Flower color and shape variation on an elevational gradient

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ABSTRACT

Many flowering plant species have coevolved with pollinator species to form fairly specialized pollination systems that involve both color and shape of flowers, for example red and orange tubular-shaped flowers are attractive to hummingbirds and white, yellow, and blue disk and head shaped flowers are attractive to insects. In Monteverde, Puntarenas, Costa Rica an elevational gradient of pollinator animals has been observed such that cool temperatures in the high altitude regions limit insect activity to low elevations, thereby leaving the high elevation pollination to hummingbirds, leading to the hypothesis that flower color and shape patterns would reflect this pollinator gradient. A patch of continuous forest on the Pacific slope of the Monteverde area was divided into 50m elevational bands from 1250m to 1400m and from 1550m to 1750m and flowering plants censused for color and shape along trails in those bands. Orange and red tubular flower were significantly more abundant in the high elevation bands and blue, white, and yellow/green disk and aster flowering plants were significantly more abundant at the lower elevations. These differences in abundance along the elevational gradients reflect the pattern of hummingbird presence domination at high elevation and insect domination at low elevation.

RESUMEN

Una porción grande de florecer la especie de planta ha coevolucionado con la especie polinizadora en tanto que ellos habido especializado sistemas de polinización en cual o pocos polinizadora, eso está en el mismo grupo taxonómico (E.G. los colibrís), poliniza una especie de planta. Esta especialización puede contribuir a un declive del elevational del color de flor y forma que corresponder con el declive de elevational en la especie polinizadora que resulta de nicho que divide debido a factores no bióticos de hábitat. En Monteverde, Puntarenas, Costa Rica un declive de elevational de animales polinizadoras se ha observado tanto que refrescado las temperaturas en las regiones altas de la altitud en la actividad Pacífica de insecto de límite de cuesta a elevaciones bajas, con lo cual saliendo la polinización alta de la elevación a colibrís y lo fue formado una hipótesis ese color de flor y las pautas de la forma reflejarían este declive. El bosque continuo de la cuesta Pacífica del área de Monteverde se dividió en 50 bandas de elevational M de 1250 M -1400M y 1550 M – 1750 M y florecer censused de plantas para el color y la forma por rastros en esas bandas. Tanto el color como la forma se vieron para estar difiriendo apreciablemente de sobra por el declive de elevational y de tal manera de reflejar como la pauta de la dominación de la presencia del colibrí en la elevación alta a la dominación del insecto en la elevación baja.

INTRODUCTION

Many flowering plants are pollinated by a variety of animals which are attracted in several different ways. Pollination systems are generally characterized by one or few related plant species having one or few related pollinator species. For instance, in the Neotropics, many related orchids rely upon *Euglossine* bees, whereas plants of the family Gesneriaceae rely upon hummingbirds (Bawa 1990). Accordingly, there is a particular suite of floral traits, including both colors and shapes that make the plants adapted to their gradient pollinators, and vice versa. The suite of floral traits displayed by a plant, along with the knowledge of the pollinator(s) allows ecologists to identify some basic "pollinator syndromes", e.g. "Hummingbird-pollination syndrome." There are many reasons suggested for why some plants are more or less specialized in their syndrome, or why certain syndromes are more or less common (Bawa 1990; Young and McDonald 2000). This study focuses on pollination syndromes as related to an elevational gradient in the Neotropics.

Elevation can be seen to influence the frequency of pollination systems in that flight in cool, cloudy conditions (as seen at high elevations) is easier for some animals than others (Murray et al 2000). This stratification can be seen as a method of avoiding direct competition between nectarivorous animals as nectar resources are distributed between competing animal species according to the habitat preferences for those species.

Temperature is a determinate factor in where a pollinating animal species lives as species differ from one another in their temperature tolerances and temperature optima. In the Monteverde area, Costa Rica, the Pacific slope of the Cordillera de Tilarán is made up of several Holdridge life zones, including premontane wet forest, lower montane wet forest, and lower montane rainforest (Haber 2000). There are warmer average temperatures at lower elevations and cooler average temperatures at higher elevations. These temperatures influence pollinator stratification in that cool temperatures limit the activity and metabolic rates of insects that depend on nectar (Murray et al. 2000). In response, insects generally stay at lower elevations. Conversely, hummingbirds are not limited in activity by the cool temperatures of high elevation, and can live successfully at high elevations.

Flower morphology has probably coevolved with pollinator species (Murray et al. 2000) so the distribution of the color and shape of flowers should reflect any niche partitioning among pollinators of Monteverde flora. As cooler temperatures dictate lower metabolic rates and activity in insects, hummingbirds become extremely important pollinators of upper elevation flowering plants (Stiles and Skutch 1989). Flowers pollinated by hummingbirds are generally red, orange, and tubular and are mainly found in epiphytes, shrubs, vines, and treelets while bees and other insects are known to visit a variety of flower colors and shapes on herbs, shrubs, and trees. Often these flowers are flat, dislike, or have a very short corolla with 'landing platform' petals and are white, yellow, or blue (Murray et al. 2000; Raven 1999).

The flowers between 1250m and 1750m on the Pacific slope of the Monteverde area should correspond with the pollinator distributions such that there should be a higher frequency of plants with red or orange tubular flowers at upper elevations and a higher frequency of small, white, yellow, or blue dis-like flowers at lower elevations.

METHODS

Observations were made along 50m elevational bands in Monteverde, Puntarenas, Costa Rica along the Pacific slope and in the continuous forest of the Estación Biológica Monteverde (EBM), Monteverde Cloud Forest Preserve (MCFP), and the Bosque Eterno de los Niños (BEN) from October 19- November 16, 2003. Elevations covered were 1250m – 1400m (BEN) and 1550m – 1750m (EBM and MCFP) and the elevational bands were divided along trails every 50m of elevational change (Figure 1).

Flowering plants were observed up to 10m on either side of a trail and from ground level to canopy. Trails used were Sendero Principal of EBM, Senderos Nuboso, Pantanoso, and Chomogo of MCFP, and Senderos Murciélago, Calandria, and del Tigre in the Bajo del Tigre area of BEN.

Data taken included numbers of individual flowering plants per species and the color and shape of the flowers. Observations were made by sight and with the aid of binoculars. The plants were photographed for identification (if possible) as well as for classification of color and shape.

Flower shape was classified using a condensed version of Heywood's common dicotyledon and monocotyledon flower shapes (1993) and with a few added categories as well. The shape categories included aster, disk, tubular, salverform, pea flower, lip, funnelform, and miscellaneous. 'Aster' included flowers with a head or with a head and disk form; 'disk' included flowers that are flat, open, and circular; 'tubular' included flowers with a long tube that may or may not have landing platform petals (e.g. trumpet) on the terminal end; 'salverform' included flowers with petals as well as a small corolla that an insect could crawl into; 'pea flowers' were Begonia flowers; 'lip' were flowers that had an extended petal as a labellum; 'funnelform' was the Morning Glory flower category; 'miscellaneous' included flowers that did not fit into any of the other categories but for which there was only one species. Color categories were blue, yellow/green, orange, pink/purple, red, and white and plants were categorized by the most dominating color found on the flower. Data were analyzed using Chi-squared tests and Contingency tables.

RESULTS

Sixty-four species of flowering plants were observed and flowers were classified by color and shape. Color categories analyzed included blue, yellow/green, orange, red, and white and shape categories analyzed were aster, disk, and tubular. Orange and red flowers were mainly tubular in shape while the majority of white, yellow-green, and blue flowers were disk or aster shaped (Figure 2).

Color Data:

There were statistically significant differences between colors along the elevational bands (X^2 = 765. 636, df = 24, p-value < 0.0001; Figure 2). Specifically, blue flowers were significantly more abundant and orange flowers significantly less abundant than expected from 1250m – 1300m. Orange flowers were significantly more abundant than expected from 1650m – 1700m. From 1700m – 1750m, orange flowers were again significantly more abundant and blue flowers significantly less abundant than expected.

Table 1. Plant flower color frequency data

	1250m	1300m	1350m	1550m	1600m	1650m	1700m	Totals
Blue	161	0	35	0	0	0	0	196
Ylw/Grn	2	1	22	4	4	9	5	47
Orange	22	2	5	19	8	67	111	234
Red	13	19	2	27	28	21	64	174
White	26	17	50	38	17	7	5	160
Totals	224	39	114	88	57	104	185	811

Shape Data:

There were also significant differences between shapes of flowers found in each band (X^2 = 411. 386, df = 12, p-value < 0.0001; Figure 4). For 1350m – 1400m, asters were significantly more abundant and tubular flowers significantly less abundant than expected. On the other hand, tubular flowers were significantly more abundant than expected between 1700m and 1750m.

Table 2. Plant flower shape frequency data

	1250m	1300m	1350m	1550m	1600m	1650m	1700m	Totals
Aster	28	0	57	2	0	2	0	89
Disk	23	12	34	13	5	6	5	98
Tubular	171	24	2	65	58	92	185	597
Totals	222	36	93	80	63	100	190	784

Discussion

I hypothesized that, due to specialization in pollination systems and differences in physiological tolerances among pollinators, red and orange tubular flowers (referred to as hummingbird flowers from here on) would be found in higher abundance in the upper elevational ranges and in lower abundance in the lower elevations. White, yellow, and blue disk-like or short-corolla/landing platform flowers (referred to bee/insect flowers from here on) would be found in high abundance at lower elevations and in low abundance at high elevations. The results support this hypothesis in that, in the ranges of 1250m – 1400m and 1550m -1750m, hummingbird flowers were observed with significantly higher abundance than bee/insect flowers while bee/insect flowers were found with highest abundance from 1250m – 1300m.

There are two possible explanations for these results. First hummingbird flowers in the lower montane wet and rainforest life zones of Monteverde (1550m – 1750m) have an annual flowering peak in the months of October to November while bee/insect flowers (trees and shrubs specifically) generally flower more during the dry season (January to April) (Haber 2000).

Also in the premontane wet forest zone (1250m-1400m) hummingbird flowers tend to bloom more during the dry season (Haber 2000). These patterns could mean that the trends I observed were due simply to seasonal flowering rather than an elevational gradient corresponding with pollinator differences. However, since at least 10% of flowering plant species are blooming during any month of the year (Haber 2000), a representative portion of the total hummingbird and bee/insect flowers were most likely present. It would be interesting to repeat this study during the dry season to determine whether the flower distribution remained the same.

A second explanation of the results is that specific flower species are found in high abundance where their pollinators are found in the highest abundance. As stated previously, floral traits likely are a product of coevolution with their specific pollinators (Murray et al. 2000). It is also thought that various flowering phonologies are adaptations by plants to avoid competition because flowering biology is strongly influenced by nectarivores (Young and McDonald 2000). In accordance with these ideas, long or short corolla (tubular) flowers that are primarily orange and red, therefore attracting hummingbirds, should be located in the upper ranges of altitude where hummingbirds occur with highest frequency. Likewise, flowers that are white, yellow, or blue and are fairly flattened or have a very short corolla with landing platform petals should occur with greatest abundance where their bee and generalist insect pollinators occur most: the lower reaches of the elevational bands chosen for this study. In other words, these results support the idea that the stratification that is observed in the major nectarivores of the Monteverde area (hummingbirds, bees, and other insects) which places the hummingbirds at the top of an elevational gradient and bees/insects near the bottom due to abiotic habitat factors has corresponding elevationally differing floral color and shape patterns.

In addition to further seasonal investigation of this idea, it would be interesting to include canopy flowers to a greater detail as bees are major pollinators of canopy trees. There are also several plant species, e.g. Besleria princeps (Gesneriaceae), which are common in both high and low altitudes and which are of a shape and color that would attract hummingbirds, yet which are so low to the ground (15cm or less above ground) that it is unlikely that hummingbirds visit them. These flowers are presumably vegetatively reproductive and should not then be found on an elevational gradient and it would be interesting to determine whether this expectation is true or not.

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Figures

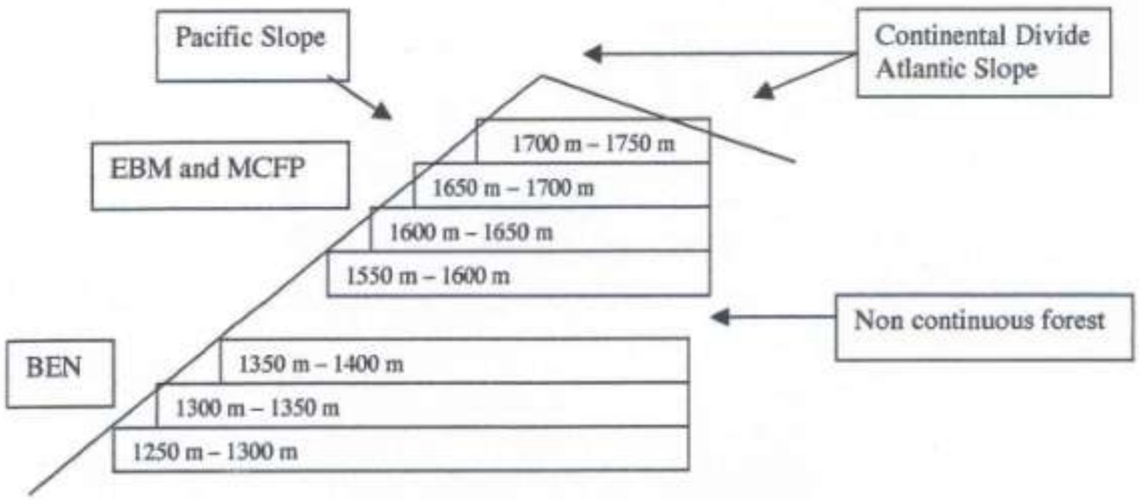

FIGURE 1. Elevational bands were made across the Pacific slope of Monteverde and flowers censused along trails for color, shape, and species.

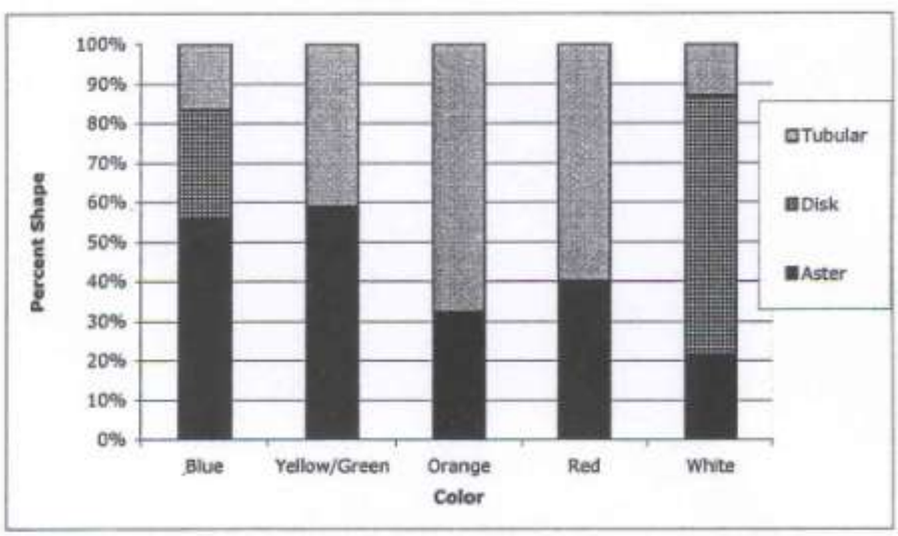

FIGURE 2. Percentage of flower shapes per color.

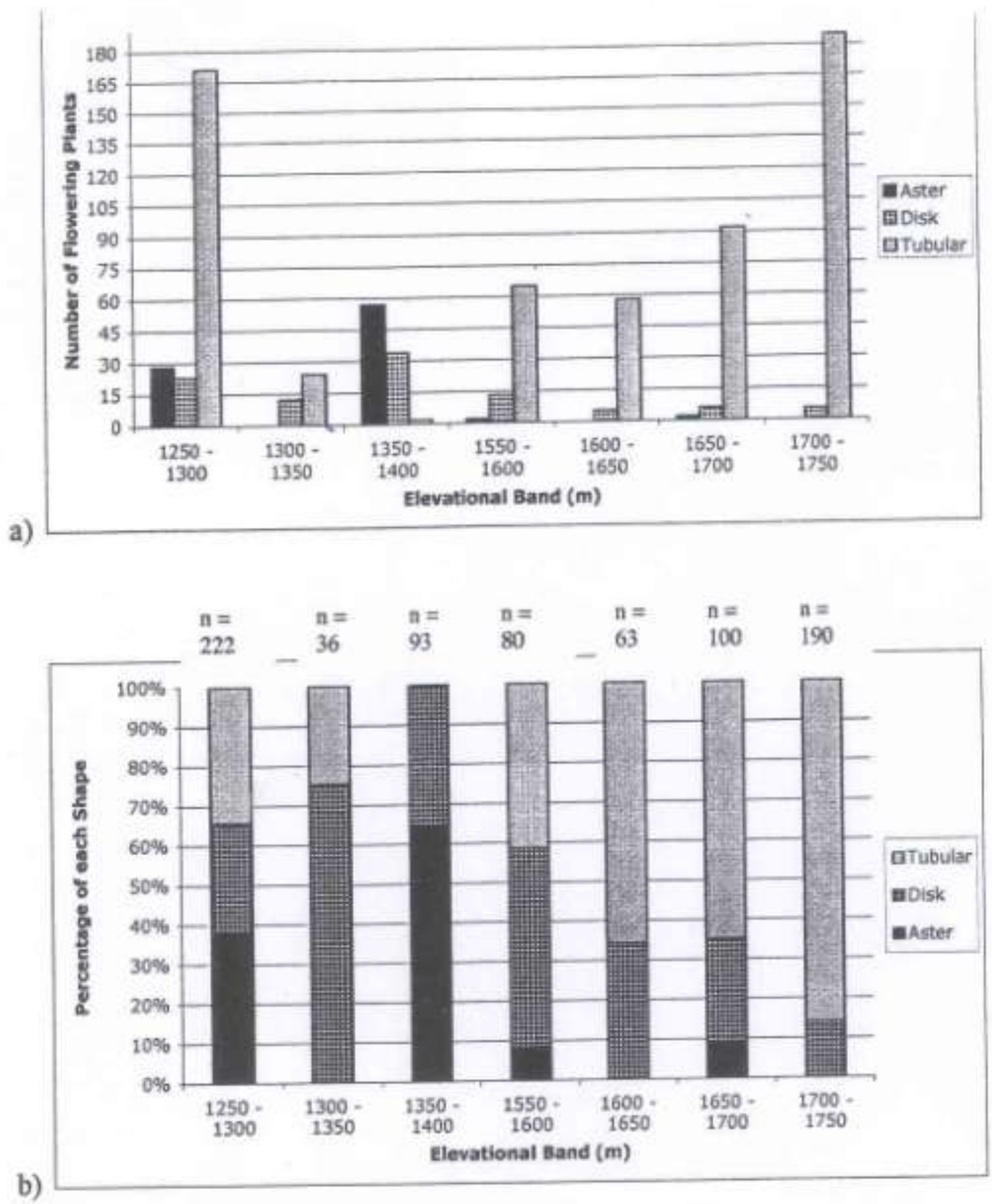

FIGURE 4. Shapes (aster, disk, tubular) per elevational band; a) tubular flowers increase in abundance as the elevation increases (in general) while asters and disks decrease with elevation; b) percentages of the shapes per elevational band.

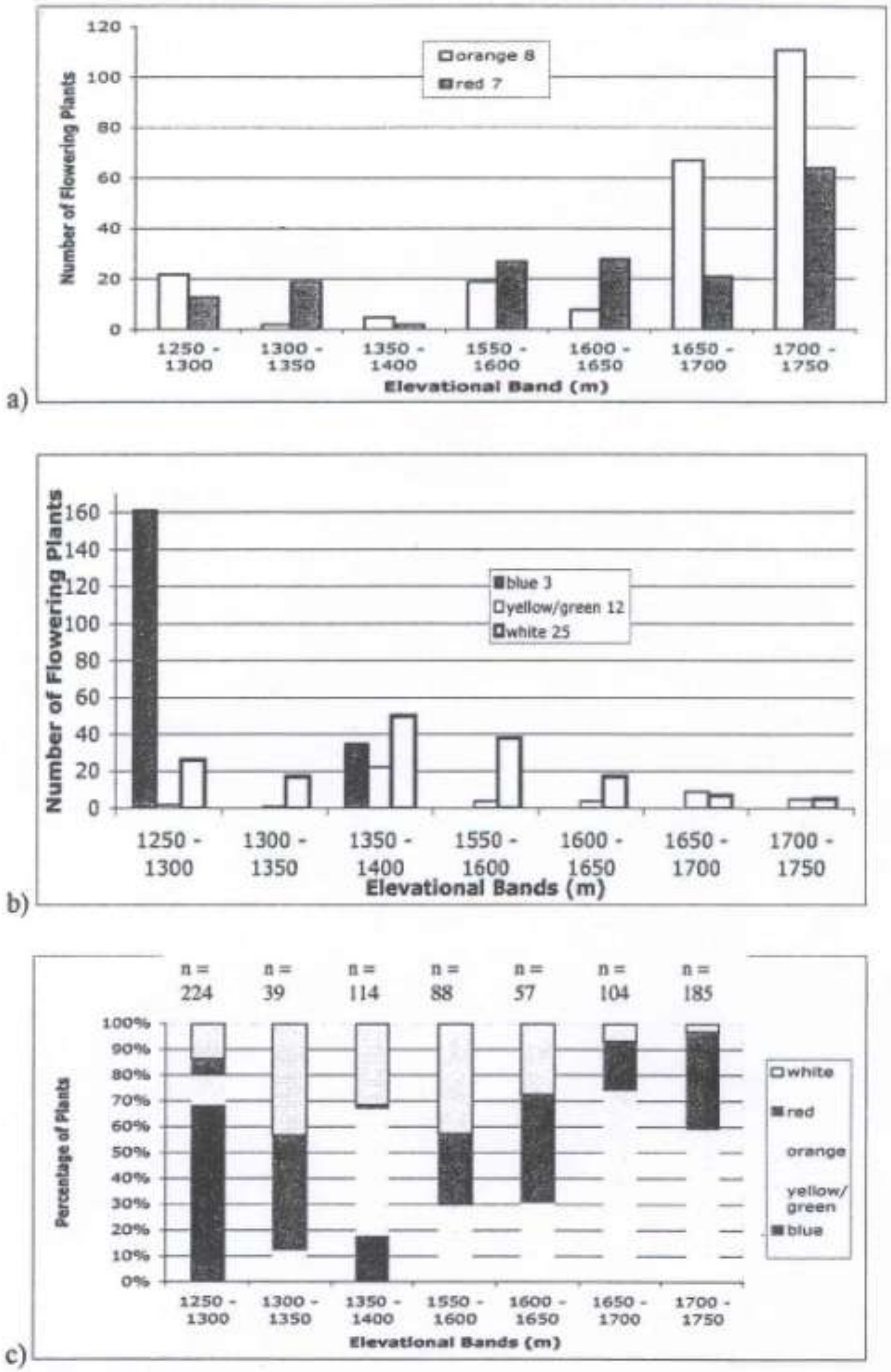

FIGURE 3. Flowering plants of certain colors per elevational band; a) red and orange flowering plants increase with elevation; b) white, blue, and yellow-green flowering plants decrease with elevation; c) percentages of flower color in each elevational band.