

## Habitat associations of herbaceous plants in Yasuní National Park, Amazonian Ecuador: A study of *Heliconia*

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### Abstract

The abundance, diversity, and distribution of herbaceous plants within tropical forests are often neglected in favor of woody tree and liana species, even though the herbaceous understory layer of these forests plays a major role in nutrient cycling and frequently encompasses a greater species diversity than trees. In a 50-ha permanent lowland Amazonian rain forest plot in Yasuní National Park, Ecuador, a census of six species of *Heliconia* (Heliconiaceae) was carried out in a stratified random manner across three topographic habitat types: valley, slope and ridge. Distribution patterns consistent with habitat niche partitioning were observed for the two most abundant species on the plot: *Heliconia stricta* was found predominantly in valley habitat and *H. velutina* in ridge habitat. Further, *H. velutina* was the only species to be present at high abundance and frequency in ridge habitat, suggesting that it can succeed in the drier ridge conditions and may even have better drought tolerance than the five other *Heliconia* species. Such habitat associations consistent with niche partitioning have been found in tree species within the plot, and likely contribute to the coexistence of these six closely related herbaceous species in this forest.

### Introduction

Many censuses of plant diversity neglect to account for herbaceous species, particularly in forest ecosystems. Herbs offer special problems to census-taking scientists because they can be small, short-lived, rhizomatous, and difficult to enumerate and tag. Because of these difficulties, many botanical species diversity studies exclude herbs from their tallies, and previous censuses in tropical forests are no exception (Gentry and Dodson 1987). For example, despite an extensive network of tree plots throughout the world's forests, very little is known about the herb flora and dynamics of many of these sites (Bass et al. 2010, Valencia et al. 2004, Feeley et al. 2011, Toriola et al. 1998, Guo-Yu et al. 2008). Still, in tropical forests, most individual plants are non-trees and terrestrial herbs account for about 13% of total plant composition (Gentry and Dod-

son 1987), suggesting important roles in ecosystem processes and services.

Herbs contribute to the forest ecosystem differently than their woody counterparts. For example, the herbaceous layer plays a crucial role in influencing the cycling of essential plant nutrients; herbaceous leaf litter decomposes more than twice as fast as tree litter (Gilliam 2007). Herbs also respond to disturbances such as tree-falls differently than trees do, so herbs may associate with such habitats differently than trees (Murphy et al. 2016).

Herbaceous plant composition and dynamics have been investigated more frequently in temperate climates than in tropical ones. Most forests in temperate North America are approaching a climax state of succession and experience annual variability with seasons (Gilliam 2014), whereas tropical forests have more recently been involved in a cycle of clearing and settling, and experience less drastic

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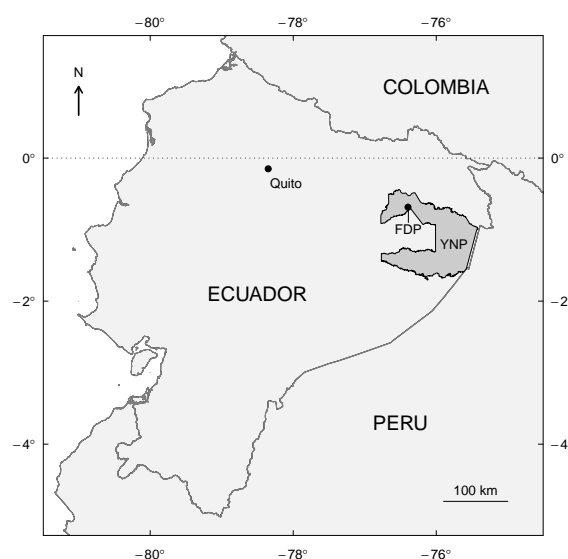
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changes in temperature. These different contexts make it harder to directly compare the dynamics of herbaceous plants between the two biomes. It seems that in temperate forests, seasonal and regional patterns in herbs are better explained by soil conditions than by climate (Gilliam 2014), though climate may play a role in driving soil conditions. Even if the rest of the forest is approaching the climax stage, the understory is a more dynamic habitat and is not usually in equilibrium because of its dependence on the dynamic canopy of trees (Gilliam 2014, Brewer 1980, Gilliam 2007). As a result, the herbaceous layer tends to increase in diversity and quantity in a forest approaching climax (Davison and Forman 1982).

Research has suggested that high diversity in woody species in tropical forests is driven in part by variation in soil resources varying in response to topography and geology (Valencia et al. 2004, John et al. 2007, Pitman et al. 2008). The catena topography gradient, ranging from the high ridgetop to the low valley, often covers a wide range of soil variation over a small area. Soil minerals are essential nutrients for plants, and can be a key axis of niche partitioning, allowing the coexistence of multiple species. For example, in some temperate studies, forb species richness has been found to strongly correlate with nitrogen mineralization rate in fertile ground (Hutchinson 1999). Interactions between the abiotic environment, such as climate and topography, affect different plant growth forms, including lianas and trees, differently, so herbs require specific study (Dalling et al. 2012).

In other Amazonian tree censuses, when compared with distance-dependent relationships, habitat associations were found to be stronger: 77% of tree species in Peruvian forests exhibited a significant habitat association (Phillips et al. 2003). More importantly, it was suggested that habitat associations were made possible due to “substrate-mediated local processes”, like soil content, which is consistent with the findings in the temperate zone (Gilliam 2014). However, habitat associations tend to vary locally – some habitat associations may

be partially or fully caused by interactions with other species (Harms et al. 2001). Other underlying factors that differ between microhabitats in certain areas may explain the instances where species display habitat associations. The semi-deciduous forest of Barro Colorado Island (BCI) in Panama is one such site of several habitat association studies where most woody species did not seem to associate with any certain type of topography (Harms et al. 2001), although topographic variation here is much less than at other forest sites.



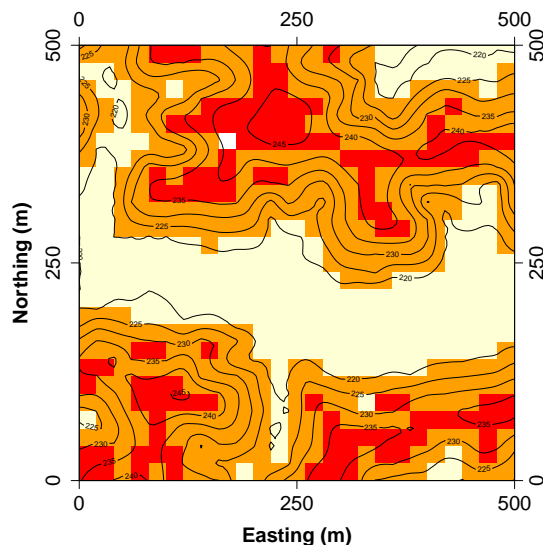
**Fig. 1.** Location of Yasuní National Park in Ecuador.

In the lowland rain forest of Amazonian Ecuador, habitat associations have been shown, dividing about a quarter of the tree community into species that occur predominantly on ridge-tops versus those that occur in valleys, and another quarter that occurs regularly in each (Valencia et al. 2004). Similar patterns have also been demonstrated among specific taxa, such as palms (Svenning et al. 1999) and the Myristicaceae (Queenborough et al. 2007). Dispersal limitation and other habitat- and topography-related factors also influence the distribution of species (Valencia et al. 2004, Dalling et al. 2012, Phillips et al. 2003,

Moeslund et al. 2013). However, very little is known about how these factors influence the distribution and potential coexistence of herbaceous plants. In this study, I examined patterns of diversity, distribution, and abundance in *Heliconia*, a genus of easily-recognizable, large, herbaceous plants, within a large 50-ha forest dynamics plot in Yasuní National Park, a lowland aseasional rain forest in the Amazon region of eastern Ecuador.

## Questions

1. Do *Heliconia* species differ in abundance, composition and diversity according to habitat?
2. Do *Heliconia* species exhibit habitat preferences according to topography?
3. Do *Heliconia* species exhibit preferential co-occurrence?



**Fig. 2.** Topographic map of the 25-ha plot in Yasuní National Park, showing valley (yellow), slope (orange), and ridge (red) categorized habitats. Sample quadrats were randomly selected within each habitat.

## Methods

### Study Site

The combined Yasuní National Park and Biosphere Reserve make up the largest protected area in the Ecuadorian Amazon at 1.6 million ha (Fig. 1). Disturbances within the forest occur from natural and anthropogenic causes, with the indigenous Wao-rani living in several recently-founded communities (Valencia et al. 2004).

Yasuní has an aseasional climate, with a mean monthly temperature of 25°C and an average annual precipitation of c.3,000 mm, with lower levels of precipitation in June–August, when this study was conducted (Pérez et al. 2014, Valencia et al. 2004). This continuous evergreen lowland wet forest is recognized worldwide for having extremely high biological diversity and maintains sizable populations of vertebrate fauna (Bass et al. 2010, Valencia et al. 2004).

A 50-ha permanent Forest Dynamics Plot (FDP, 230 meters above sea level, with 33.5 m of elevation change within it) was established in the park at 0°41' S latitude, 76°24' W longitude in 1994, about a km from the research station (Valencia et al. 2004, Pérez et al. 2014, Fig. 2). Since 1995, tree censuses have been carried out roughly every five years. All trees >1 cm DBH are mapped, tagged and identified. A total of 1,104 species are so far recognized on the plot (Valencia et al. 2004).

### Study Species

*Heliconia* L. (Heliconiaceae) is a genus of large herbs, growing up to 4 m, often with distinctive washboard-like leaves. The genus is the only genus in Heliconiaceae, with 225 species, growing primarily in the Neotropics. The inflorescences and bracts of *Heliconia* are visually striking, with an arrangement and pattern unique to each species (Fig. 3). Each ovary can produce up to three seeds, dispersed via mature purple berry (Costa et al. 2011).

*Heliconia* are ubiquitous in the understory of the Yasuní forest and they are sensitive to forest succession. Not only are *Heliconia* highly abundant

in Yasuní's state of secondary growth, but they are also highly specific and adapted to the habitats in which they thrive (Stiles 1975).

#### Sampling and Data Analysis

In the plot there are two main ridges dominated in composition by red clay, centered around a valley region characterized by brown or gray alluvium soils, and a swamp containing standing water at times (Valencia et al. 2004, Fig. 2). The Yasuní 50-ha plot is subdivided into a total of 625 20x20m quadrants. Habitat type (valley, slope, or ridge) of each quadrant was assigned based on topography according to mean elevation, slope and convexity (Harms et al. 2001, Valencia et al. 2004). Using a stratified-random sampling approach, 68 of the 20x20m quadrants were randomly selected from each habitat type (total  $n = 203$ ). Within each quadrant, all *Heliconia* individuals present were recorded and identified to species.

In each sample quadrant, I counted the total number of individuals of each species present, from small, single-leaved individuals of *H. stricta* to towering *H. vellerigera*. To test for differences in relative abundance of each species, I used a proportion test. To test for differences in the probability of a species present in a habitat, I used logistic regression. All analyses were carried out in R version 3.2.2 (R Core Team 2014).

#### Results

A total of 2,347 *Heliconia* individuals were recorded from the 203 quadrants sampled, distributed among six species (Figs. 3 and 4). All individuals were identified to species. When inflorescences were not present on the plant, leaf color and form, petiole pattern and placement on the stem were useful indicators of species.

*Heliconia communities differ in species abundance, composition, and diversity according to habitat*

In order of abundance, species documented were: *Heliconia stricta* Huber ( $n = 1135$  plants), *Heliconia*

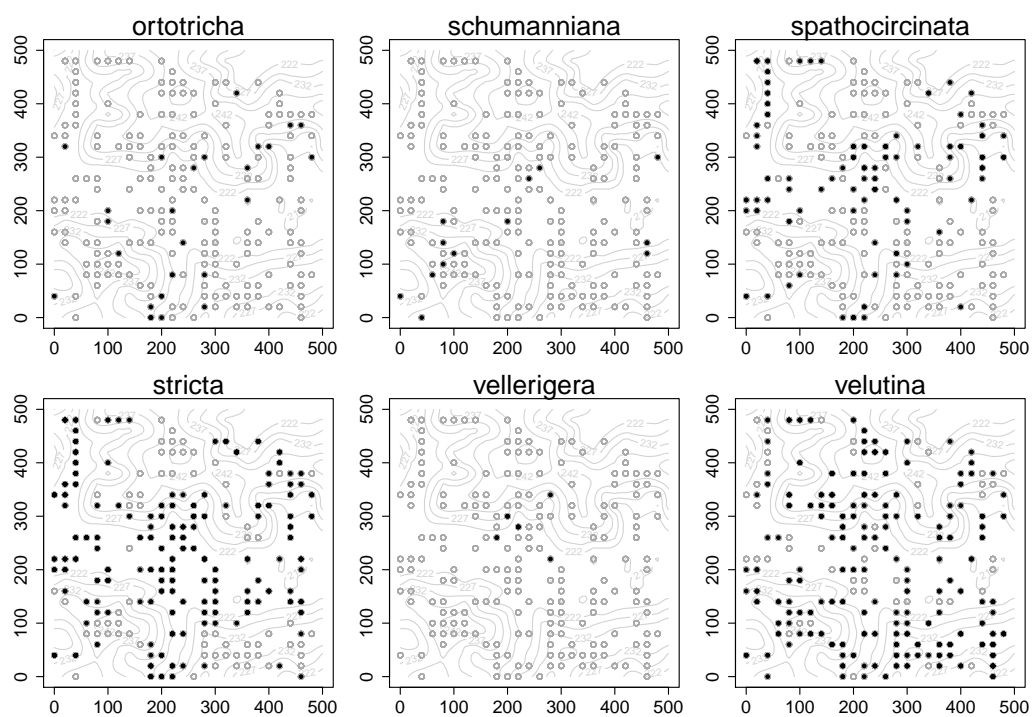


**Fig. 3.** *Heliconia* species found in the Yasuní forest dynamics plot, in order of abundance, from top left to bottom right: *Heliconia stricta* Huber, *Heliconia velutina* L. Andersson, *Heliconia spathocircinata* Aristeg., *Heliconia ortotricha* L. Andersson, *Heliconia vellerigera* Poepp. and *Heliconia schumanniana* Loes.

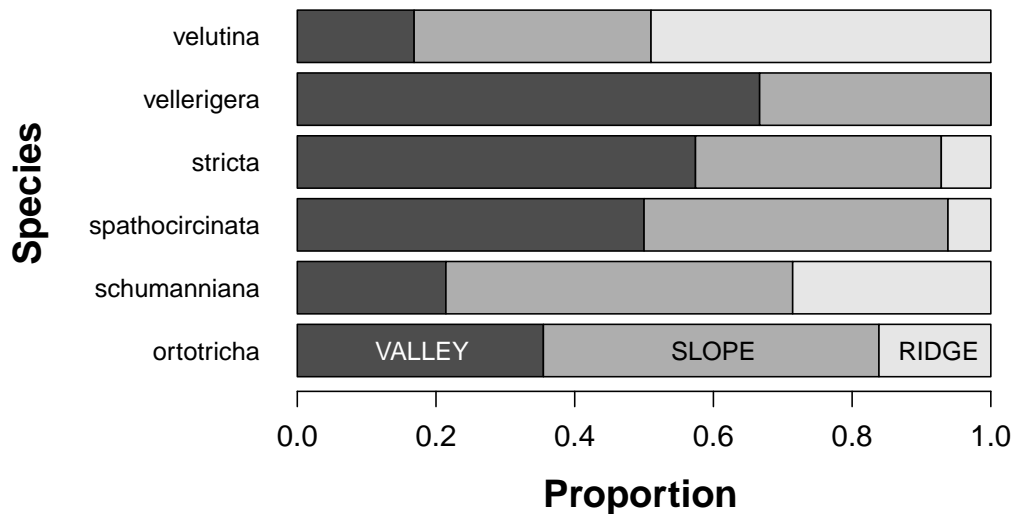
*velutina* L. Andersson ( $n = 903$ ), *Heliconia spathocircinata* Aristeg. ( $n = 239$ ), *Heliconia ortotricha* L. Andersson ( $n = 36$ ), *Heliconia vellerigera* Poepp. ( $n = 20$ ) and *Heliconia schumanniana* Loes. ( $n = 14$ ).

More *Heliconia* individuals were found in the valley (979, 41%) than on the slope (847, 35%) or on the ridge (571, 24%).

As well as differences in total abundance, these six species also differed in their abundance by habitat (Fig. 5). *Heliconia stricta* was the most common species in valley habitat ( $n = 656$ ), with about 5–6 times more individuals than either *H. velutina* ( $n = 136$ ) or *H. spathocircinata* ( $n = 120$ ). *Heliconia stricta* was the most common species on the slope ( $n = 407$ ) and in the valley, though many *H. velutina* ( $n = 292$ ) and *H. spathocircinata* ( $n = 107$ ) individuals lived on the slope as well. *Heliconia velutina* was



**Fig. 4.** Distribution of six species of *Heliconia* in the Yasuní forest plot. Circles indicate 20x20m sample quadrants; filled circles indicate the presence of that species.



**Fig. 5.** *Heliconia* species proportions by habitat. Because the *Heliconia* species differ greatly in total frequency, the proportion plot offers a more direct comparison for which habitat the species exhibits a preference. Valley = dark-grey, slope = mid-grey, pale-grey = ridge. Most *Heliconia* species were found in the valley. *H. velutina* was the only species that preferred the ridge.

the species most likely to be on a ridge ( $n = 475$ ), with 6 times more *H. velutina* individuals than the second most common species, *H. stricta* ( $n = 72$ ). No *H. vellerigera* individuals were found on a ridge.

Most of the correlations between species presence in a particular habitat were consistent and statistically significant (logistic regression of presence as a function of habitat). *Heliconia stricta* ( $t_{\text{ridge}} = 6.739$ ,  $t_{\text{slope}} = 6.695$ ,  $t_{\text{valley}} = 10.665$ , all  $p < 0.01$ ) and *H. spathocircinata* ( $t_{\text{ridge}} = 2.660$ ,  $t_{\text{slope}} = 3.261$ ,  $t_{\text{valley}} = 5.643$ , all  $p < 0.01$ ) were likely to be present in slope and valley but absent in ridge quadrants. *Heliconia ortotricha* ( $t_{\text{ridge}} = 1.843$ ,  $p = 0.068$ ;  $t_{\text{slope}} = 2.259$ ,  $p = 0.0249$ ;  $t_{\text{valley}} = 0.521$ ,  $p = 0.6027$ ) was likely to be present in slope quadrants, but not on the ridge. *Heliconia velutina* ( $t_{\text{ridge}} = 16.801$ ,  $p < 0.01$ ;  $t_{\text{slope}} = 0.720$ ,  $p = 0.472$ ;  $t_{\text{valley}} = -3.126$ ,  $p < 0.01$ ) was likely to be present in ridge quadrants and absent in the valley. *Heliconia vellerigera* and *H. schumanniana* had small sample sizes.

There was a significant difference in the number of species per quadrat by habitat (generalized linear model with Poisson counts,  $p < 0.01$ , Fig. 6). Valley habitat averaged  $2.4 \pm 0.111$  species present per quadrant, and slope  $2.3 \pm 0.128$  species. Ridge habitat was less diverse, with  $1.4 \pm 0.112$  species.

#### *Heliconia* species exhibit habitat preference with respect to topography

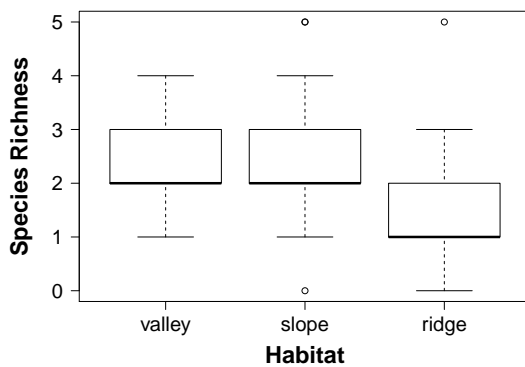
Most *Heliconia* species exhibited significant variation in their relative abundance across the three habitats, according to a proportion test of the total quantity of each species, with only *H. schumanniana* showing no significant difference from an even distribution of  $1/3$  of individuals in each habitat (Fig. 7 and 8) (test of equal proportions: *H. stricta*  $p < 2.2e-16$ , *H. velutina*  $p < 2.2e-16$ , *H. ortotricha*  $p = 0.004631$ , *H. spathocircinata*  $p < 2.2e-16$ , *H. vellerigera*  $p = 1.995e-6$ , *H. schumanniana*  $p = 0.2484$ ).

*Heliconia stricta* and *H. ortotricha* were signifi-

cantly more abundant in valley and slope habitats, *H. vellerigera* was significantly more abundant in valley habitat, *Heliconia velutina* was significantly more abundant in ridge habitat, and *H. schumanniana* in slope habitat.

*Some Heliconia species exhibit preferential co-occurrence*

Most of the *Heliconia* species pairings appear to be random in the Yasuní sample (Table 1). However, *H. stricta* and *H. velutina* exhibited a negative correlation, indicating that each grew in quadrants absent of other species more often than would be expected to occur randomly by chance. In contrast, *Heliconia stricta*, *H. ortotricha* and *H. spathocircinata*



**Fig. 6.** Mean *Heliconia* species richness per quadrat by habitat. Ridge habitat had lower richness than valley and slope.

**Table 1.** Co-occurrence of *Heliconia* species in Yasuní National Park. Species pairs exhibited positive (+), negative (-), or random (o) co-occurrence patterns.

	spath.	ortho.	stric.	vel.
spathocircinata		+	+	o
ortotricha	+		+	o
stricta	+	+		-
velutina	o	o	-	

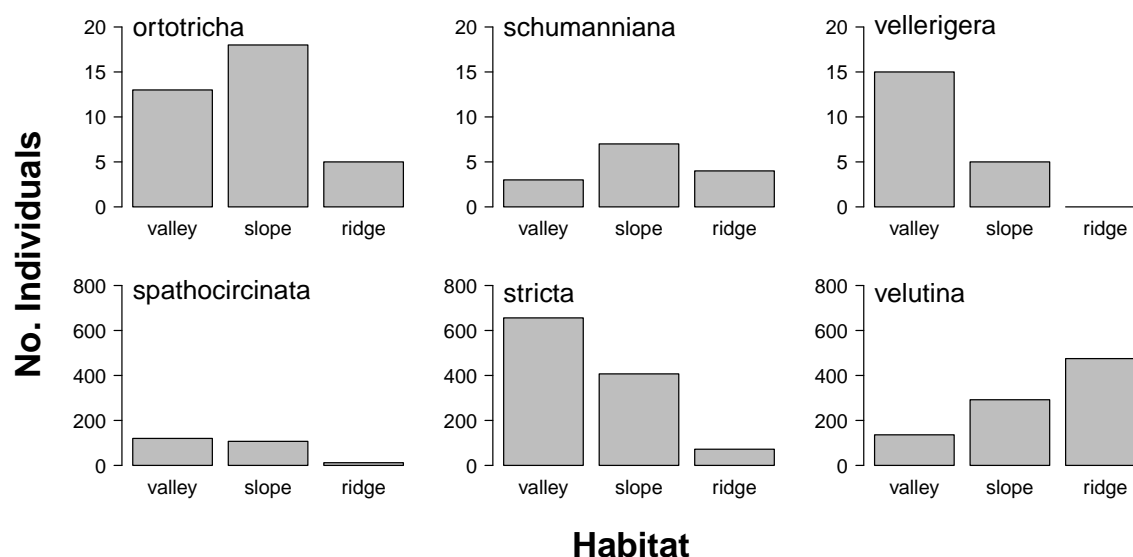
tended to display an opposite preference because they tended to coincide grow in quadrants where each with one other was also present more often than would be expected by chance.

## Discussion

The distributions of many woody tree species vary significantly according to topographic variation (Valencia et al. 2004). Similarly, this study found that species of *Heliconia* also had distinct distributions across the three habitats in the Yasuní plot. There are likely several drivers of this variation.

The most striking distribution was, when considering all the *Heliconia* individuals, most were found in the valley habitat (40%), with fewer on slopes (35%) and even fewer on ridges (25%). Major differences in water and light availability are easily seen between the valley and the ridge quadrants (Tokarz 2015, personal observation), as in previous studies (Queenborough et al. 2007, Davison and Forman 1982, Harms et al. 2001). For example, the valley often contained water running through streams or standing in swampy regions, which the ridge did not have. This correlation of species distributions with resource gradients is common. Treefalls and lower canopies were more characteristic of the valley. Increasing canopy gaps is believed to increase light and moisture conditions (Davison and Forman 1982).

In temperate zones, herb diversity and distribution fluctuates with variation in resources influenced by topography, such as soil nutrients and light availability (McEwan et al. 2011). The few studies conducted in the tropics have shown similar patterns (Tuomisto et al. 2003). The factors may overlap in influence and may not act independently. Past studies have shown that species-topography associations may be underlain by the amount of water that soil retains in each habitat type over small spatial scales such as those in the Yasuní plot (Comita and Engelbrecht 2009), as well as over much larger scales. Drought resistance has been shown to be a strong driver of the distribution



**Fig. 7.** Number of individuals of each *Heliconia* species found in each of three habitat types in Yasuní plot. *Heliconia stricta* tended to grow in lower elevation habitats and *H. velutina* tended to grow at higher elevation habitats.

and performance of tropical tree seedlings. Though habitat associations are greatly pronounced with the changing elevation and temperature gradient along a mountainside, differences in hydrology probably lead to the strongest habitat associations between species (Moeslund et al. 2013).

This pattern is exemplified by *Heliconia vellerigera*. Only found in only 2% of the quadrants surveyed, it displayed the strongest habitat association, with 75% of individuals in the valley, 25% on the slope, and none in ridge quadrants. Moreover, individuals in the valley were much larger (up to 4 m) than the individuals on the slope (1 m) (Tokarz 2015, personal observation), which suggests that *H. vellerigera* had access to better or more resources in the valley and that the species has a strong positive association with the valley.

*Heliconia ortotricha* was found in 12% of the quadrants surveyed, but was spotted frequently along the roadside en route to the plot and a large individual was situated along a trail inside the plot. If they are successful on a sunny roadside plot, *H.*

*ortotricha* presence may be indicative of a recent disturbance and greater amounts of light. *Heliconia ortotricha* were certainly least common in the ridge, and were slightly more prevalent in slope quadrants than in valley quadrants. This may show that the slope also has greater amounts of light available than the ridge, and possibly more than the valley. *Heliconia* species, in general, tend to grow in disturbed areas, though *H. ortotricha* may be more prone than the other species in this survey. Although treefalls and natural disturbances are common and expected in a tropical forest, *Heliconia* species may play a bigger role in freshly cleared areas where plenty of light is available.

*Heliconia stricta* and *H. velutina* were the most abundant *Heliconia* species found in the plot. *Heliconia stricta* was found in 67% of the quadrants surveyed. Not only is *H. stricta* the most abundant species in the plot, but it far outnumbers any other species in the valley, with six times as many individuals as the second most abundant valley *Heliconia*. *Heliconia velutina* was found in 76% of the



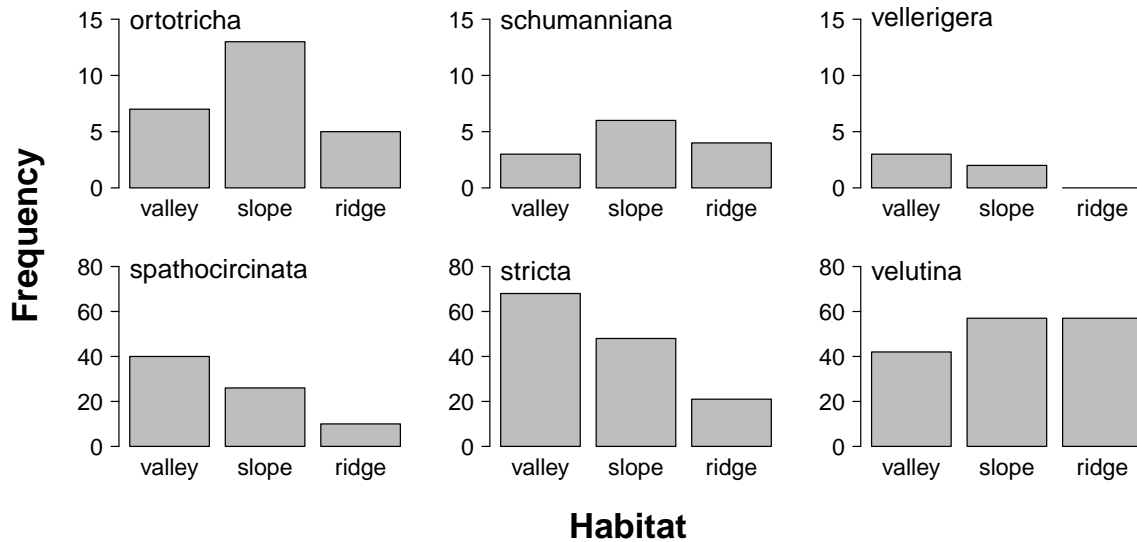
quadrants surveyed. *H. velutina* was by far the most abundant species on the ridges, with six times as many individuals as the second most abundant ridge *Heliconia*. Due to their overall greater abundance, both *H. stricta* and *H. velutina* were also the most abundant *Heliconia* on the slope, but only about 30% of the individuals of each species were on the slope for both species. 50% of each species was in the preferred habitat and about 10% of each species was in the habitat furthest removed from the one preferred. This created a distribution of about 50-35-15 for each of the most common *Heliconia* species spread across their most preferred to least preferred habitat.

*Heliconia velutina* was the species with the highest proportion of individuals on the ridge with about half of the individuals of *H. velutina* found in a ridge quadrant. The next highest proportion was that a quarter of *H. schumanniana* individuals were found in ridge quadrants, but the sample size of *H. schumanniana* is about a hundredth that of *H. velutina*. In short, *H. velutina* grew much better on the ridge than any other *Heliconia* and composed over 80% of all the *Heliconia* found on the ridge. *Heliconia velutina* also grew successfully in other habitats, so this does not necessarily mean that *H. velutina* is a dry habitat specialist, but it does suggest that *H. velutina* has a higher drought-tolerance than other *Heliconia* species, so they are able to dominate an otherwise *Heliconia*-poor habitat. Considering diversity, valley quadrants were the most diverse for *Heliconia* species with about 2.4 species found in each quadrant (compared to 2.3 species in slope quadrants), and ridge quadrants were the least diverse with about 1.4 *Heliconia* species found per quadrant. The observation that there is greater *Heliconia* diversity in the valley and the slope suggests that *Heliconia* species prefer valley and slope conditions to those of the ridge, in general.

While *H. stricta* often grew alongside other species in its preferred valley habitat, *H. velutina* was more often by itself in the ridge quadrants. Once again, this general absence of *Heliconia* species from ridge quadrants is also an absence of

*Heliconia* competition, which allows *H. velutina* to dominate the resources.

The difference in the distributions of *H. stricta* and *H. velutina* presence are not inverse, as the distributions of individual counts are (Figs. 9 and 10). *Heliconia stricta* and *H. spathocircinata* do have similar distribution shapes, present in more quadrants in the valley than in the slope or the ridge. On the other hand, *H. velutina* is present in nearly as many slope quadrants as ridge quadrants, despite having a much higher individual count on the ridges. The number of valley quadrants in which *H. velutina* is present is also rather large, especially when we see that *H. stricta* is present in half as many quadrants of its least common habitat, the ridge. The distribution of *H. velutina*, in terms of how many quadrants of each habitat in which it is present, is the most even of the six species. Gravity may play a role. Because *H. velutina* appears to consistently find success in ridge quadrants, *H. velutina* on the ridge are likely to produce seeds in larger amounts than *H. velutina* in other habitats. Ridgetop *H. velutina* individuals do not even have to compete for pollinators with other *Heliconia* species because the ridge is a less diverse place for *Heliconia*. Seeds produced by *H. velutina* on the ridge can also roll along the topography and land in either slope or valley quadrants. Because valley quadrants are more devoid of *H. velutina* than the slopes, it seems that it is easier for seeds to reach the slope because slopes are closer to the ridgetop. Even if most of the *H. velutina* that grows in non-ridge habitats are not successful enough to sustain a new population surrounding them, the seeds from the ridge will continue to tumble and create a steady supply of *H. velutina* seeds in every habitat. On the other hand, it would be more difficult for *H. stricta* seeds to ascend to different habitats. It is not impossible, but the transport of *H. stricta* seeds up to slopes or ridges may have to be facilitated in smaller increments by an animal. This upward process is slower and less trustworthy than the forces of gravity, so it may explain why *H. stricta* and *H. spathocircinata* are not found as often on the ridge as in the valley.



**Fig. 8.** Frequency of occurrence of each *Heliconia* species found in each of three habitat types in Yasuní plot. The maximum amount of quadrants a species could be found in is 68 per habitat. *Heliconia stricta* was found in almost every valley quadrant surveyed. *Heliconia vellerigera* was not found in any ridge quadrant surveyed.

Specific details about the physiological functions and traits of the *Heliconia* species in the study highlight their functional differences from trees. First, *Heliconia* are rhizomatous and clonal, meaning that one *Heliconia*'s root system can expand to support additional plant structures. This strategy gives the appearance of many *Heliconia* when all the stems actually share the same root system. Although counted *Heliconia* were counted as separate when they were more than about a meter apart from each other, the exact quantities tallied may be an overestimate of the amount of individuals.

Second, a *Heliconia*'s, inflorescence lasts for a few days before the plant is pollinated and no longer in need of attracting pollinators, but the florescence makes plant recognition and species identification easier. Without florescence, a *Heliconia* may be confused with a member of Marantaceae or simply easier to overlook. Especially with such a small team, the census is probably not an exact representation, but I confidently say that it is similar.

On a larger scale, it is uncertain how broadly

these findings generalize to other herbs. Only six species of a specific genera were counted for this survey, but the herbaceous layer in species-rich forests has historically been under-sampled (Gilliam 2014). More detailed studies and complete inventories of herbaceous plants would better reveal the mechanisms that drive variation in the abundance, distribution, and diversity of this important component of forest ecosystems.

## Conclusion

A census of six species of *Heliconia* revealed distinct variation in abundance and diversity by habitat. The two most abundant species, *H. stricta* was dominant in the valley and *H. velutina* was dominant on the ridge. Species diversity was greater in the valley and most species were more abundant in valley quadrats, probably due to local increased availability of light and water. The success of *H. velutina* on the ridge suggests an increased drought resistance in comparison to other *Heliconia*. These results suggest that habitat niche-partitioning is

a strong driver of the coexistence of herbaceous plants in tropical forests.

### Acknowledgements

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### References

- Bass M.S., Finer M., Jenkins C.N., Kreft H., Cisneros-Heredia D.F., et al. 2010. Global conservation significance of Ecuador's Yasuní National Park. *PLoS ONE* **5**, e8767.
- Brewer, R. 1980. A half-century of changes in the herb layer of climax deciduous forest in Michigan. *Journal of Ecology* **68**, 823–832.
- Comita, L.S., Engelbrecht, B.M.J. 2009. Seasonal and spatial variation in water availability drive habitat associations in a tropical forest. *Ecology* **90**, 2755–2765.
- Condit, R. 2013. *Tropical Forest Census Plots: Methods and Results from Barro Colorado Island, Panama and a Comparison with Other Plots*. Landes Bioscience. Georgetown, USA.
- Costa, F.R.C., Espinelli, F.P., Figueiredo, F.O.G. 2011. *Guia de zingiberales dos sitios PPBio na Amazonia Ocidental brasileira*. Flavia R.C. Costa. Manaus, Brazil.
- Dalling, J.W., Schnitzer, S.A., Baldeck, C., Harms, K.E., John, R., Mangan, S.A., Lobo, E., Yavitt, J.B., Hubbell, S.P. 2012 Resource-based habitat associations in a Neotropical liana community. *Journal of Ecology* **100**, 1174–1182.
- Davison, S.E., Forman, R.T.T. 1982. Herb and shrub dynamics in a mature oak forest: A thirty-year study. *Bulletin of the Torrey Botanical Club* **109**, 64–73.
- Feeley, K.J., Davies, S.T., Perez, R., Hubbell, S.P., Foster, R.B. 2011. Directional changes in the species composition of a tropical forest. *Ecology* **92**, 871–882.
- Felton, A., Felton, A.M., Wood, J., Lindenmayer, D.B. 2006. Vegetation structure, phenology, and regeneration in the natural and anthropogenic tree-fall gaps of a reduced-impact logged subtropical Bolivian forest. *Forest Ecology and Management* **235**, 186–193.
- Gentry, A.H., Dodson, C. 1987. Contribution of nontrees to species richness of a tropical rain forest. *Biotropica* **19**, 149–156.
- Gilliam, F.S. 2007. The ecological significance

- of the herbaceous layer in temperate forest ecosystems. *BioScience* **57s**, 845–858.
- Griffith, D., Veech, J., Marsh, C. 2014. *cooccur: Probabilistic Species Co-occurrence Analysis in R*. Guo-Yu, L., Yue-Hua, H., Min, C., Hua, Z., Hong, W., Shi-Shun, Z., Xiao-Bao, D., Jing-Yun, C., Jian-Guo, H., Lin-Yun, L., Hai-Long, X., Jun-Ping, S., You-Cai, H. 2008. Establishment of Mshuangbanna tropical forest dynamics plot: Species compositions and spatial distribution patterns. *Acta Phytoecologica Sinica* **32**, 287–298.
- Harms, K.E., Condit, R., Hubbell, S.P., Foster, R. 2001. Habitat associations among trees and shrubs in 50-ha Neotropical plot. *Journal of Ecology* **89**, 947–959.
- Hutchinson, T.F., Boerner, R.E.J., Iverson, L.R., Sutherland, S., Sutherland, E.K. 1999. Landscape patterns of understory composition and richness across a moisture and nitrogen mineralization gradient in Ohio (U.S.A.) *Quercus* forests. *Plant Ecology* **144**, 177–189.
- John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M., Foster, R.B. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 864–869.
- Kumar, P.P., Nathan, M.J., Goh, C.J. 1996. Involvement of ethylene on growth and plant regeneration in callus cultures of *Heliconia psittacorum* L.f. *Plant Growth Regulation* **19**, 145–151.
- McEwan, R.W., Muller, R.N. 2011. Dynamics, diversity and resource gradient relationships in herbaceous layer of an old-growth Apalachian forest. *Plant Ecology* **212**, 1179–1191.
- Moeslund, J.E., Arge, L., Bøcher, P.K., Dalgaard, T., Svenning, J. 2013. Topography as a driver of local terrestrial vascular plant diversity patterns. *Nordic Journal of Botany* **31**, 129–144.
- Murphy, S.J., Salpeter, K., Comita L.S. 2016. Higher  $\beta$ -diversity observed for herbs over woody plants is driven by stronger habitat filtering in a tropical understory. *Ecology* **97**, 2074–2084.
- Pérez, A.J., C. Hernández., H. Romero-Saltos., R. Valencia. 2014. *Árboles Emblemáticos de Yasuní*. Herbario QCA, Quito, Ecuador.
- Phillips, O.L., Vargas, P.N., Monteagudo, A.L., Cruz, A.P., Zans, M.C., Sánchez, W.G., Yli-Halla, M., Rose, S. 2003. Habitat association among Amazonian tree species: a landscape-scale approach. *Journal of Ecology* **91**, 757–775.
- Pitman, N.C., Mogollon, H., Dávila, N., Ríos, M., García-Villacorta, R., Guevara, J., Baker, T.R., Monteagudo, A., Phillips, O.L., Vásquez-Martínez, R., Ahuite, M., Aulestia, M., Cardenas, D., Cerón, C.E., Loizeau, P., Neill, D.A., Núñez, P., Palacios, W.A., Spichiger, R., Valderrama, E. 2008. Tree community change across 700 km of lowland Amazonian forest from the Andean foothills to Brazil. *Biotropica* **40**, 525–535.
- Queenborough, S.A., Burslem, D.F.R.P., Garwood, N.C., Valencia, R. 2007. Habitat niche partitioning by 16 species of Myristicaceae in Amazonian Ecuador. *Plant Ecology* **192**, 193–207.
- R Core Team 2014. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.