THE EFFECT OF DISTURBANCE ON EPILITHIC PLANT COMMUNITIES ALONG STREAMS

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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-

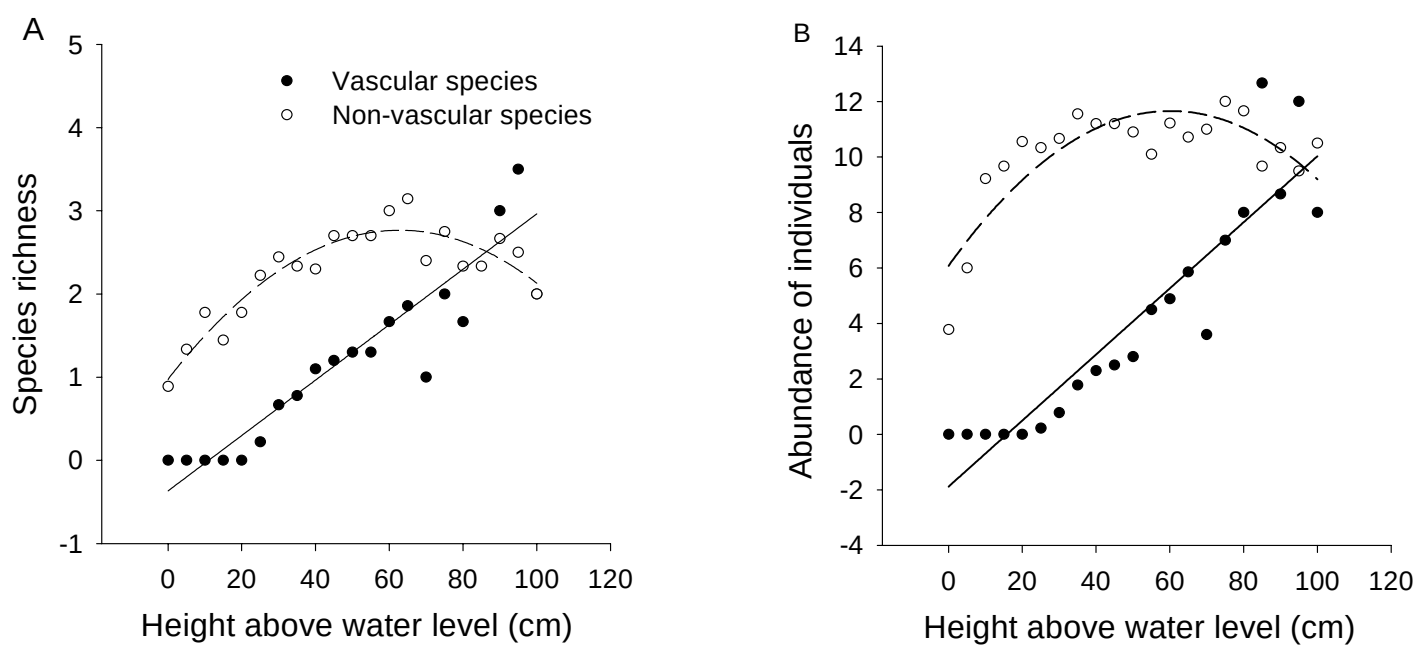

Figure 1. (A) Mean species richness of each height above water level from ten rocks for non-vascular plants ($r^2 = 0.26$) and vascular plants ($r^2 = 0.50$). (B) Mean total abundance of individuals of each height above water from ten rocks for non vascular plants ($r^2 = 0.68$) and vascular plants ($r^2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

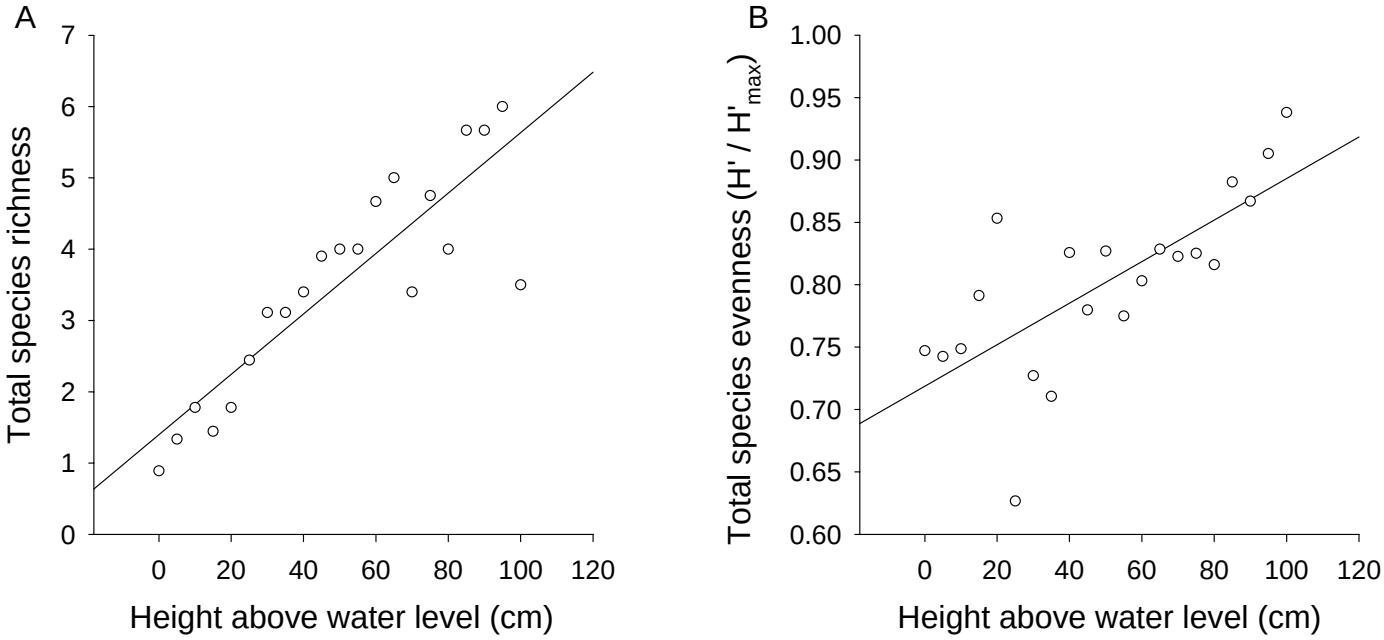

Figure 2. (A) Mean species richness of each height above water level from ten rocks ($r^2 = 0.49$). (B) Mean species evenness of each height above water from ten rocks ($r^2 = 0.09$).

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.

LITERATURE CITED

Begon, M., J. L. Harper and C. R. Townsend. 1990. Ecology: individuals, populations and communities. Second edition. Blackwell Scientific Publications: Cambridge, MA.