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DOI: <https://doi.org/10.1111/j.1570-7458.2010.01063.x>

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Journal Article

Originally published at:

Abrahamczyk, S; Steudel, B; Kessler, M (2010). Sampling Hymenoptera along a precipitation gradient in tropical forests: the effectiveness of different coloured pan traps. *Entomologia Experimentalis et Applicata*, 137(3):262-268.

DOI: <https://doi.org/10.1111/j.1570-7458.2010.01063.x>

Sampling Hymenoptera along a precipitation gradient in tropical forests: the effectiveness of different coloured pan traps

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Accepted: 7 September 2010

Key words: measuring biodiversity, Bolivia, bee, wasp, forest edge, assemblage composition, canopy cover

Abstract

Measuring species richness of tropical insects is an important but considerable challenge. Several techniques have been developed to quantitatively sample the non-formicid Hymenoptera (bees and wasps). One of the most common is the use of colored pan traps. Although it is known that Hymenoptera are attracted differently by different colors, it is not yet known if these preferences shift in different habitats and hence affect comparisons of Hymenoptera diversity. We studied the effectiveness of differently-colored pan traps along a latitudinal, climatic, and forest structure gradient from tropical to subtropical forests. Overall, we found a strong increase in individual numbers from north to south. Yellow traps sampled significantly more individuals than blue ones, mainly due to the responses of the families Ichneumonidae, Nyssonidae, Pompilidae, and Crabronidae, but trap catch was also related to canopy cover. Notably, traps located at forest edges had yellow/blue ratios similar to those of forests with comparable canopy cover. This suggests that, in contrast to the overall number of individuals caught, the relative effectiveness of yellow vs. blue traps was driven by canopy cover and hence light conditions or visibility of the traps. Thus comparisons of pan trap results between forests having different structures should only be made with great care.

Introduction

With over 115 000 known species, Hymenoptera are one of the four most species-rich insect orders (Goulet & Hubler, 1993). Even excluding the ants, this order comprises more than 100 000 species of mostly flying bees and wasps. Hymenoptera include the most important pollinators worldwide and are keystone species in most terrestrial habitats (Bawa et al., 1985). Other Hymenoptera play important roles as predators, parasites, or parasitoids on arthropod species.

For conservation issues, measuring this diversity is an important challenge. Over the years, a number of techniques have been developed to quantitatively sample Hymenoptera diversity, including pitfall, malaise, flight intercept, and colored pan traps (Campbell & Hanula, 2007; Wilson et al., 2008; Missa et al., 2009). The latter, in which pans of different colors (usually white, yellow, and/or blue) attract insects to a solution in which they

drown, is one of the most commonly-used techniques. However, it is known that the sampling efficiency of traps may be influenced by the color of the traps, both for all Hymenoptera combined and for individual families (Aguilar & Sharkov, 1997; Hoback et al., 1999; Toler et al., 2005; Campbell & Hanula, 2007; Roulston et al., 2007; Wilson et al., 2008). This has been documented mainly in open or semi-open habitats in temperate North America and Europe, and predominantly looking at the Apiformes (bees). To date, only one study of this kind has been conducted in a forested ecosystem (North American pine forest) (Campbell & Hanula, 2007). Pan traps have also been used to sample Hymenoptera in tropical forests, but without assessing the influence of color on the collection results (Noyes, 1989; Kitching et al., 2001; Wells & Decker, 2006; Missa et al., 2009). Of these studies, most focused on disturbance gradients, and one covered an elevational forest gradient (Noyes, 1989).

In our study, we provide the first data on the influence of color on the sampling results for a wide range of hymenopteran families along a precipitation and seasonality

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gradient in tropical and subtropical lowland forests. To assess the influence of color, we addressed several questions: (a) Do traps of different color attract different numbers of individuals and families of Hymenoptera? (b) Do different Hymenoptera families show preferences for different trap colors? (c) Are these patterns influenced by vegetation structure, which changes along the precipitation gradient of our study?

Materials and methods

Our study was conducted at six sites along a latitudinal gradient from the tropics to the subtropics in Bolivia (Villa Tunari: 16°57'S, 65°24'W; Sacta: 17°06'S, 64°47'W; Buena Vista: 17°30'S, 63°38'W; Santa Cruz: 17°46'S, 63°04'W; Río Seco: 18°42'S, 63°11'W; and Corbalán: 21°36'S, 62°27'W). Along this gradient, mean annual precipitation decreases from 6 258 mm at Villa Tunari to 410 mm at Corbalán, while seasonality in temperatures and precipitation increases. Climatic data were taken from a climate model for Bolivia (Kessler et al., 2007; Soria-Auza et al., 2010; Table 1).

Study sites consisted of primary, occasionally slightly disturbed, forest at 200–440 m a.s.l. During the dry season between May and October 2008, each site was sampled once for a period of 8 days. The sites were sampled in a mixed order to avoid time of the season as a factor. At all sites, we established a 1.5-km long transect along a path through the forest whose minimum distance to the forest border was 150 m to avoid edge effects (Murcia, 1995; Debinski & Holt, 1999; Hausmann et al., 2005; Grimbacher et al., 2006). Tree height and cover were estimated at four random places along each transect during the sampling period. Along each transect during five consecutive days, we placed 13 pairs of yellow and blue pan traps on the ground at distances of approximately 120 m. Pans of a pair were touching each other. All pans were 27 cm in diameter and 5 cm high, and were sprayed with UV-reflecting color. The traps were filled with water, a drop of honey, and dishwashing detergent. We emptied the traps daily in the late afternoon. On the remaining 3 days we

placed the 13 pairs of traps along a 350 m long section of a sharp forest border. The pairs of traps were placed 25–28 m away from each other at the forest edge. At forest edges, tree cover in the adjacent forest was estimated at four random places 10–12 m into the forest. For statistical analysis, we divided the tree cover by two due to the position of the traps at the edge where only one side was covered.

All non-formicidae Hymenoptera were collected and dried. Later we prepared all individuals and identified them to family level using Goulet & Hubler (1993).

With a linear model in R 2.10 (R Development Core Team, 2007) we correlated the total number of individuals and the number of individuals per family collected per site against latitude to find out which family contributes most to the diversity pattern. We then conducted linear regression analyses of the total number of individuals and families and the number of individuals per family at each site against the environmental factors to explain family diversity patterns. We adjusted P-values with the sequential Bonferroni correction method (Rice, 1989). Then we calculated G-tests to find out whether the sampled number of individuals per site were equally distributed between sampling days. For sites with significant results, we then calculated Spearman Rank correlation factors of individual numbers against sampling days to test if differences between days showed consistent temporal patterns. To test for differences in sampling effectiveness of the differently colored traps and sites, we used Mann-Whitney U-test and Kruskal-Wallis tests. With a Wilcoxon test for matched pairs, we tested if the proportion of individuals and families collected was different inside the forests and at the forest edges. For this comparison, we multiplied the number of individuals collected in the forest by 0.6 to account for the different number of collection days between forests and forest edges. We utilized this method and did not reduce the sampling days to be consistent with all other statistical analyses and to avoid discarding data. Linear regressions were used to assess the relationship of the ratio of individuals collected in yellow and blue traps inside the forest and at the forest edge and the forest cover. Further,

Table 1 Environmental characteristics of the six study sites (mean \pm SD)

| | Elevation (m) | Precipitation total (mm) | Temperature amplitude (°C) | No. arid months | Minimum temperature (°C) | Tree height (m) | Canopy cover (%) | Canopy cover edge (%) |
|--------------|---------------|--------------------------|----------------------------|-----------------|--------------------------|------------------|-------------------|-----------------------|
| Corbalán | 268 | 410 | 7 | 8 | -3 | 3.50 \pm 0.58 | 28.75 \pm 4.79 | 14.75 \pm 1.81 |
| Río Seco | 434 | 729 | 5 | 6 | -1 | 8.00 \pm 0.00 | 33.30 \pm 17.08 | 16.63 \pm 5.24 |
| Santa Cruz | 397 | 1166 | 5 | 2 | 1 | 18.25 \pm 2.36 | 42.50 \pm 11.90 | 22.19 \pm 4.38 |
| Buena Vista | 424 | 2000 | 4 | 0 | 3 | 18.00 \pm 1.63 | 65.00 \pm 7.07 | 33.13 \pm 4.33 |
| Sacta | 204 | 3457 | 4 | 0 | 5 | 20.00 \pm 1.63 | 60.00 \pm 7.07 | 31.25 \pm 4.46 |
| Villa Tunari | 400 | 6258 | 3 | 0 | 6 | 15.50 \pm 3.79 | 62.50 \pm 11.90 | 32.50 \pm 5.40 |

we used G-tests for each site to assess if families were unequally collected in traps of different colors. Later, we used Species Indicator Analyses (Dufrene & Legendre, 1997) in PCOrd 5 (McCune & Mefford, 1999) to find out which families were significantly more common in one type of trap. We only calculated species indicator values for families with more than five individuals per site. Finally, we calculated pair-wise site comparisons of family composition with the quantitative Sorensen similarity (Bray-Curtis) index and applied a linear model in R 2.10 to test whether blue or yellow traps were more similar across sites in the families that they attracted. We decided to define an additional level of marginal significance at $P = 0.1$ because of the low number of study sites.

Results

In total, we collected 1 829 individuals of non-formicidae Hymenoptera belonging to 22 families. In the yellow traps, we collected 864 individuals (19 families) inside the forests and 418 individuals (13 families) at the forest edges. In the blue traps we collected 326 individuals (11 families) inside the forests and 185 individuals (8 families) at the forest edges (Table 2).

The linear models correlating the total number of individuals and the number of individuals per family collected per site against latitude recovered significant relationships for the total number of individuals ($R^2 = 0.94$, $P = 0.002$) and for Crabronidae ($R^2 = 0.85$, $P = 0.009$), Halictidae ($R^2 = 0.90$, $P = 0.004$), Ichneumonidae ($R^2 = 0.71$, $P = 0.035$), and Vespidae ($R^2 = 0.94$, $P = 0.002$; Figure 1). For

all analysis except for Ichneumonidae we found a positive relation to latitude.

The G-tests for sampling effectiveness between collecting days per site revealed significant differences (all $P < 0.01$) in the number of collected individuals per day for Río Seco ($G = 108.8$, d.f. = 4), Santa Cruz ($G = 14.2$, d.f. = 4), Buena Vista ($G = 247.8$, d.f. = 4), and Sacta ($G = 68.4$, d.f. = 4). But only in Buena Vista did we find a marginally significant increase in collected individuals from the first to the last day ($R^2 = 0.75$, $P = 0.057$). These differences are most likely related to weather conditions but because we do not have weather data for each sampling day, we will not further discuss these results. The number of individuals and families differed significantly among sites for forests and forest edges [Kruskal-Wallis tests: individual number (forest: $H = 64.1$, d.f. = 5; forest edge: $H = 55.35$, d.f. = 5), family number (forest: $H = 36.15$, d.f. = 5; forest edge: $H = 49.25$, d.f. = 5; all $P < 0.001$)]. We found similar results for the number of individuals and families among colors (Mann-Whitney U-tests: individual number (forest: $U = 1\ 816$, d.f. = 1; forest edge: $U = 2\ 127$, d.f. = 1) and family number (forest: $U = 1\ 506$, d.f. = 1; forest edge: $U = 2\ 053$, d.f. = 1; all $P < 0.001$). When we checked which environmental variables caused the significant differences between the sites by linear regression analyses, we found that mainly climatic but also structural characters had an effect on the total number of individuals and on the number of individuals of several families (Table 3). We found no significant relationships for the number of families against any environmental variable.

| | Corbalán | Río Seco | Santa Cruz | Buena Vista | Sacta | Villa Tunari |
|-----------------|----------|----------|------------|-------------|-------|--------------|
| Apidae B | 4 | 30 | 0 | 3 | 2 | 1 |
| Apidae Y | 11 | 76 | 0 | 4 | 0 | 5 |
| Bethylidae B | 1 | 1 | 0 | 1 | 1 | 0 |
| Bethylidae Y | 0 | 2 | 0 | 8 | 0 | 3 |
| Braconidae B | 0 | 4 | 0 | 0 | 0 | 0 |
| Braconidae Y | 0 | 3 | 0 | 1 | 1 | 0 |
| Crabronidae B | 4 | 0 | 0 | 3 | 0 | 0 |
| Crabronidae Y | 17 | 3 | 3 | 5 | 9 | 0 |
| Halictidae B | 186 | 16 | 8 | 4 | 1 | 0 |
| Halictidae Y | 337 | 6 | 5 | 10 | 1 | 0 |
| Ichneumonidae B | 1 | 5 | 3 | 9 | 9 | 9 |
| Ichneumonidae Y | 3 | 13 | 15 | 31 | 38 | 21 |
| Nyssonidae B | 0 | 0 | 0 | 0 | 0 | 0 |
| Nyssonidae Y | 5 | 1 | 3 | 1 | 0 | 2 |
| Pompilidae B | 7 | 14 | 0 | 14 | 1 | 0 |
| Pompilidae Y | 18 | 35 | 12 | 74 | 6 | 9 |
| Vespidae B | 9 | 3 | 1 | 1 | 0 | 0 |
| Vespidae Y | 20 | 4 | 0 | 3 | 0 | 0 |

Table 2 Number of individuals of the nine main hymenopteran families sampled in the yellow (Y) and blue (B) traps in the different forest study sites

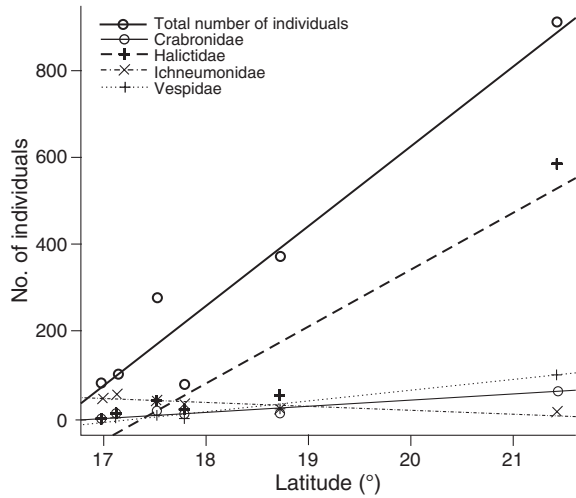


Figure 1 Linear models of the total number of individuals ($P = 0.002$) and the individual number of the four families Crabronidae ($P = 0.009$), Halictidae ($P = 0.004$), Ichneumonidae ($P = 0.035$), and Vespidae ($P = 0.002$) against latitude.

With Wilcoxon test matched pairs we were able to document that only Ichneumonidae ($P = 0.036$) and Nyssonidae ($P = 0.009$) showed a significant difference in collection rates between blue and yellow traps whereas Crabronidae ($P = 0.079$) and Pompilidae ($P = 0.092$) showed marginally significant ones. G-tests showed that at all sites, the family composition differed significantly between the blue and yellow traps in the forests. This was also true for the forests edges with the exception of Santa Cruz and Villa Tunari (Table 4). There was no significant difference between the total number of individuals (Wilcoxon test for matched pairs: $P = 0.485$) and families ($P = 0.375$) collected inside the forests and the adjusted number collected at the forest edges. With a linear regression of the ratio of individuals collected in yellow and blue traps inside the forest and at the forest edge against forest cover we found a significant positive relation ($R^2 = 0.40$, $P = 0.036$; Figure 2).

To be able to show individually for each site which families were significantly more common in one type of trap we used Species Indicator Analyses, which found that all families showing significant differences were more numerous in yellow traps. As predicted by the more general G-tests, at each site inside the forest we found at least one family to be significantly more common in one type of trap. However, at the forest edges, the Indicator Species Analyses did not recover significant results at Sacta and Corbalán, which partly contradicted the results of the G-tests. For the nine most numerous families, Table 4 gives an overview of their occurrence and of significant dif-

Table 3 R^2 values for the linear regression analyses of the number of individuals (ind.), families (fam.), and individuals of the most important hymenopteran families of the six sites against environmental factors

| | No. ind. | No. fam. | Apidae | Bethylidae | Braconidae | Crabronidae | Halictidae | Ichneumonidae | Nyssonidae | Pompilidae | Vespidae |
|----------------------------|----------|----------|--------|------------|------------|-------------|------------|---------------|------------|------------|----------|
| Elevation (m) | 0.07 | 0.03 | 0.04 | 0.12 | 0.27 | 0.22 | 0.17 | 0.02 | 0.00 | 0.28 | 0.15 |
| Precipitation total (mm) | 0.21 | 0.00 | 0.33 | 0.01 | 0.12 | 0.22 | 0.23 | 0.52 | 0.15 | 0.11 | 0.25 |
| No. arid months | 0.74* | 0.03 | 0.67* | 0.01 | 0.02 | 0.53 | 0.61 | 0.83* | 0.05 | 0.00 | 0.69* |
| Minimum temperature (°C) | 0.66* | 0.02 | 0.53 | 0.00 | 0.04 | 0.46 | 0.52 | 0.87** | 0.15 | 0.02 | 0.57 |
| Temperature amplitude (°C) | 0.75* | 0.06 | 0.28 | 0.01 | 0.01 | 0.70* | 0.74* | 0.75* | 0.22 | 0.00 | 0.76* |
| Tree height (m) | 0.78* | 0.00 | 0.66 | 0.00 | 0.02 | 0.56 | 0.64 | 0.67* | 0.07 | 0.00 | 0.72* |
| Canopy cover (%) | 0.48 | 0.15 | 0.54 | 0.11 | 0.00 | 0.33 | 0.42 | 0.89** | 0.01 | 0.03 | 0.48 |

* $P \leq 0.05$, ** $P \leq 0.01$.

Table 4 Results of G-tests and Species Indicator Analyses per site. In each cell, the first result refers to the forest, the second to the forest edge. All significant results showed a preference for yellow traps; -, not calculable because too few individuals of that family were collected at this site

| | Corbalán | Río Seco | Santa Cruz | Buena Vista | Sacta | Villa Tunari |
|---------------|------------------------|------------------------|--------------------|------------------------|-----------------------|--------------------|
| G-test forest | $G_{10} = 276.45^{**}$ | $G_{12} = 102.96^{**}$ | $G_7 = 26.08^{**}$ | $G_{14} = 102.26^{**}$ | $G_{10} = 31.74^{**}$ | $G_8 = 25.77^{**}$ |
| G-test edge | $G_9 = 125.42^{**}$ | $G_6 = 67.60^{**}$ | $G_3 = 1.06$ | $G_7 = 45.31^{**}$ | $G_5 = 11.33^*$ | $G_6 = 1.05$ |
| Apidae | ns/ns | (*)/ns | -/- | ns/* | -/- | ns/- |
| Bethylidae | -/- | -/- | -/- | ns/- | -/- | -/- |
| Braconidae | -/- | ns/- | -/- | ns/- | -/- | -/- |
| Crabronidae | */(*) | (*)/- | -/- | ns/- | **/- | -/- |
| Halictidae | ns/ns | ns/ns | ns/- | ns/* | -/ns | -/- |
| Ichneumonidae | ns/ns | **/- | (*)/ns | */- | (*)/ns | **/- |
| Nyssonidae | ns/- | -/- | -/- | -/- | -/- | -/- |
| Pompilidae | **/- | **/** | **/ns | **/** | (*)/ns | */- |
| Vespidae | */ns | ns/ns | -/- | ns/- | -/- | -/- |

ns, not significant; (*) $P \leq 0.1$, * $P \leq 0.05$, ** $P \leq 0.01$.

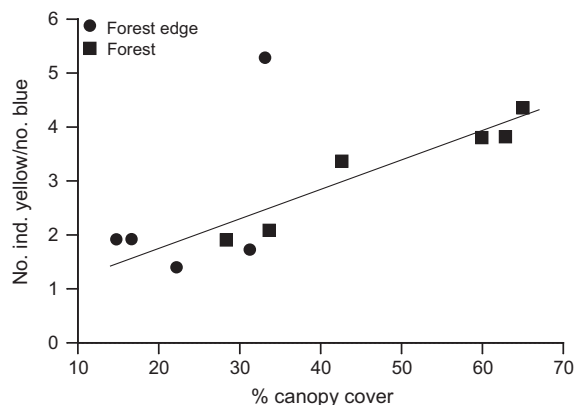


Figure 2 Linear regression of the ratio of the number of individuals (ind.) collected in yellow and blue traps per site against canopy cover. Squares: forest, circles: forest edge; $R^2 = 0.40$, $P = 0.036$. Data for the forest edge at Villa Tunari were excluded because only a single individual was caught in the blue trap, making this site a statistical outlier (yellow/blue ratio >25).

ferences between habitat types and trap colors. Finally, a linear model of pair-wise comparison of similarity in family composition (Bray-Curtis) against distance between sites for the two types of traps showed that yellow traps collected significantly more similar families at different sites compared with blue traps (Figure 3). Further, it demonstrates that similarity in trap samples decreased with increasing site distance.

Discussion

The total number of hymenopteran individuals collected increased significantly from the northern, humid tropical

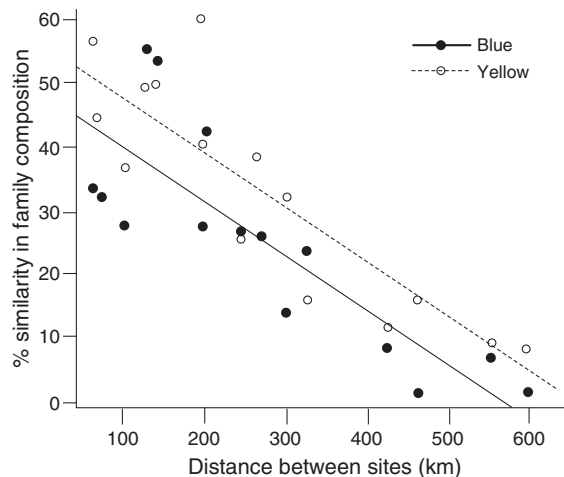


Figure 3 Linear model of pair-wise comparison of similarity in family composition (Bray-Curtis) against distance between sites for the yellow and blue traps; color $P = 0.033$, site distance $P < 0.001$; $R^2 = 0.74$, $P < 0.001$. Note that the P -values given are inflated because we used the data in more than one comparison, but we consider that the overall pattern is evident nonetheless.

rainforest sites to the southern, seasonal deciduous forest sites. This gradient also reflects a decrease in canopy cover. At first glance, this pattern appears to correspond to previous studies from single sites finding higher abundances of Hymenoptera in open habitats (Noyes, 1989; Wells & Decker, 2006; Missa et al., 2009). However, when we compared collecting densities within forests and at forest edges at our study sites, we found no significant differences between them. This suggests that the latitudinal trend in Hymenoptera density was driven by climatic seasonality or some related factor, rather than by vegetation density as

such. We found that the latitudinal trend was mainly driven by Crabronidae, Halictidae, and Vespidae, whereas Ichneumonidae showed the opposite pattern. In this latter family, the number of individuals caught was apparently directly related to canopy cover.

We found a highly significant difference in sampling effectiveness between blue and yellow traps for the whole set of families. Overall, yellow traps collected significantly more individuals and families than blue ones and no family was found significantly more often in blue traps than in yellow ones. These patterns shifted between sites and apparently were affected by forest structure. Thus, among the traps located inside the forests, the ratio between the number of individuals caught in yellow vs. blue traps decreased significantly with decreasing canopy cover. Importantly, traps located at edges had ratios similar to those of forests with comparable canopy cover. This suggests that, in contrast to the overall number of individuals caught, the relative effectiveness of yellow vs. blue traps is driven by forest structure (and accordingly by light conditions or visibility) and not by some other factor that also differed between sites, such as climatic seasonality. Possibly, yellow traps are more conspicuous and thus attractive in shady forests compared to the blue ones, or else, insects are potentially adapted to more readily find bright yellow coloured flowers in dense forest habitats.

There is considerable discrepancy in the literature regarding the sampling efficiency of differently-colored traps for Hymenoptera. After reviewing the literature, we believe that this at least partly relates to the taxa included in the studies. Thus, the majority of studies focusing on Apiformes found no color preferences at the family level (Toler et al., 2005; Roulston et al., 2007; Wilson et al., 2008), although Campbell & Hanula (2007) collected more individuals of mainly, but not exclusively, Apiformes in blue traps compared to yellow ones in a pine forest in North America. In contrast, studies of non-Apiformes using sticky color traps found preferences for yellow in the Braconidae, Aphelinidae, Encyrtidae, and Mymaridae, but not in other taxa (Neuenschwander, 1982; Samways, 1986; Redak & Bethke, 1995; Hoback et al., 1999). This agrees with our results, with significant preferences for yellow being noted primarily in non-Apiformes families such as Ichneumonidae and Nyssonidae.

Linking the above patterns, we are thus faced with a situation in which overall diversity patterns are mainly determined by regional factors such as climatic seasonality, whereas the effectiveness of differently colored traps is influenced by local, structural factors, for example canopy cover. Furthermore, these trends are mainly determined by a few families, and the higher sampling efficiency of yellow traps is primarily driven by exactly those families for

which we found an overall preference for dense, shaded habitats. These results call into question the comparability of pan traps across habitats gradients at different spatial scales. Because the abundant families Ichneumonidae and Pompilidae are primarily found in dense forests and because they prefer yellow traps, these traps located in open, seasonal habitats will by default collect relatively fewer Hymenoptera. Using traps of different colors may thus result in different perceptions of diversity patterns. If, for example, a study aims to quantify the impact of selective logging on Hymenoptera assemblages, yellow traps will give different results than blue ones.

At the same time, our study also shows that biogeographical analyses using pans of different color may also reach different conclusions. We found that the similarity in family composition was consistently lower, suggesting higher spatial turnover, in blue than in yellow traps. This may at least partly be driven by the lower sampling efficiency of blue traps, leading to less complete sampling and hence lower similarity between samples.

In conclusion, sampling of Hymenoptera in colored pan traps is influenced by taxonomic color and habitat preferences, regional shifts in family composition of the assemblages, and both regional and local changes in vegetation structure. This leads to complex interactions that may influence the perception of patterns of diversity and calls for careful sampling designs and analyses. Our study suggests that especially when studying strong geographical or ecological gradients, the inclusion of different colors may generally be preferable to using a single color, even if one of the colors has an overall better collecting efficiency than the other.

Acknowledgements

We thank our colleagues Thomas Delhotal, Yuvinka Garcia, Caroli Hamel, Sebastian K. Herzog, Steffen Reichle, Vanessa Sandoval, and Julian Q. Vidoz for their support and advice during field work, Jürgen Kluge and Daniele Cicuzza for their help during data analysis, Barbara Seitz and Elena Benetti for their help with literature search, Rodrigo W. Soria-Auza for providing the climatic data, and Helge Schuirman for technical advice. We are grateful to the Botanical Garden in Santa Cruz, the University of Cochabamba, Prometa, the municipal governments of Villa Tunari and Río Seco, and Robin Clarke Gemuseus for the permission to work on their land, and to the National Herbarium in La Paz as well as the Ministry of the Environment for supporting our study. Funding was provided by the Konrad-Adenauer-Stiftung and the DFG (Deutsche Forschungsgemeinschaft). The experiments comply with the current laws of Bolivia.

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