Distribution patterns of the tree ferns Alsophila erinacea and *A. polystichoides* (Cyatheaceae) in cloud forests of Monteverde, Costa Rica

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Abstract

The effects of elevation on the tree ferns *Alsophila erinacea* and *A. polystichoides* (Cyatheaceae) distributions were examined between 1550 m and 1800 m in Monteverde, Costa Rica. *Alsophila erinacea* and *A. polystichoides* prefer similar habitat types and overlap almost completely in their elevational ranges, making them ideal species for comparison. Six transects were made in each of five-50 m elevational blocks between 1550 m and 1800 m for a total of 30 transects. Transects along a ridge trail were compared with those on a trail on the side of a slope and were found to contain considerably less *Alsophila* tree ferns at all elevations (a total of 5 individuals on six ridge transects compared with 36 individuals on four slope transects). There was a slight decrease in these two species' abundances on an increasing elevational gradient. Both species of fern were found to be patchy based on an index of dispersion, Poisson comparison, and Chi-squared tests (X^2 = 710 and 33063; df = 9 and 18; P = 0.001 and 0.001 for *A. erinacea* and *A. polystichoides* respectively). Finally, microclimate variations likely did more to influence *A. erinacea* and *A. polystichoides* distributions than did elevation.

Resumen

Se examinaron los efectos de la elevación en los helechos *Alsophila erinacea* y *A. polystichoides* (Cyatheaceae) entre 1550 m y 1800 m en Monteverde, Costa Rica. Estos helechos prefieren tipos de hábitat similares y se traslapan casi completamente en sus ámbitos altitudinales. Por esta razón *A. erinacea y A. polystichoides* son especies buenas para comparar. Se hicieron seis transectos en cinco bloques de elevación, de 50 m cada uno, entre 1550 m y 1800 m para un total de 30 transectos. Se compararon los transectos a lo largo de un sendero en una cresta con los de un sendero empinado y se encontró muchos menos helechos *Alsophila* en todas las elevaciones de la cresta (cinco individuos en seis transectos de la cresta comparados con 36 individuos en cuatro transectos de la cuesta). Hubo una leve disminución en la abundancia de estas dos especies del helecho en un gradiente de elevación ascendente. Se encontró que las dos especies de helecho están agrupadas con base en el índice de dispersión, el test de comparación Poisson, y el test Chi-cuadrado (X^2 = 710 y 33063; df = 9 y 18; P = 0.001 y 0.001 para *A. erinacea* y *A. polystichoides* respectivamente). Finalmente las variaciones en el microclima influyeron más las distribuciones que la elevación.

Introduction

Elevation is known to have a significant influence on community composition and species abundances in tropical forests (Kappelle and Gomez 1992; Lee et al. 1986; Lieberman et al. 1996). In general, tree fern abundances tend to increase slightly with increases in elevation (Gomez 1983). For two Cyatheaceae ferns, A. *erinacea* and A. *polystichoides,* the role of elevation in their abundances and distributions is largely unknown. These two species have overlapping elevational ranges (800m - 2100m for A. *erinacea,* and 700m - 2000m for A. *polystichoides)* and both are forest understory or riverbank trees making them ideal species for comparison (Rojas 1999).

By comparing these two species, one can determine how closely related tree ferns interact with each other. Direct competition, facilitation, and allelopathic inhibition are all possible interactions to consider between these two species. Direct competition would be a result of one species using a resource thereby limiting the resource availability for the other species (Ricklefs 1990). Facilitation would result from the activities of one species enhancing the population of the other species (Ricklefs 1990). Because these two tree fern species prefer the same habitats and have similar growth forms, one of these two interactions is likely to occur. Finally, allelopathy is a known mechanism in some ferns for eliminating other plants by inhibiting germination, growth and/or development (Cooper-Driver 1980). Thus it makes sense that the presence of one species of tree fern may limit the presence of the other.

The purpose of this study was to determine whether elevation affected the abundances of these two species and to determine the distributions of each. One would predict that, based on some of the above mentioned experiments, abundances for these tree ferns would increase on an elevational gradient, and that they would limit each other's abundance due to similar habitat selection, similar growth habits, and allelopathic inhibition.

Study Site and Methods

Thirty transects were made between 1550m and 1800m in both leeward cloud forest and elfin forest behind the Estación Biológica de Monteverde (EBM) and the Centro de Educación Creativa (CEC) in Monteverde, Costa Rica. Five 50-meter elevational blocks were established between 1550m and 1800m using a handheld altimeter. For each elevational block a total of six transects were made, three on CEC property and three on EBM property up to 1750m. For the 1750m - 1800m block all six transects were made on EBM land as CEC trails did not reach this elevation. Both CEC and EBM transects included one on-trail transect and two off-trail transects. The CEC on-trail transects all were located along a ridge whereas the EBM on-trail transects were on the side of a slope (except for the 1750m - 1800m transect of course). The on-trail transects were 125 meters long and extended two meters into the forest on either side of the trail for a total of $500m^2$. In each case 125 meters were measured down slope

along the trail from the upper limit of the elevation block. The off-trail transects were made on plots 25 meters long and ten meters wide, also for a total of 500m^2. Each transect had to begin and end in the same elevational block, and the off trail transects began two meters out from the trail so as not to overlap the trail transects. Slope, aspect, and nearest neighbor distances were measured for each tree fern found in a transect. Nearest neighbor distances were rounded to the nearest whole meter.

An index of dispersion was taken for the nearest neighbor values. Chi-squared tests were used to determine whether or not A. *polystichoides* and A. *erinacea* tended to occur in the presence or absence of one another. A Chi-squared test was also used to compare each tree fern's frequency distribution against a Poisson distribution to determine whether or not distributions were random. Formulas for index of dispersion and Poisson distribution were taken from Southwood (1978).

Results

I found a total of 100 *Alsophila* tree ferns in my 30 transects (81 A. *erinacea* individuals and 19 A. *polystichoides* individuals. Both A. *polystichoides* and *Alsophila erinacea* abundances seemed to decrease along an elevational gradient (Figure 1). 1550 m -1600 m had the highest total *Alsophila* abundance (27 individuals) as well as the most A. *erinacea* (22 individuals). *Alsophila polystichoides* was most abundant in the 1600 m - 1650 m block with 7 individuals. The fewest individuals of each species were found in the 1650 m -1700 m block, 11 individuals for A. *erinacea* and one individual for A. *polystichoides.* Both species *of Alsophila* appeared to prefer moderate slopes (30-60 degrees), and aspects from South-East (100 degrees from North) to South-West (250 degrees from North) (Figure 2). Overall, transects made on land behind the Estación Biológica de Monteverde contained more *Alsophila* of both species than the Centro de Educación Creativa land. Specifically, ridge-line transects, most of which were on CEC property, contained far fewer individuals (five individuals) than the trail transects on the slope of EBM property (36 individuals) despite being sampled more (six ridge transects compared to four slope transects).

The index of dispersion for A. *erinacea* and A. *polystichoides* was 570 and 158 respectively, which makes both species significantly 'patchy', or non-randomly dispersed (for A. *erinacea* and A. *polystichoides* respectively: df = 80, 18; $P < 0.001, 0.001$). The Poisson distribution comparison also demonstrates this 'patchiness' (for A. *erinacea* and A. *polystichoides* respectively: $X^2 = 710$ and 33,063; df = 9, 18; $P < 0.001, < 0.001$). 88.9 percent (72 of 81 individuals) of A. *erinacea* and 73.7 percent (14 of 19 individuals) of A. *polystichoides* were within ten meters of a conspecific individual (Figure 3). Although A. *erinacea* was encountered separately from A. *polystichoides* in 14 of 30 transects (47% of the time), A. *polystichoides* never occurred without A. *erinacea* in all 30 transects; these findings were significant ($X^2 = 14.27$; df = 3; $P = 0.005$).

Discussion

I expected the distributions *of Alsophila erinacea* and *Alsophila polystichoides* to increase with elevation and to niche partition so that neither would be found in the same place as the other. The data I found do not support this hypothesis. There was an overall decrease in abundances for both species on an elevational gradient, and a much lower abundance for both in the 1650 m -1700 m block (Figure 1). While these findings do contradict my hypothesis and the general findings of Lee et al. 1986, they may be consistent with other studies that show 'life form' abundance in general varies greatly over elevational gradients (Lieberman et al. 1996). There is also evidence that tree ferns are strongly dependent on microhabitat characteristics such as presence of light gaps, water availability, and slope (Gomez 1983). These dependencies may be more important than mere changes in elevation in encountering these two species of tree fern, and may explain the lower abundances of both in the 1650m - 1700m block (perhaps fewer ideal microhabitats were encountered on these transects).

The co-occurrence of *A. polystichoides* with *A. erinacea* throughout these transects suggests a lack of significant partitioning of space. If these species were partitioning space we would expect to find them separate from each other most of the time. The lower abundance of *A. polystichoides* in each elevation suggests it is outcompeted by A. *erinacea* for space, however, this study does not overwhelmingly support this hypothesis, nor does it rule out facilitation as a viable interaction. More studies need to be done across these ferns' elevational ranges as well as in ideal *Alsophila* habitat (wet areas, light gaps) to better understand the dynamics of the relationship between *A. erinacea* and *A. polystichoides.*

I determined both species of tree fern to be patchily distributed using index of dispersion, Poisson distribution, and the Chi-squared tests, and that they tended to be within 11 meters of conspecifics. These results could give support to the hypothesis that microhabitat was perhaps more important than elevation in examining abundances. For example, light gaps or water drainages could cause *A. erinacea* or A. *polystichoides* individuals to clump together in the same habitat. It also appears that the habitat on ridges is far less favorable than habitat on slopes (see Results). Ridges tend to have drier and warmer conditions than canyons on the Pacific side and are especially vulnerable to desiccating trade winds during the dry season (Haber 2000). We may expect this drop in tree fern abundances along the ridges considering they prefer wet environments (Gomez 1983). It is clear that any future studies on an elevational gradient should consider these microclimate associations more closely.

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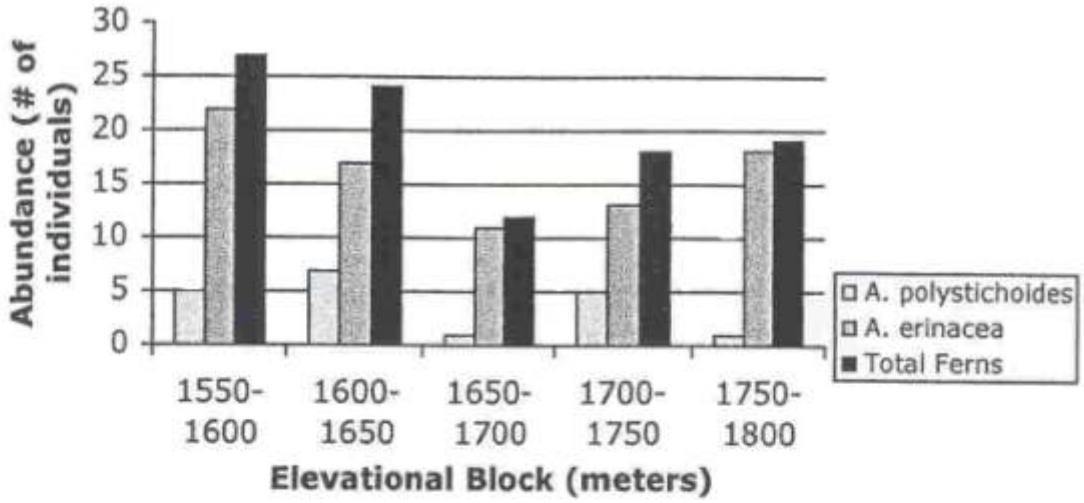

Figure 1. *Elevational block abundances of Alsophila erinacea and Alsophila polystichoides between 1550m and 1800m. Abundances for each fern species decrease overall as elevation increases.*

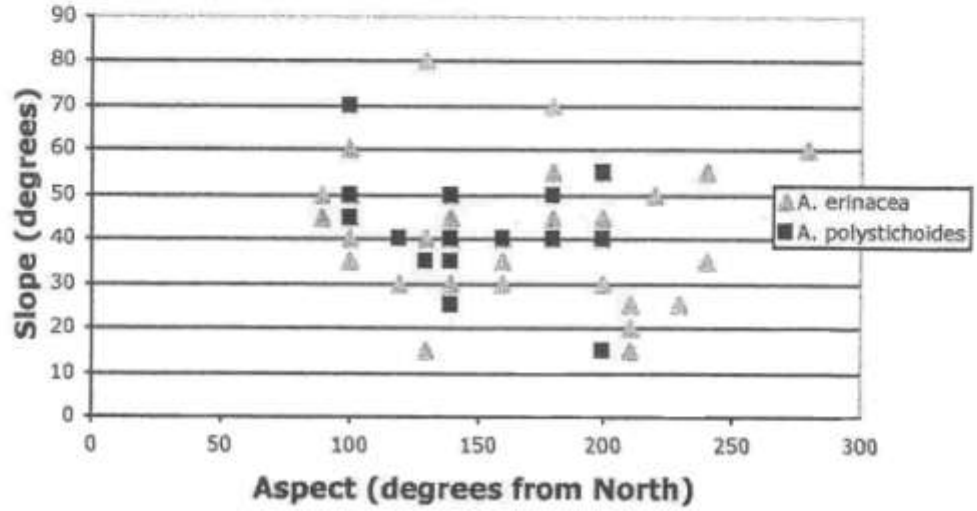

Figure 2. *Distribution of Alsophila erinacea and Alsophila polystichoides on slope and aspect.*

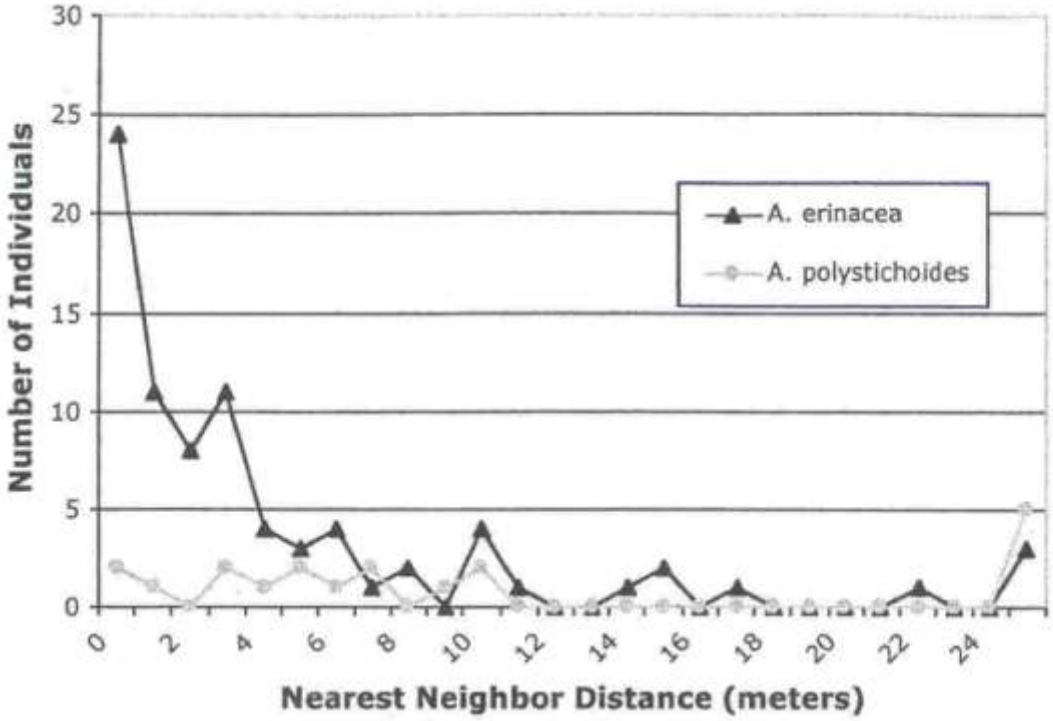

Figure 3. *Nearest neighbor distances for Alsophila erinacea and Alsophila polystichoides. Chi-squared test shows significant difference between these distributions and a Poisson distribution.*