Shifts in flowering phenology in response to irregular precipitation and temperature patterns in Monteverde

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ABSTRACT

Studies of plant flowering phenology have the potential to provide essential information on the structure and functioning of communities. Additionally, shifts in flowering phenology as a response to local weather variability have been observed in the tropics, and may worsen as the effects of anthropogenic climate change increase. Unfortunately, comprehensive data on the phenology of many Monteverde plant species is unavailable. This survey of 79 flowering plants of Monteverde in October and November of 2009 aimed to determine the effects of El-Niño on the timing of anthesis as well as provide new information on the phenology of local plant species. Seventy-nine species of flowering plants were identified, ten of which were flowering irregularly. The atypical flowering was not significantly distributed over geographic areas or pollinator type. This suggests that the effects of local climate variation extend across plant types and may have large implications for the functioning of this community.

RESUMEN

Estudios fenológicos en plantas tienen el potencial de proveer información esencial en la estructura y función de las comunidades. Adicionalmente, cambios en la fenología de flores como respuesta a la variación del clima local se han observado en los trópicos, y pueden deberse a cambios climáticos antropomórficos. Desafortunadamente, datos exhaustivos en la fenología de la mayoría de las plantas de Monteverde no están disponibles. En este trabajo 79 especies de plantas en Monteverde entre octubre y noviembre de 2009 con el objetivo de determinar el efecto de El Niño en la producción de flores y a la vez para proveer nueva información en la fenología de las plantas locales. Setenta y nueve especies de plantas con flores fueron identificadas, de las cuales diez estaban floreando en forma irregular. La afloración atípica no está significativamente distribuida sobre áreas geográficas o tipo de polinizador. Esto sugiere que el efecto en la variación del clima local se extiende a través de los tipos de plantas y puede tener implicaciones para el funcionamiento de la comunidad.

INTRODUCTION

The study of plant phenology, or the timing of events, contributes significantly to our understanding of ecosystems. In the tropics, where flowering plants often influence highly specialized interspecies interactions, phenology can play a large role in ecosystem composition and function (Feinsinger 1978, van Schaik 1993, Harrington *et al.* 1999, Visser & Holleman 2001).

Tropical cloud forests create unique opportunities for the study of phenology (Koptur *et al.* 1988). For example, the compression of life zones in Monteverde, Costa Rica has facilitated the growth of numerous plant species specialized for different amounts of precipitation, temperature, and exposure (Koptur *et al.* 1988). Additionally, seasonal flowering is observed for many cloud forest species (Koptur *et al.* 1988). Since many species flower at distinct periods rather than year-round, shifts in flowering phenology can be detected.

Climate change has altered the weather patterns in the Monteverde cloud forest, resulting in longer dry periods and a shift in the cloudbank towards higher elevations (Pounds *et al.* 1999). Though altitudinal migration has been noted in several species (Pounds *et al.* 1999, Chaves-Campos *et al.* 2003), there have been few comprehensive studies of phenological shifts in the plant community in Monteverde. Phenology is a response to abiotic as well as biotic conditions (van Schaik 1993); thus one would expect that changes in local climate (e.g. precipitation and temperature) would lead to shifts in phenology. Moreover, information on changing phenologies of flowering plants could aid in understanding the response of tropical communities to human-induced climate change.

This year, an El Niño year (Masters, pers. comm.), is an ideal one for studying phenology. In Monteverde, plants respond to the dry conditions of El Niño in the same way they respond to human-induced climate change–by flowering earlier (Haber 2000). Since the decrease in precipitation associated with ENSO events may exacerbate the larger patterns of global warming (Pounds *et al.* 1999), shifts in phenology may be easily detectable this season. Any observed differences in reproductive timing may be a result of El Niño and not global warming; however, since the two have similar effects, this data could be used to predict the effects of climate change.

To determine whether the plants of Monteverde have undergone shifts in flowering phenology during the current season, I surveyed the area for flowers and created an inventory of all species in bloom during October and November 2009. This inventory was compared to historical data to determine whether significant shifts in phenology have occurred. I hypothesized that, due to the combined effects of El Niño and climate change, there would be a considerable amount of early blooming species. Additionally, I expected to find irregularly blooming species preferentially on the Pacific slope, since this slope is more seasonal (Haber 2000), and therefore might contain a higher proportion of seasonally flowering plants.

MATERIALS AND METHODS

Historical Weather Data

I analyzed monthly temperature and precipitation data (Pounds, unpub. data) from this year and previous years to determine the deviation in climate due to El Niño. Weather data was collected at Campbell Station, located at the Monteverde Institute.

Study sites

Plants were sampled in October and November 2009 along the forested trails in Monteverde area reserves, from altitudes of 900m in Bajo del Tigre to 1800m on the Continental Divide. The survey locations comprised six life zones (Haber 2000):

1. Bajo del Tigre (Pacific slope): premontane moist and premontane wet forest.

2. Monteverde Cloud Forest Reserve (Pacific slope): lower montane rain forest, lower montane wet forest
3. Estación Biológica Monteverde (Pacific slope and continental divide): premontane wet forest, lower montane rain forest,
4. Selvatura (Caribbean slope and continental divide): lower montane rain forest, premontane rain forest.

Flowering Plant Surveys

To survey the flowering plants in the Monteverde region, I identified species in bloom that were less than 2 meters tall (to ease in specimen collection). Surveyed plants therefore excluded canopy and other mature trees, as well as some epiphytes and vines that grew too high to easily collect.

For each open flower observed, I photographed the sample and, where possible, collected a specimen to aid in identification. The number of observed flowering individuals for each species was also noted, as well as the date and location.

To identify plants, I used field guides, expert opinion, primary literature, and online databases (see Table 1 for sources). Past studies and expert opinion were used to determine whether their phenology was unusual. In addition, I compared the quantity of flowering individuals to the estimated abundance of each species, as determined by field guides and expert opinion. This allowed me to determine whether the flowering was characteristic for the entire population; for example, if a species is common in Monteverde, but I observed only a few flowers of that species, the population as a whole was not determined to be in bloom.

I compiled a list of species that I determined to be atypically flowering, as well as a list those that were flowering normally. Next, I identified the pollinators of the flowers to compare whether shifts in phenology disproportionately affected certain guilds of plants. Finally, a geographic comparison was used to test for disproportionate effects of climate on certain life zones.

RESULTS

Historical Weather Data

Recent weather data show that the climate in Monteverde is affected by the current El Niño event (see Figs. 1-3). Precipitation levels for 2009 are low when compared to other years, especially the previous year. Moreover, the temperatures in the months preceding this survey were historically high.

Flowering Plant Survey

I found and identified 79 species of flowering plants (see Table 1). Of these, ten exhibited irregular phenology (eight flowering early, two flowering late). Forty-four species were observed flowering normally, of which 18 were seasonal flowers blooming in the correct season. There was incomplete phenological information on 25 of the surveyed plants, preventing an assignment of "typical" or "atypical"(see Fig. 4). The plants for which phenological data was incomplete were not included in statistical tests, because they may have been either typical or atypical.

Atypical flowers were found in all four of the study sites (see Fig. 5). Moreover, there was no significant difference between atypical and typical flowers in their geographic distribution. This was true when only seasonal flowers were included (χ^2 = 0.28; df = 3; P = 0.964) and when both seasonal and non-seasonal flowers were included (χ^2 = 0.88; df = 3; P = 0.829).

Seasonal flowers were not found disproportionately on the Pacific slope, as was predicted (χ^2 =1.724; df = 3; P = 0.631).

Figure 6 illustrates the pollinator type for seasonal typical and atypical plants. Phenological shifts were not disproportionately noted for a particular pollinator type. Again, this was true when both seasonal (χ^2 = 2.59; df = 2; P= 0.274) and all typical flowers (χ^2 = 4.06; df = 5; P = 0.54) were considered.

DISCUSSION

Weather data from 2009 shows higher-than-average temperatures and lower-than-average precipitation for the months preceding this study. High temperatures and low precipitation are consistent with El-Niño events (Haber 2000); therefore, this data implies that the 2009 El-Niño event is affecting the local climate in Monteverde.

Furthermore, a drop in precipitation in the months preceding the dry season should, as expected, cause early, rather than late anthesis, because the effect imitates the onset of the dry season (Haber 2000). Several species of flowers were blooming in October and November, but should be blooming at the beginning of the dry season. Seasonal flowering occurs in peaks, after which flowering may severely decrease (Koptur *et al.* 1988). This suggests that only a few flowers may be present during these species' usual flowering season.

There were no significant differences in pollination strategy between atypical and typical blooming flowers. Therefore, pollinators across taxa will be affected by the shifts in phenology. Hummingbirds, which pollinate the majority of flowers surveyed, may suffer from the shifts in their resource base. Studies have shown that hummingbird distribution and life history is tightly coevolved with the flowering times of certain species (Feinsinger 1978, Stiles 1985). In particular, staggered flowering seasons have evolved to provide a year-round nectar source for hummingbirds (Feinsinger 1978). Should these flowering patterns be disrupted, this could have serious consequences for the hummingbird population.

The geographic distribution was similar for both atypical and typical flowers. Contrary to predictions, the Pacific slope was not disproportionately affected by climatic shifts. Additionally, the Pacific slope did not contain a higher proportion of seasonal flowers than the Atlantic slope. This has worrying implications for the fauna that depend on these plants. If plants in all geographic areas are affected by changes in climate, there may be no refuge for pollinators or dispersers. For instance, species that span a range of life zones may bloom early in all these life zones; thus, organisms dependent on those flowers will be unable to relocate to find them.

Finally, this study found 25 species of plants for which Cloud Forest flowering data was incomplete or unknown. This indicates the need for more comprehensive studies of flowering phenology in the Monteverde area, especially with durations of several years. The flowering of plants contributes to community-wide patterns in structure and phenology, and thus, it is vital to understand the impacts of phenological shifts that result from local and global climatic change. Without this knowledge, it is difficult to recognize when large shifts have already occurred, and more difficult to predict the future impacts of global climate change.

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TABLE 1. List of all flowering species surveyed in Monteverde in October and November 2009, along with their locations, phenologies, and pollinators. (unk = unknown, incomplete, or conflicting information)

Family	Species	Bajo del Tigre	Pacific slope	Contin-ental Divide	Caribb-ean slope	Flowering Typical		Seasonal	Pollinator*	References **
Acanthaceae	*Dicliptera iopus*		x	x		n	early	y	bird	11,15,17,18
Acanthaceae	*Hybrid sp. (Razisea & Stenostephanus)*		x			unk		unk	unk	17
Acanthaceae	*Justicia aurea*		x		x	y		y	bird	4,11,17
Acanthaceae	*Justicia macrantha*		x			unk		unk	bird	17
Acanthaceae	*Justicia valerii*		x			n	early	y	bee	4,10,11,17
Acanthaceae	*Poikilacanthus macranthus*		x	x	x	y		y	bird	4, 11,17
Acanthaceae	*Pseuderanthemum cuspidatum*		x			y		y	butterfly	10,17
Acanthaceae	*Razisea spicata*		x	x	x	n	early	y	bird	2,4,11,17,18
Acanthaceae	*Stenostephanus blepharorachis*		x			n	early	y	bird	16,17,18
Araceae	*Anthurium obtusilobum*		x			y		y	bee	10, 16, 17
Arecaceae	*Calyptrogyne sp.*		x		x	y		n	butterfly	11, 17
Arecaceae	*Chamaedora sp.*	x				y		n	wind	11, 17
Asclepiadaceae	*Asclepias curassavica*	x				y		n	butterfly	4
Asteraceae	*Ageratum petiolatum*	x				unk		unk	butterfly	17
Asteraceae	*Clibadium surinamense*	x				y		n	butterfly, bee	1, 3, 17
Asteraceae	*Conyza canadensis*				x	y		n	insect	17
Asteraceae	*Galinsoga parviflora*		x			unk		unk	bee	17
Asteraceae	*Hidalgoa ternata*		x			unk		unk	butterfly	10, 17
Asteraceae	*Koanophyllon pittieri*				x	y		y	moth	10, 17
Balsaminaceae	*Impatiens walleriana*		x			y		n	unk	4
Begoniaceae	*Begonia involucrata*		x			y		y	bee	4, 15
Brassicaceae	*Cardamine sp.*		x	x		unk		unk	insect	17
Campanulaceae	*Burmeistera parviflora*		x			unk		unk	bird	17
Campanulaceae	*Centropogon granulosis*		x		x	y		n	bird	4
Commilanaceae	*Tradescantia zanonia*		x		x	y		n	bee	4
Costaceae	*Costus montanus*		x			unk		unk	bird	17
Ericaceae	*Cavendishia bracteata*				x	y		n	bird	4
Gesneriaceae	*Alloplectus tetragonus*		x	x		y		n	bird	8, 15
Gesneriaceae	*Besleria notabilis*		x			y		n	bird	8, 11, 17
Gesneriaceae	*Besleria princeps*		x	x		n	late	y	bird	8, 11, 17
Gesneriaceae	*Besleria solanoides*		x			n	early	y	bird	8, 11, 17
Gesneriaceae	*Columnea lipidocaulis*		x	x		y		y	bird	8
Gesneriaceae	*Drymonia conchocalyx*		x			y		n	bird	8
Gesneriaceae	*Drymonia rubra*		x	x	x	y		n	bird	8, 16
Gesneriaceae	*Kohleria spicata*		x			n	early	y	bird	4, 8, 11, 16
Gesneriaceae	*Moussonia strigosa*		x			y		y	bird	8
Heliconiaceae	*Heliconia tortuosa*	x				y		y	bird	17, 18
Lamiaceae	*Salvia costaricensis*	x				y		y	bee	10, 17
Lythraceae	*Cuphea appendiculata*	x				y		n	bird	4
Malvaceae	*Malaviscus palmanus*		x	x	x	y		n	bird	15, 17
Malvaceae	*Malviscus arborescens*	x				unk		y	bird	11, 17
Malvaceae	*Sida rhombifolia*				x	y		n	bee	3, 17
Marantaceae	*Calathea marantifolia*		x			unk		unk	bee	10, 17
Melastomataceae	*Arthrostemma ciliatum*	x				y		n	bee	4
Melastomataceae	*Centradenia inaequilateralis*		x			y		n	bee	4
Myrsinaceae	*Ardisia guianensis*		x			unk		unk	bee	17
Nyctaginaceae	*Pisonia sylvatica*	x				unk		unk	moth	10, 17
Orchidaceae	*Cranichis lankesteri*		x			y		y	unk	13
Orchidaceae	*Masdevallia sp.*		x			unk		unk	unk	12, 13, 17
Orchidaceae	*Maxillaria fulgens*		x			y		y	unk	12, 13
Orchidaceae	*Pleurothallis sp.1*			x		unk		unk	unk	13
Orchidaceae	*Pleurothallis sp.2*		x			unk		unk	unk	13
Orchidaceae	*Pleurothallis sp.3*		x			unk		unk	unk	13
Orchidaceae	*Pleurothallis tonduzii*		x			y		n	unk	13
Orchidaceae	*Sobralia leucoxantha*		x			y		y	unk	13, 17
Orchidaceae	*Stelis sp.*		x			unk		unk	unk	13, 17
Orchidaceae	*Stenorrhynchos speciosum*				x	n	early	y	bird	13, 17
Orchidaceae	*Unknown sp.*			x		unk		unk	unk	
Orchidaceae	*Xylobium elongatum*		x			y		y	unk	13, 17
Passifloraceae	*Passiflora capsularis*		x			y		y	bee	11, 17
Phytolaccaceae	*Phytolacca rivinoides*			x		y		y	bee	4, 11,16
Piperaceae	*Peperomia hernandiifolia*		x			unk		unk	insect	10, 15, 17
Poaceae	*Lasiacis oaxacensis*	x				unk		unk	wind	17
Rosaceae	*Rubus roseifolius*	x				y		y	bee	4, 15
Rubiaceae	*Coccocypselum hirstutum*		x			y		n	bee	4
Rubiaceae	*Hamelia Patens*	x	x			y		n	bird	4, 11
Rubiaceae	*Hoffmannia congesta*		x			y		y	bee	4, 17
Rubiaceae	*Psychotria aggregata*		x			unk		unk	bee	17
Rubiaceae	*Psychotria chiriquiensis*		x			unk		unk	bee	10, 17
Rubiaceae	*Psychotria quinqueradiata*	x				n	early	y	bee	9, 10, 17
Rubiaceae	*Spermacoce asurgens*	x				y		n	insect	4
Solanaceae	*Solanum cordovense*	x	x			n	late	y	bee	6, 17
Solanaceae	*Solanum longiconicum*			x		y		n	bee	14, 17
Solanaceae	*Witheringia meiantha*		x			y		n	bee	7, 17
Solanaceae	*Witheringia sp.*		x	x		unk		unk	bee	17
Urticaceae	*Pilea hyalina*		x			unk		unk	wind	17
Valerianaceae	*Valeriana scandens*				x	unk		unk	insect	17
Violaceae	*Viola stipularis*		x			y		n	bee	4, 10
Zingiberaceae	*Renealmia ceruna*		x			y		n	bird	4

*Pollination data is from: Haber, W.A. 2000. Vascular Plants of Monteverde.

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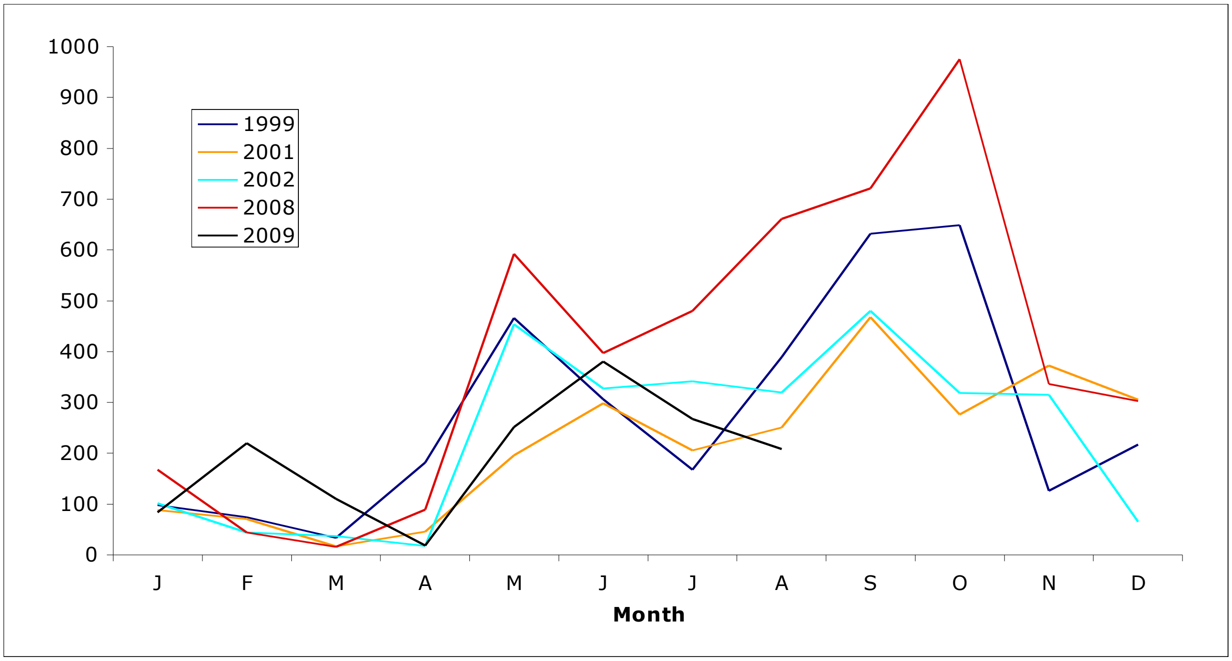

FIGURE 1. Monthly precipitation totals for different years in Monteverde. 1999 is a La Niña year, 2001 is a normal year, 2002 is an El Niño year, and 2008 is a normal year (NOAA/National Weather Service 2009). The current year, 2009, has relatively low precipitation, especially in the months directly preceding this study.

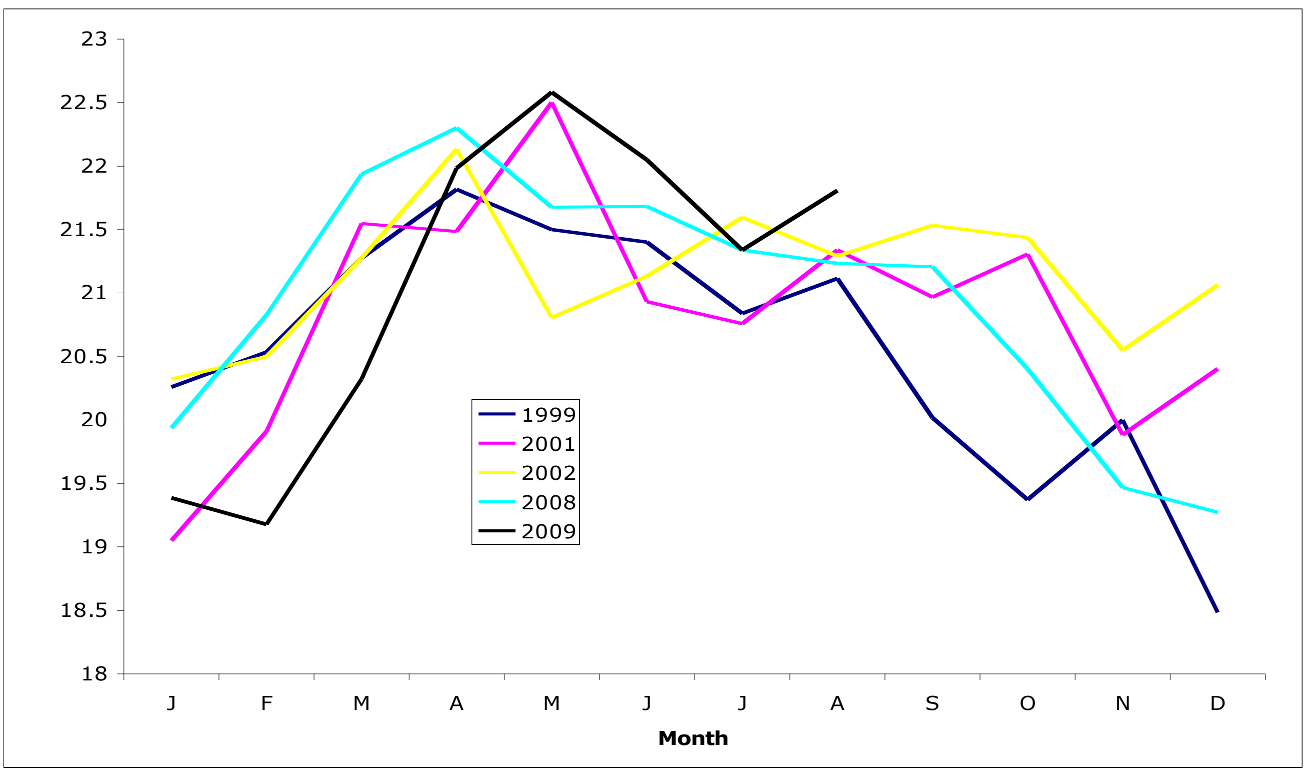

FIGURE 2. Monthly maximum temperatures for different years in Monteverde. The most recent months of 2009 have increased temperatures when compared to historical trends.

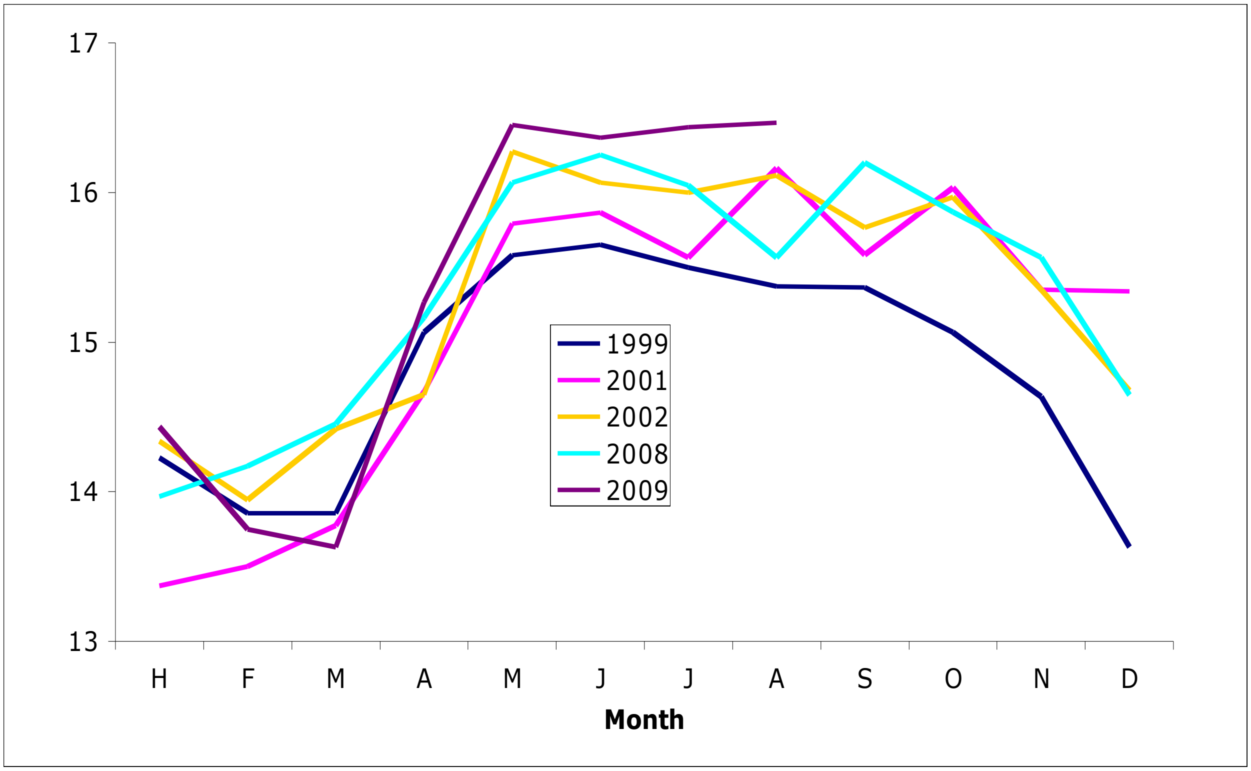

FIGURE 3. Monthly minimum temperatures for different years in Monteverde. 2009 has higher than normal minimum temperatures.

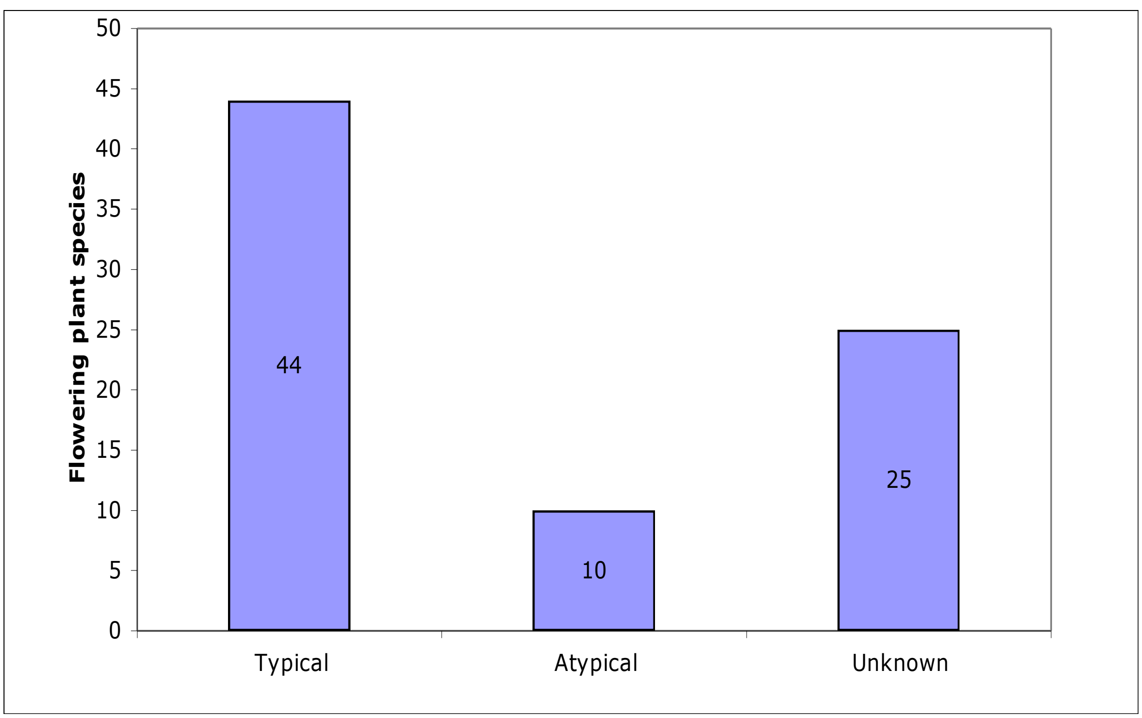

FIGURE 4. Identified plant species in Monteverde during October and November of 2009, classified as flowering in an atypical or typical fashion. If information was incomplete, classified as unknown.

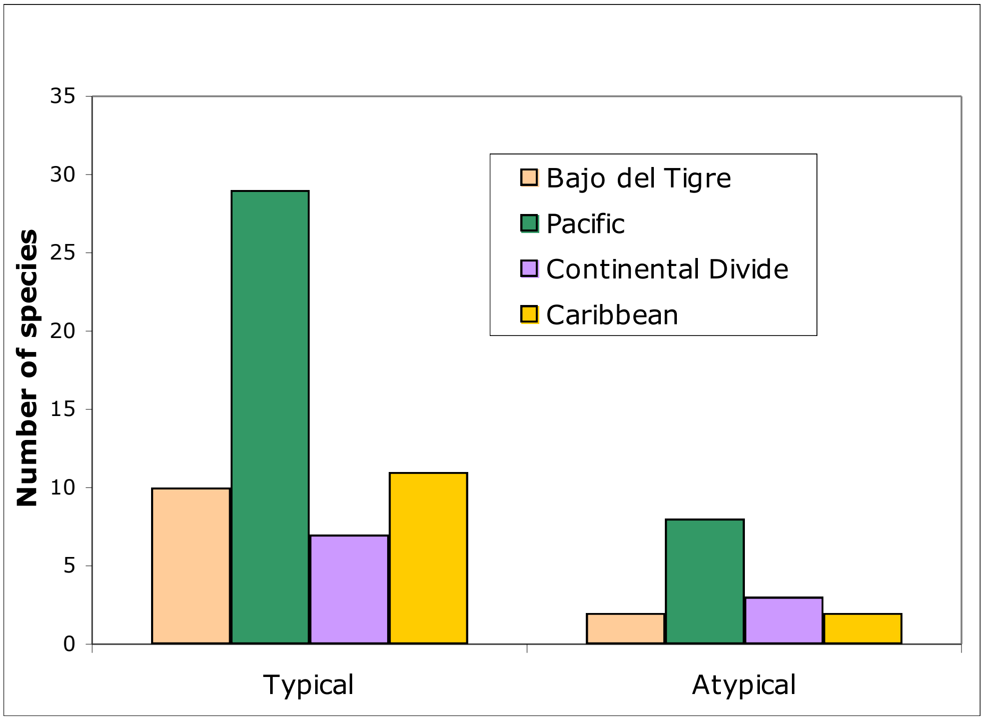

FIGURE 5. The geographic distribution of typical and atypical plants across four survey sites in Monteverde in October and November 2009. The typical plant species counts include both seasonal and aseasonal plants.

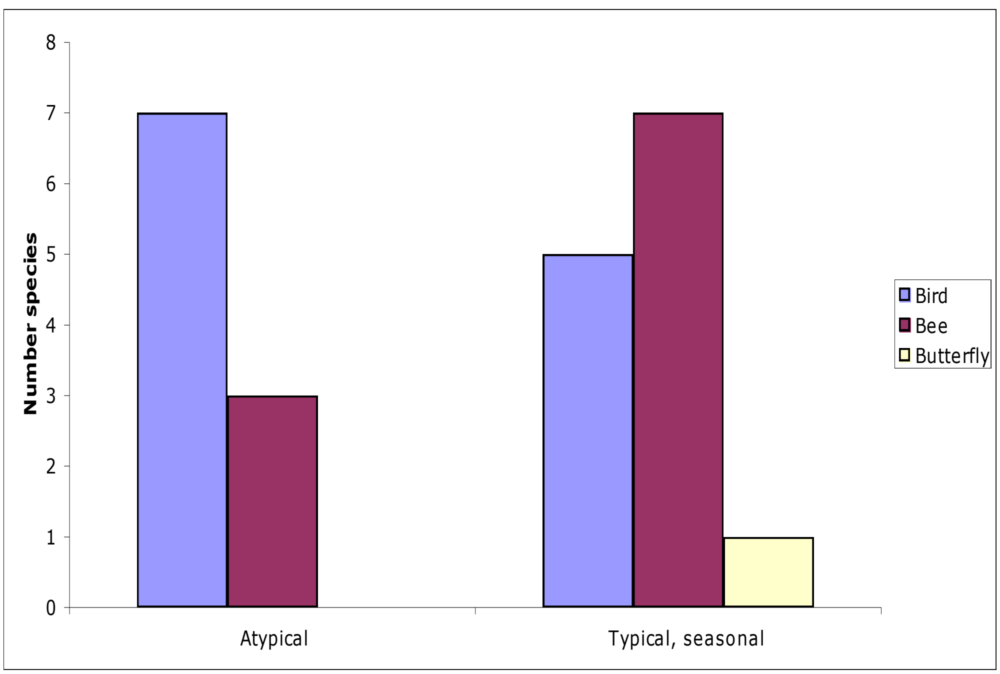

FIGURE 6. Pollinators for both atypical and seasonal typical plants in Monteverde for October and November 2009. There was no significant difference in pollinator type between atypical and typical plants