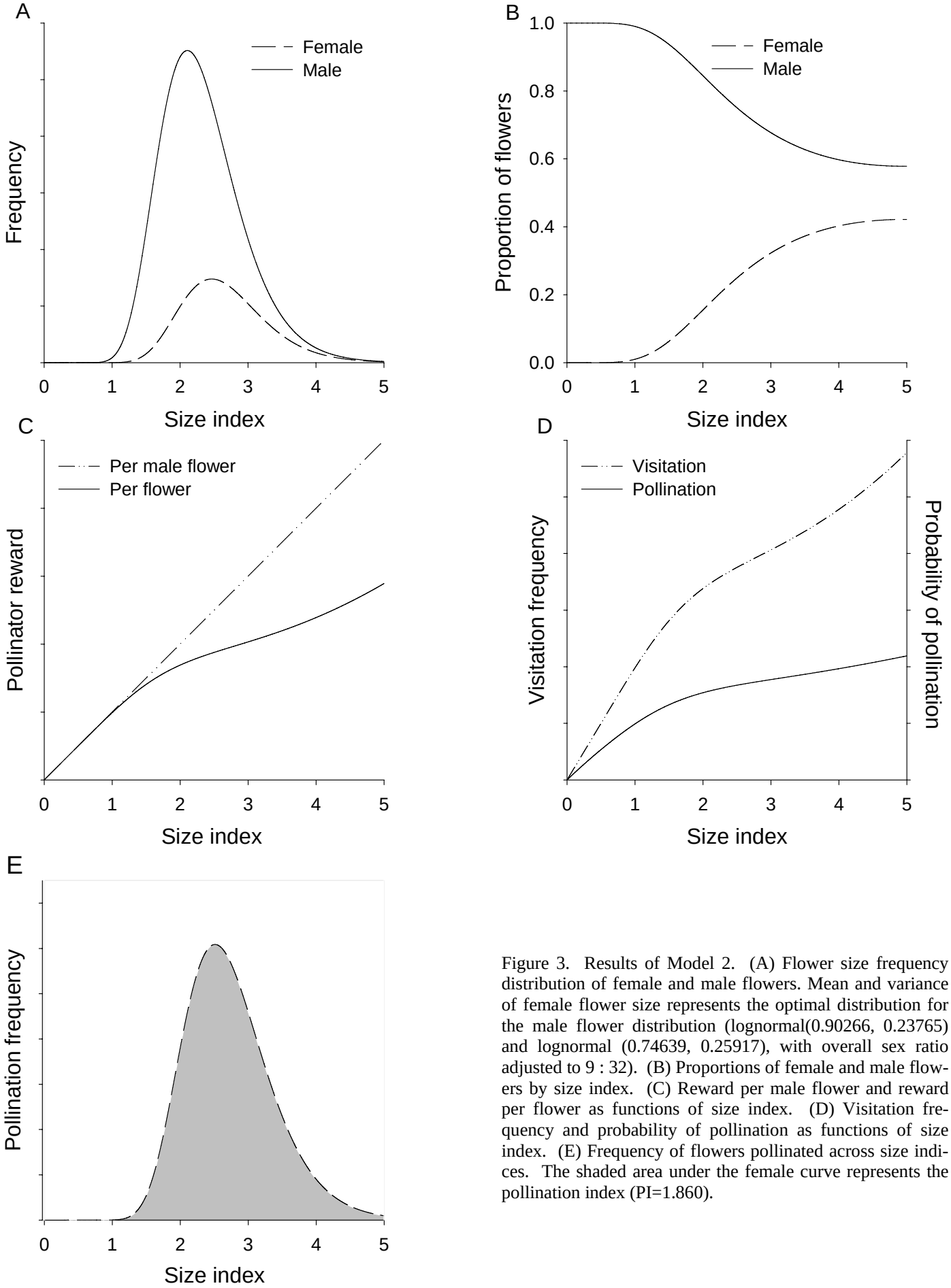

Figure 3. Results of Model 2. (A) Flower size frequency distribution of female and male flowers. Mean and variance of female flower size represents the optimal distribution for the male flower distribution (lognormal(0.90266, 0.23765) and lognormal (0.74639, 0.25917), with overall sex ratio adjusted to 9 : 32). (B) Proportions of female and male flowers by size index. (C) Reward per male flower and reward per flower as functions of size index. (D) Visitation frequency and probability of pollination as functions of size index. (E) Frequency of flowers pollinated across size indices. The shaded area under the female curve represents the pollination index (PI=1.860).

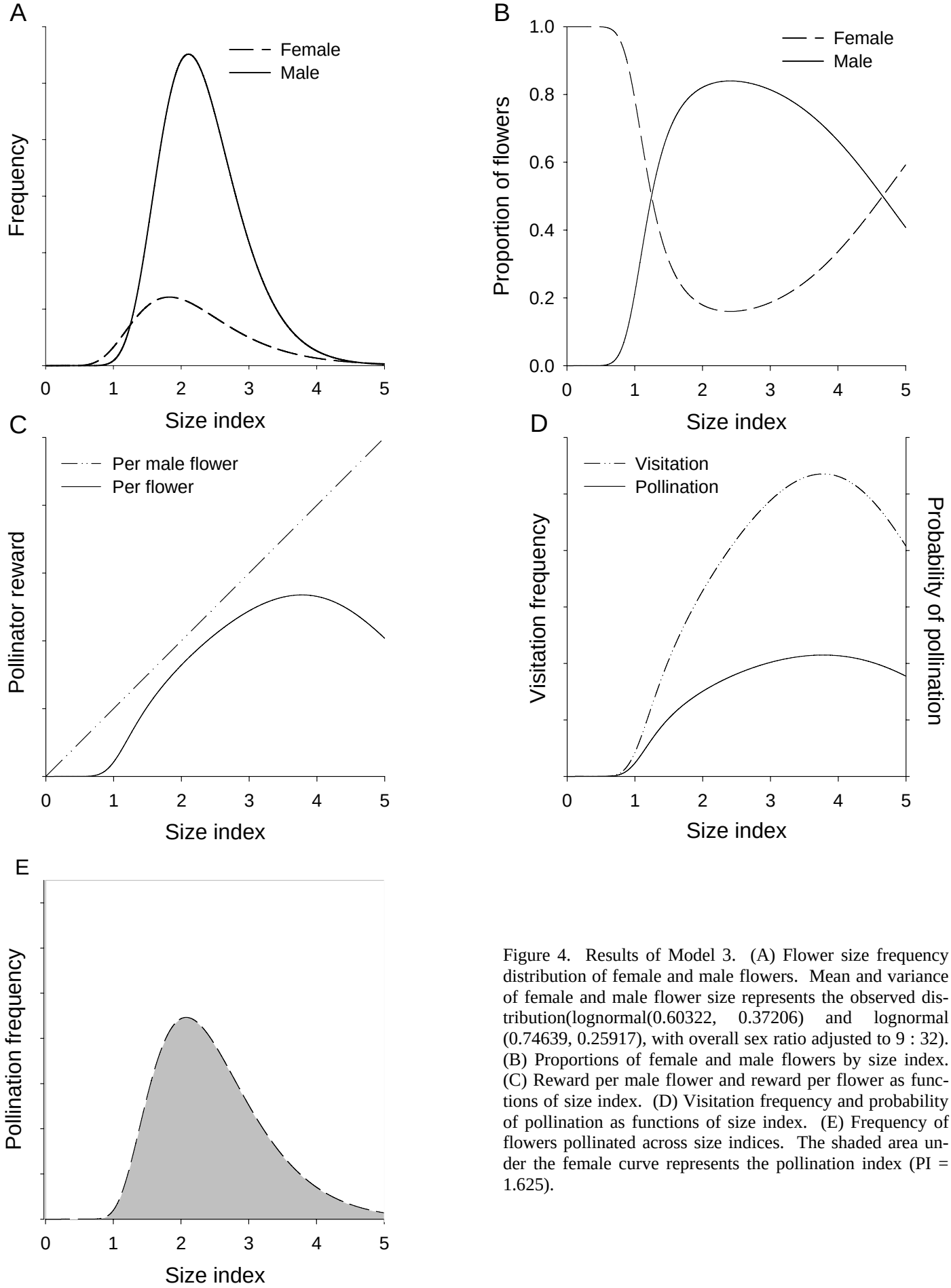

Figure 4. Results of Model 3. (A) Flower size frequency distribution of female and male flowers. Mean and variance of female and male flower size represents the observed distribution(lognormal(0.60322, 0.37206) and lognormal (0.74639, 0.25917), with overall sex ratio adjusted to 9 : 32). (B) Proportions of female and male flowers by size index. (C) Reward per male flower and reward per flower as functions of size index. (D) Visitation frequency and probability of pollination as functions of size index. (E) Frequency of flowers pollinated across size indices. The shaded area under the female curve represents the pollination index (PI = 1.625).

TABLE 1. Nested ANOVA comparing variance of female and male flower size at different spatial levels.

		Female flowers		
Source	df	F	P	% variance
Quadrats	6	2.70	0.065	32
Inflorescence (quadrat)	14	5.22	<0.001	34
Flowers (inflorescence)	87			34
		Male flowers		
Source	df	F	P	% variance
Quadrats	11	1.92	0.051	7
Inflorescence (quadrat)	67	2.71	<0.001	25
Flowers (inflorescence)	305			67

(2.11) (Fig. 5). This difference is small, but statistically significant (oneway ANOVA assuming unequal variances, t = 3.51, df = 137, P = 0.0003). We also found highly significant variance in flower size, both male and female, among inflorescences within quadrats, and marginally significant variance among quadrats (Table 1). Spatial structure of the variance differed among male and female flowers, with females having relatively more variance among quadrats and inflorescences within quadrats.

We used the observed size distribution of male flowers to create Model 1 based on the first mimicry strategy (mean female size equals mean male size) and Model 2 based on the second mimicry strategy (mean female size is greater than mean male size). Model 2 (PI = 1.86) resulted in a pollination index that was 5.4% higher than that of Model 1 (PI = 1.77) (Figs. 2 and 3). The lognormal distributions of observed female and male flower sizes were different than the size distributions of Models 1 and 2 (Goodness-of-fit test, D = 0.27, P < 0.01, n = 108 for Model 1; D = 0.48, P < 0.01, n = 108 for Model 2). Therefore we created Model 3 based on the best-fit lognormal distributions for the observed size distributions (Fig. 4). The pollination index value resulting from this model was 1.63, which was 8 - 13% lower than that of Models 1 or 2. The qualitative results comparing the pollination indices of the three models did not change even when other increasing functions were used in place of assumed linear relationships, including power, exponential, saturation, and sigmoidal functions. However, the magnitude of the differences in PI was affected by using alternate relationships. Altering the value used for the proportion of visits that result in successful pollination similarly changed the magnitude, but not the qualitative result.

DISCUSSION

The observed size distributions of female and male *B. involucrata* in our field sample from Monteverde did not conform to either of the mimicry strategies proposed by Ågren and Schemske (2000). Our models suggested that mimicry of large male flowers would result in the most pollination. According to our models, the observed size distribution of female flowers would result in the least pollination of the three scenarios. Assuming that our models are valid, our hypothesis was not supported.

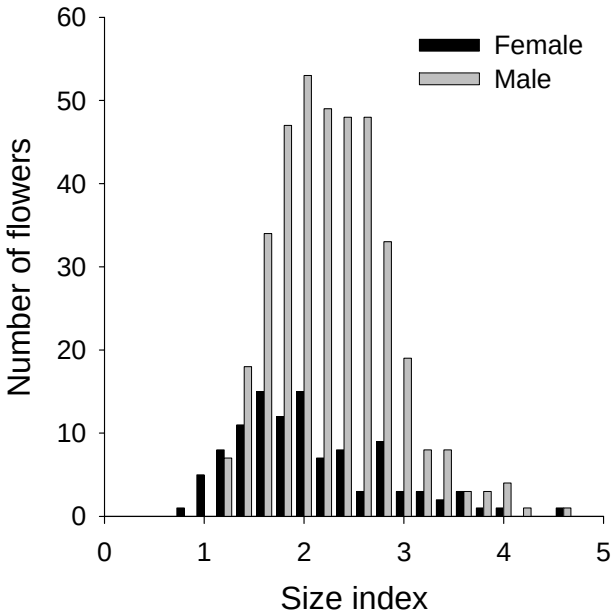

Figure 4. Size distribution of female (N = 108) and male (N = 384) *B. involucrata* flowers. Mean female flower size = 1.83; 95% confidence interval: 1.70 - 1.96. Mean male flower size = 2.11; 95% confidence interval: 2.06 - 2.16.

We assumed that the size mimicry strategy employed by female *B. involucrata* in nature ought to be biologically optimal. This assumption, however, is either incorrect, or our models failed to account for other biological factors that contribute to realized reproductive success. For example, if frequency of visitation by pollinators is not the limiting factor in reproduction, then our pollination index value is not meaningful. However, Ågren and Schemske (1991) suggest that pollination is limiting, citing a 40% increase in seed production resulting from pollen addition.

Alternately, the observed size distribution of female flowers may be the result of tradeoffs. The potential 13% increase in pollination suggested by our model may be outweighed by the cost of producing larger flowers. Also, female flowers may face greater physiological costs to reach the same flower size as males if, for example, ovary production is more energetically costly than male pollen and nectar production. If female flower size is limited by energetic costs and therefore more sensitive than male flowers to spatial differences in resource availability, this may explain the differences found between the spatial structure of variance between female and male flowers. It is also possible that genetic or developmental constraints preclude optimization, given that pollination by deceit is common within the genus *Begonia,* and may therefore be an ancestral trait for *B. involucrata.*

An interesting feature suggested by our models is frequency dependence. Natural selection will favor individual plants that produce female flowers of a size that has the highest probability of pollination. For example, in Model 1, probability of pollination, and therefore fitness, is highest for individuals with female flowers that are larger (Fig. 2d). However, as the frequency of large female flowers increases, the proportion of male flowers at that large size decreases, and therefore, reward per male flower, visitation rate, and probability of pollination also decrease. Thus, the most favorable female flower size oscillates as the population shifts towards the continually changing optimum. Since this appears to be a frequency dependent system in dynamic equilibrium and we only sampled at one point in time, one would expect that the observed female flower size distribution would not be at a stable optimum.

Our model assumed that pollinators are able to perceive and compare flowers sizes among all flowers in a population. However, pollinators may operate at smaller spatial scale, perhaps only comparing among nearby inflorescences or adjacent flowers. Given that there is heterogeneity among quadrats (Table 1), we may expect a different outcome from a model based on this scale.

To improve our model, future studies should determine the form of important relationships that we had to assume, such as reward versus male size and visitation rate versus polli-

nator reward. Future studies should also evaluate the other biological factors that may affect reproductive success of *B. involucrata*, such as dispersal and survival, as well as determine energetic costs associated with flower production. Longer-term studies could examine the possibility of yearly shifts in female flower size due to frequency dependence.

Pollination by deception requires complex strategies and tradeoffs that may be further complicated by physiological constraints. Individuals must balance energy expended in attracting pollinators with their other reproductive energy requirements such as seed production.

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THE EFFECT OF BARK MORPHOLOGY ON EPIPHYTE COMPOSITION AND ABUNDANCE

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Abstract: Diverse bark morphologies among trees in tropical cloud forests may be an adaptation to discourage epiphytic growth. Moss growth is influenced by moisture availability, while vine growth is affected by having suitable attachments. We investigated how rough and flaky bark morphologies affect the abundances of epiphytic mosses and vines. We predicted that rougher bark would support increased moss and vine growth, while flaky bark would encourage moss growth but discourage vine growth. Contrary to our predictions, mosses were most abundant at an intermediate bark roughness. Apparently, the roughest bark does not provide the best growing surface for moss, perhaps because deep bark grooves reduce water-retention. Roughness, as we measured it, actually seemed to hinder vine growth. Flakiness did not affect either vine or moss abundance. These results suggest that bark morphology is only a partial determinant of epiphyte composition and abundance.

Key words: evolutionary arms race, Monteverde, mosses, vines

INTRODUCTION

Particularly heavy epiphyte loads and a variety of bark morphologies that may have evolved in part to discourage epiphyte growth characterize trees in the pre-montane tropical cloud forest. Epiphytes can be detrimental to host trees in several ways: moss may provide a substrate for the establishment of heavier epiphytes that are structural parasites and vines may block sunlight to the tree (Forsyth and Miyata 1984).

Because epiphytes attach to trees via the bark, bark morphologies may affect epiphyte growth. Smooth bark sheds water which decreases moss coverage (Forsyth and Miyata 1984). Trees with rough bark are conducive to small vines that use tendrils to cling to small bumps or crevices (Forsyth and Miyata 1984). Flaky bark has increased water retention, which facilitates moss growth, but flaky bark may dislodge heavier epiphytes by sloughing off both bark and attached epiphytes (Kim et al. 1997). We examined the correlations between bark morphology and moss and vine growth, hypothesizing that bark morphology affects the composition and abundance of epiphytes on trees. We predicted that (1) as bark roughness increases, moss coverage and vine abundance will increase, and that (2) as flakiness increases, moss coverage will increase and vine abundance will decrease.

METHODS

We observed bark morphology and epiphytic distribution in 123 trees of the cloud forest above the Estación Biologia Monteverde, Costa Rica, on 22 - 23 January 2004. We sampled all trees that we encountered that matched the criteria of (1) 15 - 30 cm diameter and (2) growing at an elevation of 1520 - 1560 m. We measured flakiness by estimating the percentage of bark removed by a 2 x 10 cm strip of duct tape. We categorized roughness by the depth of grooves in the trunk on a relative scale of 0 to 3, with 0 being least rough. We focused our measurements of epiphyte distribution on mosses, lianas, and vines (the latter two hereafter combined and referred to as vines). We measured the percentage of moss coverage and the diameter of each vine on the trunk at 1 - 2 m height. Our flakiness measurement failed on the second day of data collection because of rain, which lessened the stickiness of the duct tape. Analyses of flakiness were restricted to the first day of

measurements (n = 70 trees).

We transformed vine area and flakiness as $\log_{10}(x + 1)$ to correct for non-normality. We calculated tree cross-sectional area (hereafter called tree size) from tree diameter, and vine area from the combined cross-sectional area of each vine, calculated from vine diameters. We standardized vine area and moss coverage by using the residuals of regressions that related each to tree size. We then evaluated all seven possible regression models predicting moss coverage residuals on vine area residuals based upon bark roughness, bark flakiness, and/or roughness*flakiness.

RESULTS

Epiphytes were abundant: mean ± SD = 27 ± 23% moss coverage and 3.0 ± 6.0 cm^2 of vines at 1 - 2 m height. Among the five variables measured on each tree, there were significant correlations between flakiness and roughness, tree size and roughness, tree size and moss coverage, and tree size and vine area (Table 1). Percent moss coverage decreased significantly with tree size ($r^2 = 0.08$, df = 122, P = 0.002; Fig. 1). Regression analyses of the residuals revealed that only roughness explained significant additional variance in moss coverage residuals, and a second-degree polynomial best described the relationship ($r^2 = 0.10$, df = 122, P = 0.002; Fig. 2).

Increasing tree size had a marginally significant positive effect on vine area ($r^2 = 0.03$, df = 122, P = 0.07; Fig. 3). The best model to predict vine area residuals was one that only included roughness, but this relationship was only marginally significant ($r^2 = 0.03$, df = 122, P < 0.06; Fig. 4).

DISCUSSION

Our prediction that moss coverage would increase with roughness was not supported by

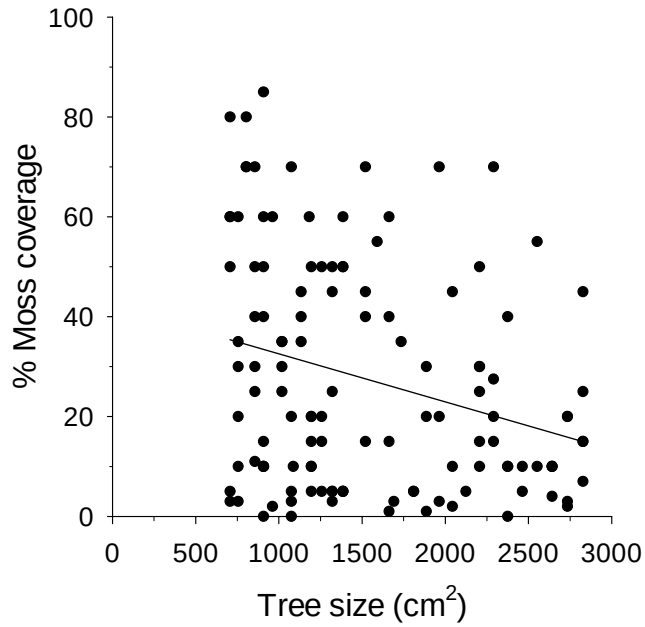

Figure 1. Moss coverage varies with tree cross-sectional area. Moss coverage decreases significantly with tree size (P = 0.002), so we analyzed residuals from this relationship instead of pure moss coverage.

Table 1. Correlations among tree characteristics.

	A	B	C	D	E
A. log(% flakiness + 1)	1.00	-	-	-	-
B. scale roughness	**0.41	1.00	-	-	-
C. log(vine area + 1)	0.07	-0.10	1.00	-	-
D. tree size	0.17	**0.37	*0.17	1.00	-
E. % moss coverage	0.17	0.08	-0.10	**-0.28	1.00

* P < 0.07; ** P < 0.05

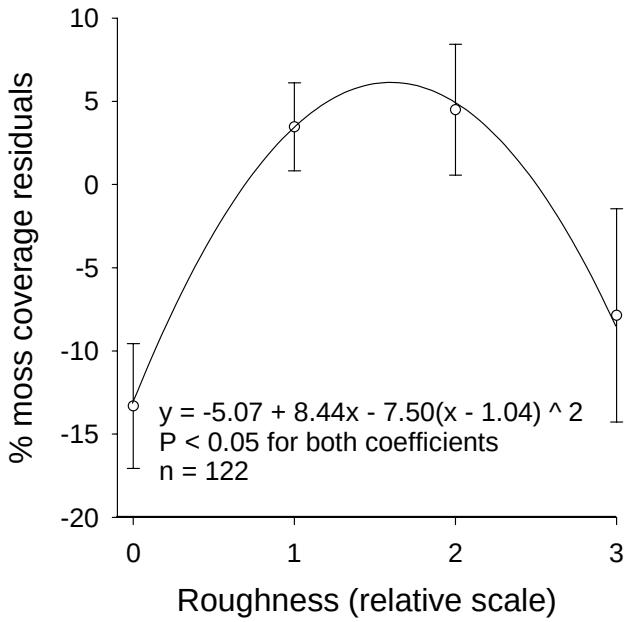

Figure 2. Percent moss coverage (residuals from Fig. 1) versus roughness (means ± SE for each roughness class).

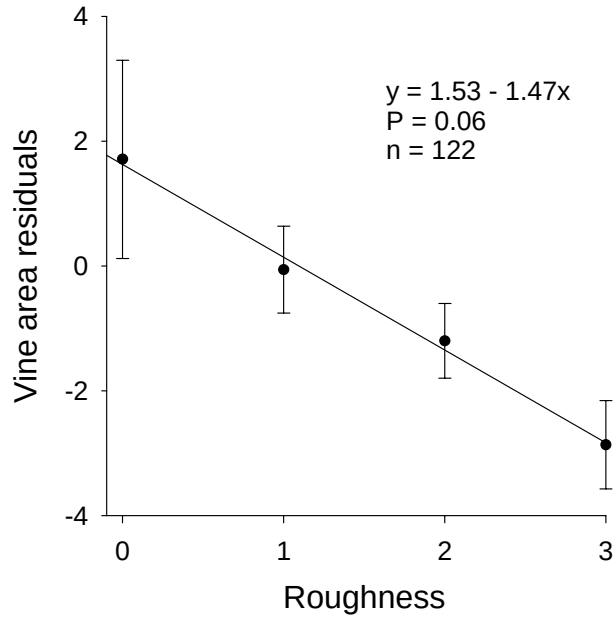

Figure 4. Vine area (residuals from Fig. 3) versus roughness (means ± SE for each roughness class).

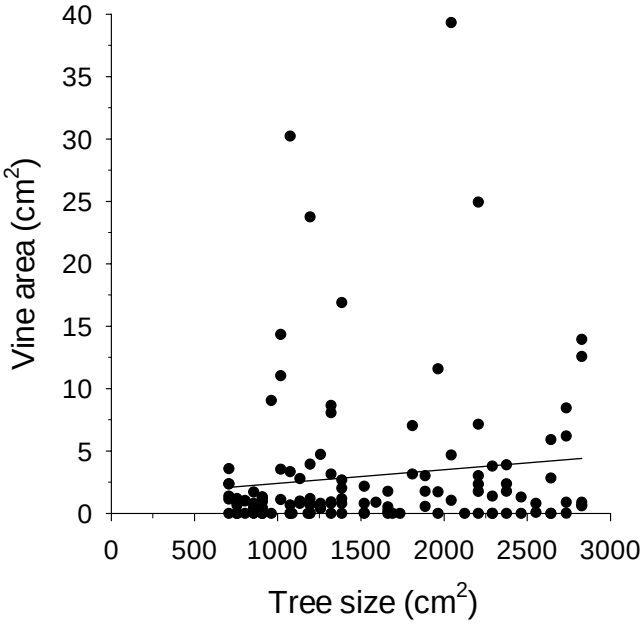

Figure 3. Correlation between tree size and vine area. Vine area varied marginally significantly (P = 0.07) with tree size, so subsequent analyses used residuals from this relationship.

these results. Percent moss coverage was highest at an intermediate roughness, suggesting that maximum roughness may not be the optimal growing conditions for moss. Deep grooves (more rough) may not increase the retention of water, and thus moss growth, as we predicted. Deep grooves may actually channel water, thereby discouraging moisture buildup and moss growth in the same manner as smooth bark. Examining stem flow as a function of bark morphology could test this possibility.

Although we predicted that rougher bark would provide better support to vine tendrils and thus encourage increased vine growth, our results indicated roughness hinders vine growth. Roughness on the scale measured in this study may not be relevant to vine tendrils. Perhaps vine tendrils need small-scale roughness or tiny crevices to attach. Conversely, large-scale roughness may create more barriers for the vines to grow across, costing the vine more energy and reducing vine area. Examining the correlation between small-scale roughness and vine area could test this hypothesis.

Flakiness did not have a significant effect on moss coverage, which refutes our prediction that bark flakiness would encourage moss growth. Flakiness may not influence water retention as we had speculated. Also, moss may be too light to be affected by loose flakes. Bark flakiness may only be an effective deterrent of

heavier epiphytic growth, such as the bromeliads or orchids that are facilitated by mosses (Forsyth and Miyata 1984). Kim et al. (1997) supported this idea by noting differences in bromeliad and orchid abundances between trees with shedding and non-shedding bark. Flakiness may not have any effect on moss growth except when moss encourages heavier epiphytes capable of tearing flakes off the tree. The relationship between moss growth, heavy epiphyte growth, and bark morphology would be an interesting area for further research.

Our results also refuted the prediction that flakiness would discourage vine growth, perhaps because flakes cannot slough off vines completely as long as they have several strong holds on the tree. We noted several vines with free-hanging tendrils that had visible bark pieces attached. Examining vine attachment mechanisms and bark morphology may test this hypothesis.

Our results suggest that bark morphology is not the single determining factor of moss and vine growth on mid-elevation cloud forest trees. Trees and epiphytes may be taking part in an evolutionary arms race to compete for light and nutrients: the trees struggle to remove epiphyte growth while the epiphytes fight to remain and grow. Our results seem to indicate that epiphytes are generally successful at growing on trees. Other factors, such as tree shape, bark chemistry, and microhabitat may combine with bark morphology to affect epiphyte growth. In addition, bark morphology serves functions other than discouraging epiphyte loads, such as preventing insect infestation or fungal growth. Our study examined the effects of bark morphology in only one environment with necessarily subjective measurements of flakiness and roughness. A broader study, including a larger environmental range and more varieties of epiphytic growth, could better define the effects of bark morphology on epiphytes.

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DO BUTTRESSES CONFER A COMPETITIVE ADVANTAGE FOR TROPICAL TREES?

R. QUINN THOMAS AND SARA M. HELLMUTH

Abstract: Many hypotheses have been proposed to explain why some tropical trees form buttresses. We examined the competitive advantage hypothesis, which predicts that buttressed trees will have fewer surrounding trees and fewer vines. However, we found no difference in basal area or number of saplings surrounding buttressed versus non-buttressed trees. Additionally, we found that the two tree types did not differ in vine abundance. Our results tend to refute the competitive advantage hypothesis for buttressed trees in the Monteverde region. Further research on the function of buttresses should focus on other explanations.

Key words: basal area, Monteverde, vines

INTRODUCTION

There has been a continuing debate over why some tropical trees form buttresses. An early explanation was that buttresses provide structural stability (Janzen 1983). However, this hypothesis has failed some tests (Young and Perkocha 1994, Bansak et al. 1993). Black and Harper (1979) proposed (1) that buttresses prevent competing trees from growing in the space that the buttresses occupy around the base of the trunk and (2) that buttresses deter potentially harmful vines from growing on the trunk by forcing the vines to deplete their resources growing over the buttresses, and by severing vines as the buttresses grow outward. To test this competitive advantage hypothesis, we evaluated the predictions that tree and sapling abundance around buttressed trees would be fewer than around non-buttressed trees, and that buttressed trees would have fewer vines growing on them than would non-buttressed trees.

METHODS

We examined the saplings and tree density around 15 buttressed and 15 non-buttressed trees on 22 - 23 January 2004 in a pre-montane cloud forest at Monteverde Biological Station, Costa Rica. Buttressed trees were selected by walking the trails around the station and measuring trees (at least 2 m off the trail) that appeared to be buttressed. For each buttressed tree, we selected the closest non-buttressed tree of a similar diameter (sans buttresses). We calculated a buttress index for each tree as *diameter at ground level / diameter at breast height.* To quantify competition, we measured the number of vines growing on each trunk, basal area (of trees) using a 10X forestry prism (count x 10 = ft^2/ acre), and the number of saplings (DBH < 6 cm) within a 2 m radius of each tree (saplings were not included in basal area measurements). We measured vine abundance by counting the number of vines attached to the tree at breast height, and classified vines into three size classes based on diameter (< 2 cm, 2 - 4 cm, > 4 cm). An index of vine abundance (IVA) was created to account for the increasing impacts of larger sized vines: IVA = *(# of size class one vines + (# of size class two vines * 2) + (# of size class three vines * 3))*. We measured the percent canopy cover beneath each focal tree by taking four measurements with a spherical densiometer, one at each cardinal direction around the focal tree, 1 m from the trunk. Prior to analyses, the number of saplings and the vine index were log-transformed to improve normality.

RESULTS

The buttress index ranged from 0.85 to 1.75 for trees that we classified *a priori* as not buttressed and from 1.64 to 4.02 for trees that we classified as buttressed. Because the natural variation in the extent of buttresses appeared to be continuous rather than categorical, all our subsequent statistical analyses used buttress index instead of the buttress type category. Buttress index was not significantly correlated with basal area, number of saplings, or vine index (Fig. 1; Table 1). None of the possible linear regression models involving buttress index and/or percent open canopy explained significant variation in basal area, number of saplings, or vine index.

DISCUSSION

Our findings tend to refute the hypothesis that buttresses provide a competitive advantage by preventing the establishment of competitive trees and decreasing vine abundance. However, one limitation to our study was our

Table 1. Correlation matrix between buttress index, percent open canopy, basal area, log (# of saplings), and log (vine index)

	A	B	C	D
A. Buttress index	-	-	-	-
B. Percent open canopy	- 0.02	-	-	-
C. Basal area	- 0.03	- 0.10	-	-
D. Log (# of saplings)	- 0.06	- 0.25	0.45 *	-
E. Log (vine index)	- 0.07	0.35	- 0.47 *	- 0.47*

* P < 0.05

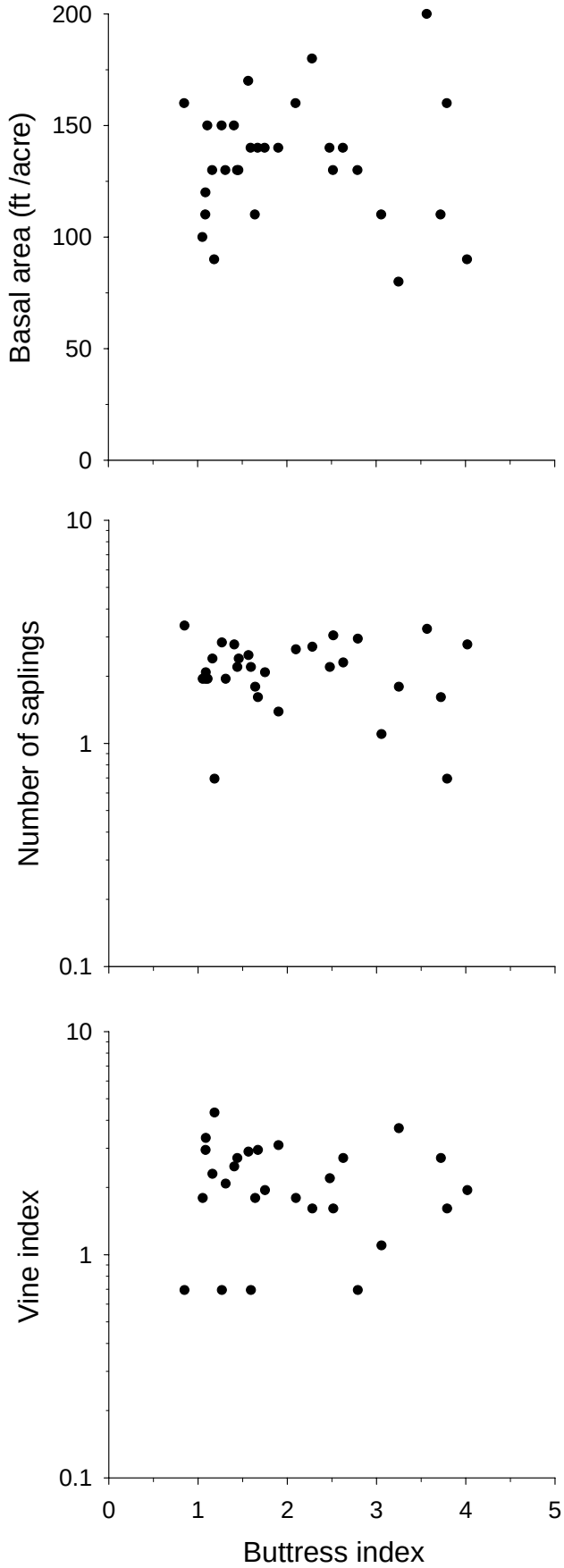

Figure 1. Extent of buttressing was unrelated to basal area (top), number of saplings (middle), or vine index (bottom).

definition and measurement of vine abundance. We could not differentiate between vine-like growth forms that germinate in the canopy and those that establish themselves in the ground first. The vines establishing in the ground are what we expected to be harmed by buttresses because expanding buttresses could sever their roots. There would be value in future studies that focus on vines that establish on the ground

If buttresses are not just for structural support, and if the competitive advantage hypothesis is rejected, some other explanation is needed for the prevalence of buttresses in tropical forests. One possibility is that buttresses can collect leaf litter, thus improving soil quality immediately beneath the tree and facilitating growth (Dallison et al. 1999).

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THE EFFECT OF DISTURBANCE ON EPILITHIC PLANT COMMUNITIES ALONG STREAMS

LUKE EVANS, BRENDA WHITED, HEATHER LAPIN AND MATTHEW KEMP

Abstract: Disturbance regimes strongly influence the structure and diversity of plant communities. We tested theories of succession and diversity on the plant community that occupies boulders in a Costa Rican cloud forest stream. We hypothesized that vascular plants would replace non-vascular plants as height above water increased, and that total species richness and evenness would be greatest at medium height above water (i.e., at a height that experienced intermediate disturbance frequencies). As predicted, vascular plants replaced non-vascular plants as height above water increased, and species richness of non-vascular plants was highest at intermediate heights. However, overall plant richness and evenness continued to increase over the full height gradient we measured. The intermediate disturbance hypothesis offers a promising conceptual framework for understanding these epilithic plant communities, but further studies are needed to test the predicted mechanisms, and evaluate the apparent inconsistencies.

Key words: diversity, intermediate disturbance hypothesis, non-vascular, species richness, succession, vascular

INTRODUCTION

Disturbance regimes strongly influence the structure and diversity of many plant communities, from fires in grasslands to windblown treefalls in mature forests (Begon et al. 1986). The frequency of disturbance can alter the species composition of a community greatly. Where disturbances are frequent, late-successional species will be unable to establish themselves and pioneer species will dominate. However, where disturbances are infrequent, pioneer species cannot compete with late-successional species, which will then dominate. Thus, the Intermediate Disturbance Hypothesis states that species diversity is maximized at intermediate disturbance frequencies, which allow both early- and late-successional species to co-exist.

We tested this hypothesis using the non-vascular and vascular plant community growing above water on boulders within a tropical cloud forest stream. The plant community experiences disturbance periodically as the water level rises. Lower plants on the rocks experience more frequent disturbances than those higher on the rock. We hypothesized that species richness (total number of species) and evenness (the distribution of individuals across species) would be greatest at medium height (i.e., a height where the frequency of disturbance was intermediate).

As succession is a facet of the Intermediate Disturbance Hypothesis, we also tested for evidence of succession in this system. Non-vascular plants (mosses and liverworts) are likely early successional species because they can effectively colonize and grow on bare rock. Vascular plants (ferns and flowering plants) are only able to grow on the boulders after sufficient dirt or organic matter has collected, and therefore would be late successional species because they competitively dominate the prostrate non-vascular plants by usurping the available light. Thus we predicted that maximum non-vascular plant richness would occur at a lower height than maximum vascular plant richness, and that vascular plants would replace non-vascular plants as height above water increased.

METHODS

We conducted our study in Quebrada Móquina, south of the Monteverde Biological

Station on 22 - 23 January 2004. We studied ten stream boulders that sometimes experienced disturbance when they were partly submerged during peaks of stream discharge, and were of a size that supported a community of vascular and non-vascular plants. We standardized the intensity of disturbance by studying the upstream face of each boulder, which was greater than 90° to the water. The size of each face was at least 0.50 x 0.60 m.

We placed a series of horizontal transects parallel to the waterline, each transect consisting of 11 points, 5 cm apart. We began at waterline and placed one transect every 5 cm vertically up to 100 cm above waterline, or on smaller rocks, to the top of the rock. We recorded each plant morphotype that occurred at each of the 11 points on each transect (i.e., each plant species that would be penetrated by an imaginary needle striking the rock perpendicular to the rock surface). If plants overlapped at a point, all were included.

Richness was calculated as the total number species along each 50 cm transect above the water level. Evenness was calculated as equitability ($J = H' / H'_{max} = - \sum(p_i * ln(p_i)) / ln(\# spp.)$) for each 50 cm transect above the water level. We evaluated 2nd order polynomial regressions to test for the predicted pattern of a nonlinear unimodal relationship between species richness and height above water (presumed index of disturbance frequency). Second order models were accepted and reported if both coefficients in the regression model (for height and height^2) were significantly different than zero.

RESULTS

Non-vascular plant species richness showed a unimodal relationship with height above water, peaking at 60 cm ($P < 0.0001$; Fig 1a). Vascular plants did not appear until 20 cm above water, after which richness increased linearly with height ($P < 0.001$; Fig 1a). Non-vascular plant abundance was hump-shaped, peaking at 60 cm above water, while vascular plants began to increase linearly at 20 cm above water, eventually replacing non-vascular plants ($P < 0.0001$ for both non-vascular plants and vascular plants; Fig 1b). Total plant species' rich-

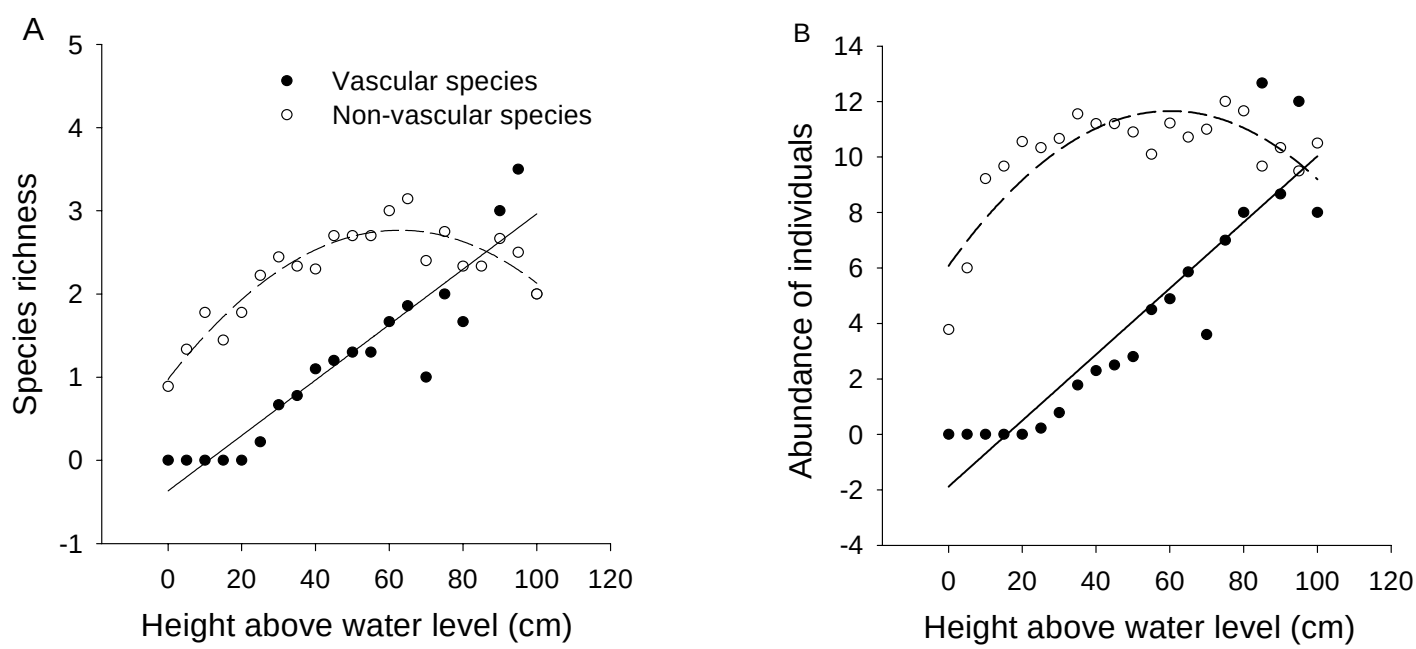

Figure 1. (A) Mean species richness of each height above water level from ten rocks for non-vascular plants ($r^2 = 0.26$) and vascular plants ($r^2 = 0.50$). (B) Mean total abundance of individuals of each height above water from ten rocks for non vascular plants ($r^2 = 0.68$) and vascular plants ($r^2 = 0.49$).

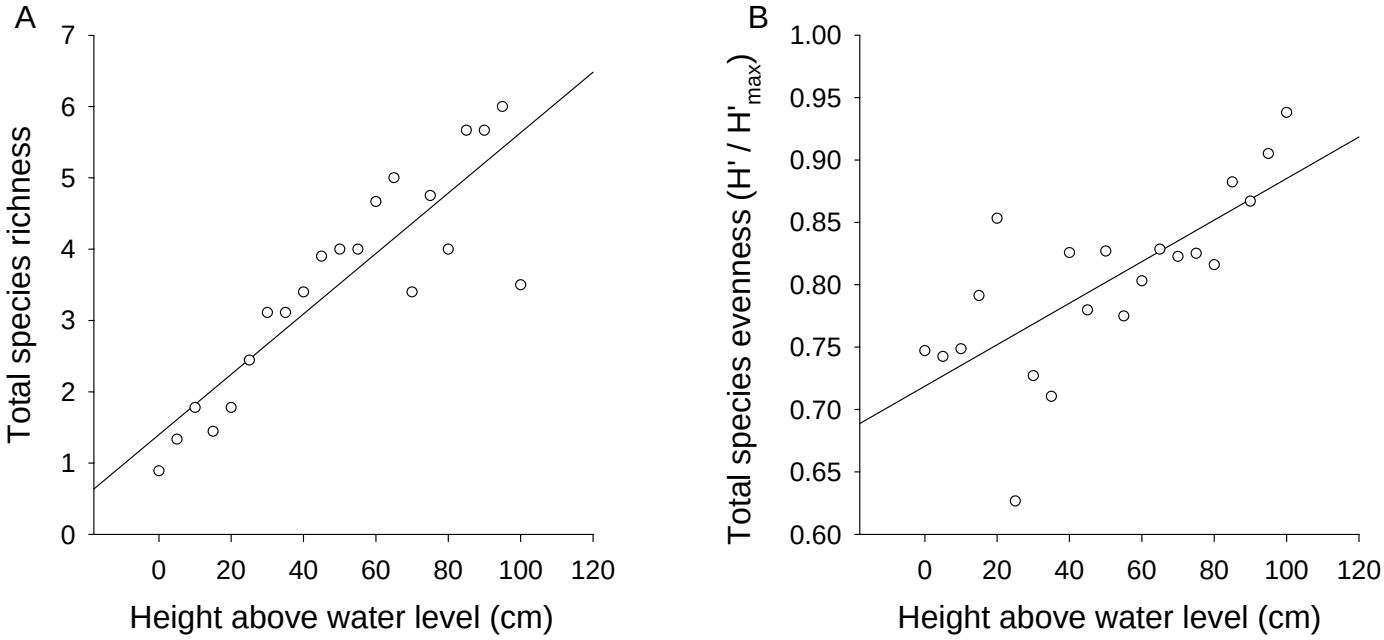

Figure 2. (A) Mean species richness of each height above water level from ten rocks ($r^2 = 0.49$). (B) Mean species evenness of each height above water from ten rocks ($r^2 = 0.09$).

ness and evenness (including both vascular and non-vascular plants) increased linearly with height above water level ($P < 0.0001$, $P = 0.0002$ for richness and evenness respectively; Fig 2).

DISCUSSION

The Intermediate Disturbance Hypothesis was partly supported in that species richness of non-vascular plants was greatest at medium frequencies of disturbance. The suggestion is that disturbances at medium heights were frequent enough to maintain pioneer non-vascular plant species, but infrequent enough to allow late-successional non-vascular plant species to dominate. However, we did not test competitive dominance among species, so we cannot specifically evaluate these details of succession mechanisms within the non-vascular plant community.

Vascular species richness as well as total species richness and evenness increased linearly across the full range of height above water, which did not support our predictions from the Intermediate Disturbance Hypothesis. This might be because niche partitioning increases at lower disturbance frequencies, and the diversification of niches in stable environments outweighs richness contributions from having a mix of successional strategies. Alternatively, it is possible that we did not take measurements far enough along the disturbance-stability continuum (at locations high enough above the water line) to allow for the decrease in richness and evenness that is expected due to competitive exclusion (Begon et. al., 1986).

Our results revealed an apparent successional pattern in which non-vascular plants tend to dominate on lower, more frequently disturbed rock faces; they can be regarded as the pioneer species. This is consistent with the typical life history of non-vascular plants in that they are able to survive on bare rocks. Non-vascular plants then provide a substrate for vascular plants to germinate upon (facilitation), which would be expected in areas with infrequent disturbances. Vascular plants did replace non-vascular plants at heights with less frequent disturbances, and this suggests they are the late-successional species. Further studies would be

needed to test corollaries regarding the colonization and competitive ability of these plants.

Our study supported the Intermediate Disturbance Hypothesis in part, and indicated that different frequencies of disturbance can maintain a series of successional stages in a community. However, there are undoubtedly other factors that affect diversity. For example, intensity of disturbance was not evaluated as part of our research, and neither did we consider effects of different micro-environments within stream rock communities, such as light, and orientation to the flow of water.

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THE EFFECTS OF TANK WATER VOLUME ON COMMUNITY ABUNDANCE IN *GUZMANIA*

STEPHEN WELLER AND SCOTT CUSHMAN

Abstract: The abundance of macro-invertebrates in bromeliad tanks in *Guzmania monostachyia* has been shown to be positively correlated to the volume of detritus and water in the tank. *G. monostachyia* occur on both sides of the continental divide in the Monteverde Biological Preserve, where they are subject to different precipitation. Because detritus input should be similar between the two slopes, this provided a means of separating the effects of water and detritus on tank fauna. We measured water volume, detritus dry mass and macro-invertebrate abundance and diversity for eight *G. monostachyias* on each slope. Caribbean tanks had higher water volumes, but there was no difference between the slopes in the number of macro-invertebrates. As predicted, detritus mass did not differ between slopes. There was a significant positive correlation between detritus dry mass and macro-invertebrate abundance on the Pacific slope, but, not on the Caribbean slope. The lack of water and very low number of inhabitants was in stark contrast to previous studies. The frequency and duration of droughts in tank bromeliads might be quite important for the structure of tank communities. Recent decreases in regional precipitation might be making such droughts more common.

Key words: Caribbean slope, macro-invertebrates, Monteverde, Pacific slope, phytotelmata

INTRODUCTION

Phytotelmata are a common source of standing water in forest ecosystems, and provide habitat and breeding grounds for multiple macroorganisms (Varga 1928). Tank bromeliads such as *Guzmania monostachyia* (Bromeliaceae) are important phytotelmata in areas with high levels of atmospheric moisture and precipitation. *G. monostachyia* is an epiphytic plant that collects water and detritus in a tank created by its interlocking leaves, and can support a community of insect larvae, zooplankton, and other invertebrates (Forsyth and Miata 1984, Yanoviak 2001). Previous studies have shown that the volume of both detritus and water in the tanks influence the abundance of organisms in the tank communities (Yanoviak 2001, Licona 2003). Tank bromeliads occur on both the Caribbean and Pacific slopes of the continental divide in the Monteverde Biological Preserve, Costa Rica. The two slopes are subject to different moisture regimes. The prevailing easterly winds from the Caribbean Sea drive clouds up the Caribbean slope, where precipitation is generated as moist air rises and cools. The air masses continue across the divide to the Pacific slope with a reduced moisture load. We hypothesized that *G. monostachyia* would have higher water volumes on the Caribbean slope than on the Pacific slope, and that the organismal abundance in the tank communities would be higher as a result of the greater water volume.

METHODS

On 22 January 2004, within the Monteverde Biological Preserve, Monteverde, Costa Rica, we sampled eight bromeliads on the Pacific side of the continental divide and eight on the Caribbean side. Sampling occurred at 1700 - 1720 m elevation, on plants that were 0.5 ± 0.1 m at their greatest diameter from leaf tip to leaf tip. We removed all detrital matter and visible organisms with forceps before collecting water from the tanks using a 600 cc syringe and surgical tubing.

For each bromeliad, we weighed (1) the water, and (2) the water plus all detritus and macroorganisms. Using a dissecting microscope, we removed and identified (to morphotype) all macroscopic organisms in our samples.

We then dried the detritus to determine its dry mass.

RESULTS

In *G. monostachyia* tanks of similar size, water volume was low overall (0 - 1.74 mL/tank) but was modestly higher on the Caribbean slope than on the Pacific slope ($F_{1,14} = 3.60$, $P = 0.079$; Fig. 1). The amount of detritus did not differ between the Caribbean and Pacific slope ($F_{1,14} = 0.016$, $P = 0.90$; Fig. 1). There were surprisingly few invertebrates within the tanks (total of 16 individuals, representing seven recognizable taxa, within 16 tanks; Table 1). The fauna, including chironomids of the diptera family, appeared to be normal inhabitants of bromeliad phytotelmata, and not incidental captures from the terrestrial environment. The number of individual organisms per tank did not differ between slopes ($F_{1,14} = 1.80$, $P = 0.21$; Fig. 2).

There was a positive correlation between organismal abundance and detrital load on the Pacific slope ($P = 0.04$), but not on the Caribbean slope ($P= 0.16$; Fig. 3). There were no other significant correlations, on either slope, among water volume, number of organisms, and detrital mass ($P > 0.50$).

Table 1. Total captures of macroorganisms in eight tanks of *G. monostachyia* on either slope.

	Caribbean slope	Pacific slope
Dipterans	4	1
Nematoda	2	2
Hemiptera	1	1
Eubrachiopoda	1	1
Isopoda	1	0
Coleoptera	1	0
Copepoda	0	1

DISCUSSION

The lack of water in bromeliad tanks was surprising. There was a major discrepancy between the water volumes found in our study (largest volume = 1.74 mL) and those of Licona et al. (2003), who reported volumes of 31 - 189 mL in approximately the same population of tank bromeliads. While a simple lack of precipitation over a week may explain our low volumes, Lawton, et al. (2001) suggests that lowland deforestation may be systematically reducing the amount of rainfall received at Monteverde.

We found macro-invertebrate abundances in the tank communities to be very low. Licona et al. (2003) found abundances of 10 - 299 individuals *per tank sampled*, while our total catch for 16 plants was 16 individuals. A portion of the fauna found by Licona et al. (2003) were probably facultative inhabitants of phyto-

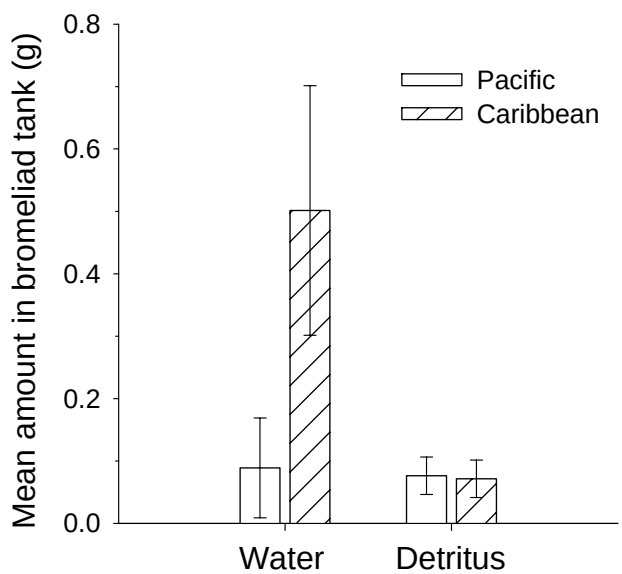

Figure 1. Mass of water and dry detritus (± SE) in the central tanks of G. monostachyia bromeliads on the Carribean slope versus the Pacific slope.

telmata. We found so few organisms in total that it is impossible to judge whether we found a lower or higher proportional representation of obligate inhabitants of phytotelmata. However, with the low water volumes found in our study, it is possible that facultative inhabitants were largely absent, and even obligate macro-invertebrates exhibited low abundances in drier conditions.

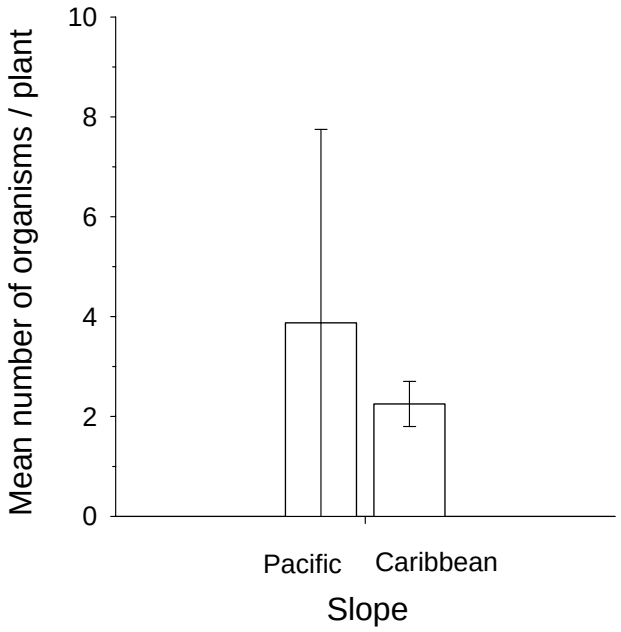

Figure 2. Mean number of organisms (± SE) per *G. monostachyia* tank on Carribean and Pacific slopes.

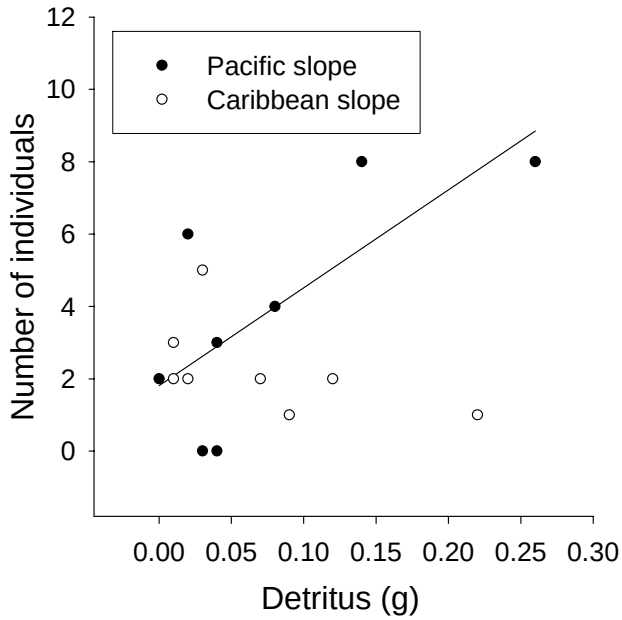

Figure 3. Number of individuals vs. detritus mass within tank bromeliads. Regression for Pacific slope: y = 0.019x + 0.002, r^2 = 0.52. There was no correlation on the Caribbean slope (no line shown).

The severe lack of water and very low organismal abundance of inhabitants prevented us from obtaining a satisfying comparison of Pacific vs. Caribbean fauna. However, the interested unexpected result was that tank bromeliad communities in this environment could be so impoverished. Even at the continental divide, it seems that neither precipitation nor condensation were enough to provide tank water volumes necessary for what we assumed to be the normal tank fauna (Laconia et al. 2003). While this may be a function of a brief lack in precipitation, our data could be a biological harbinger of Lawton et al.'s (2001) suggestion that regional precipitation is declining due to deforestation. Future studies could investigate the bromeliad community to determine if the stark contrasts between our study and 2003's study (Licona et al.) are a simple year to year variation or the sign of a broader and potentially significant change in biological communities.

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