Sampling Methods for Assessing Syrphid Biodiversity (Diptera: Syrphidae) in Tropical Forests

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ABSTRACT When assessing the species richness of a taxonomic group in a specific area, the choice of sampling method is critical. In this study, the effectiveness of three methods for sampling syrphids (Diptera: Syrphidae) in tropical forests is compared: Malaise trapping, collecting adults with an entomological net, and collecting and rearing immatures. Surveys were made from 2008 to 2011 in six tropical forest sites in Costa Rica. The results revealed significant differences in the composition and richness of syrphid faunas obtained by each method. Collecting immatures was the most successful method based on numbers of species and individuals, whereas Malaise trapping was the least effective. This pattern of sampling effectiveness was independent of syrphid trophic or functional group and annual season. An advantage of collecting immatures over collecting adults is the quality and quantity of associated biological data obtained by the former method. However, complementarity between results of collecting adults and collecting immatures, showed that a combined sampling regime obtained the most complete inventory. Differences between these results and similar studies in more open Mediterranean habitats, suggest that for effective inventory, it is important to consider the effects of environmental characteristics on the catchability of syrphids as much as the costs and benefits of different sampling techniques.

KEY WORDS Costa Rica, entomological net, phytotelmata, immature stages, Malaise trap

Assessments of biodiversity often rely on species inventories for recognizing and prioritizing conservation targets, such as biodiversity hotspots and centers of endemism (Pimm et al. 1995) and for studies on functional biodiversity that are basic in ecosystem functioning (Tscharntke et al. 2008, Cadotte et al. 2011). In addition to biodiversity assessments and conservation priorities, species inventories also facilitate environmental monitoring, for example, by comparing results of repeat surveys based on standardized sampling methods (Kohlmann 2011).

Hence, for making inventories of species as comprehensive as possible, specifying and testing sampling methods are high priorities. Because of the diverse characteristics of taxa and their environments, it is proved impossible to generalize over what are the most effective methods. Thus, it is important to compare techniques and determine which are the most effective in particular cases (Southwood and Henderson 2000). Moreover, the selected methods need to be easily replicable in space and time (García-López et al. 2010), which is especially significant in the tropics where, because of environmental characteristics, inventory and survey is relatively complex.

In selecting target taxa for inventorying, priority might be given to a group that has important roles in the structure and function of the target ecosystem, habitat, or geographical area (García-López et al. 2010). In terms of selecting target groups that relate to ecosystem functioning, syrphids (Diptera, Syrphidae) are an important candidate. Syrphids comprise ≈6,000 species and 202 genera. The greatest richness occurs in the Neotropical Region (Evenhuis et al. 2008, Thompson et al. 2010) where many species await discovery and description. Syrphids interact directly with vegetation because of their trophic requirements (Rotheray and Gilbert 2011). Adults are relatively uniform in feeding habits and feed on pollen and nectar. Immatures are more diverse and three functional groups can be recognized: phytophages of many vegetal species, saprophages of decaying vegetal media and zoophages, and predators of other arthropods (Seifert 1982; Rotheray et al. 2005, 2007, 2009b; Speight and Castella 2006; Ricarte et al. 2007; Thompson et al. 2010). Because of these roles, in the Old World syrphids have been used frequently in assessments of biodiversity (Gittings et al. 2006, Ricarte and Marcos-García 2008, Petanidou et al. 2011) and functional diversity (Schweiger et al. 2007), as bioindicators (Burgio and Sommaggio 2007), for measuring the effects on biodiversity of vegetation and landscape (Ouin et al. 2006; Ricarte et al. 2009, 2011) and in

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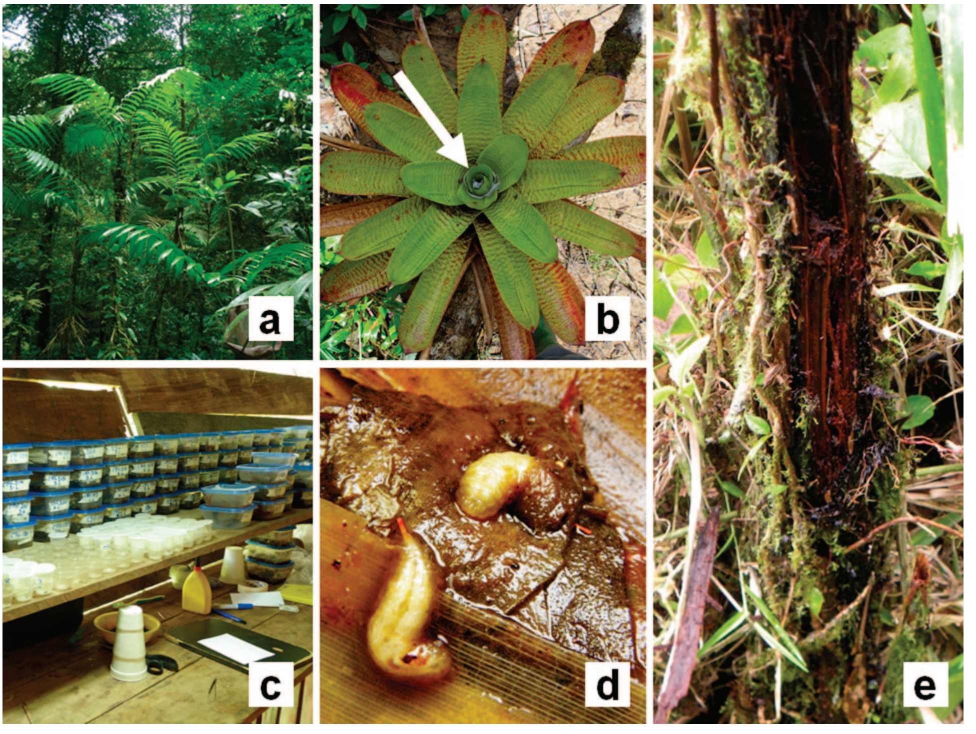

Fig. 1. (a) Example of the structure of the sampled plots in the forests, (b) Phytotelmata in living bromeliad, (c) breeding containers of immature stages at the Tenorio field station, (d) larvae of *Copestylum* in decaying bromeliad, (e) decomposing tree ferns. (Online figure in color.)

agriculture as agents of biological control and pollination (Freier et al. 2007, Haenke et al. 2009, Petanidou et al. 2011). In the Neotropics, however, fewer quantitative data are available that demonstrate similar levels of environmental significance. In Neotropical xeric habitats, saprophagous hoverflies have been shown to be of primary importance in recycling dead cacti (Martínez-Falcón et al. 2011). In Neotropical forests, hoverflies could be considered a group of high value for assessing biodiversity, recognizing conservation targets, and monitoring environmental change. In terms of the latter, syrphids may be particularly valuable as indicators of climate warming. This is because several, species-rich syrphid lineages appear to have diversified in relation to larval development sites that, in plants, contain wet or moist conditions (Fig. 1b, d, e). Such contained aquatic habitats, many formed naturally by plants, are known as phytotelmata (Srivastava et al. 2004) and they are probably highly sensitive to the drying effects of climate change (Benzin 1998). For instance, in the syrphid lineages *Ocyptamus* Macquart, 1834; *Quichuana* Knab, 1913; and *Copestylum* Macquart, 1846 extensive species radiations have occurred in association with water pockets in live and dead bromeliads (Bromeliaceae) (Rotheray et al. 2000, 2007; Marcos-García 2002; Ricarte et al. 2012). Furthermore, there is evidence of large radiations of syrphid species in a diverse array of wet, decaying plant parts, including flowers, leaves, stems, fruits, and exudations of plant sap across a wide range of plant groups and Neotropical habitats (Fig. 1b, d, e) (Rotheray et al. 2007; M.A.M.-G. and G.E.R., unpublished data).

Malaise traps and hand nets have been used widely to improve knowledge of syrphid biodiversity, faunistics, and phenology, both in the Old World (Simic and Vujic 1984, Castella et al. 1994, Castella and Speight 1996, Burgio and Sommaggio 2002, Ouin et al. 2006, Birtele 2011, Petanidou et al. 2011) and the New World (Marinoni and Bonatto-Sionei 2002, Marinoni et al. 2004, Céuli et al. 2007). However, no study has measured their performance in tropical forests, nor has the effectiveness of these traditional methods been assessed against another method infrequently used in biodiversity studies: collection of immature stages. This latter method consists of targeting development sites and rearing early stages or immatures, such as eggs, larvae, and puparia (Marcos-García 2002; Rotheray et al. 2007, 2009b; Ricarte et al. 2009, 2012). This method not only provides data for species inventories but simultaneously and uniquely among the three methods, acquires data on breeding requirements. Moreover, within a habitat, assigning resident taxa to functional groups based on a knowledge of development sites and determining how specialized they are, provides an important tool for predicting and monitoring responses to environmental change; for instance, the tendency of generalists to replace specialists under conditions of habitat loss and environ-

Table 1. Syrphid survey sites and periods along an altitudinal gradient of forest in Costa Rica

Sampling site	Latitude	Longitude	Elevation (m)	Sampling period
Buenavista	10° 48′12.71″ N	84° 53′15.22″ W	100	Nov. 2009–Sept. 2010
Cabanga	10° 35′23.82″ N	84° 51′10.19″ W	500	Nov. 2009–Sept. 2010
Tenorio 1	10° 42′13.20″ N	84° 59′25.20″ W	800	Apr. 2008–Sept. 2008
				Nov. 2009–Sept. 2010
				Nov. 2010–Aug. 2011
Tenorio 2	10° 41′45.00″ N	85° 0′58.20″ W	1,160	Apr. 2008–Sept. 2008
				Nov. 2010–Aug. 2011
Tenorio 3	10° 41′42.60″ N	85° 1′10.20″ W	1,300	Apr. 2008–Sept. 2008
				Nov. 2010–Aug. 2011
Tenorio 4	10° 41′31.80″ N	85° 1′25.20″ W	1,510	Apr. 2008–Sept. 2008
				Nov. 2010–Aug. 2011

mental deterioration or degradation (Tscharntke et al. 2005, Ouin et al. 2006).

We test the effectiveness of Malaise traps, hand nets, and collection of immatures to inventory the diversity of syrphids in six forest sites of Costa Rica. The tropical forests of this country are part of the Mesoamerican Biodiversity Hotspot where high levels of species density and endemism occur (Gotelli and Colwell 2001, Obando 2002, Mittermeier et al. 2004). This is particularly evident in plants groups such as Araceae, Bromeliaceae, Cyatheales, Palmae, and Strelitziaceae that provide important development sites for Neotropical syrphids (Rotheray et al. 2007; M.A.M.-G. and G.E.R., unpublished data). Hence, high levels of syrphid diversity probably exist in these forests, making assessment of their biodiversity a priority target and for which appropriate methods are required. Specifically, we measure 1) the most efficient sampling method in terms of abundance and species richness, and in the pattern found based on functional group and season; and 2) the effect of sampling method on species composition.

Materials and Methods

Study Sites. Syrphids were surveyed at six sites along an altitudinal gradient of forest, ranging from tropical wet forest at 100 m above sea level to lower montane rain forest at 1,500 m on the summit of Montezuma Hill (Holdridge 1967), on the Caribbean slope of the northern Guanacaste Mountain Range in Costa Rica (Table 1). These forests have different ecological characteristics (temperature, humidity, vegetation) related to the differences in elevation that allow survey techniques to be tested under different environmental conditions. In all cases sampling sites were located in primary forests.

Sampling Methods. Sampling took place in three annual periods: April–September 2008, November 2009–September 2010, and November 2010–August 2011. However, only the site Tenorio 1 was sampled during all these periods (Table 1).

1) Hand Collection of Adults With an Entomological Net (HCA). Hand netting took place at each of the six sites along a linear 50-m-long transect for one hour per month. Transects were resampled for 11 mo in the case of the three lowest sites (Buenavista, Cabanga, and Tenorio 1) and 16 mo in Tenorio 1–4 (Table 1). Hand netting was carried out during sunny mornings by experienced people and consisted in walks along the transect collecting individual syrphids as they were observed. The adult flies were transferred to a cyanide killing jar and later pinned and labeled. The extended sampling period, including dry and rainy seasons, made possible the establishment of a relatively complete spectrum of the species given that the populations of flower and plant visiting insects vary significantly in space and time (Moldenke 1979, Herrera 1988, Williams et al. 2001, Price et al. 2005, Petanidou et al. 2008).

2) Hand Collection of Immatures (HCI). The three lowest sites (Buenavista, Cabanga, and Tenorio 1) were sampled for 11 mo (Table 1). Sites Tenorio 1–4 were sampled for 16 mo (Table 1). At each site, a 100-m^2 plot was sampled each month (Fig. 1a). Each plot was walked over systematically and larval microhabitats sampled by hand searching. These included tree holes; bromeliads (Fig. 1b, d); sap runs; bamboo stems; decomposing tree ferns (Fig. 1e); palm stems and leaves; decaying tree logs; fallen fruits; and predatory and phytophagous syrphids on foliage. To find larvae in bromeliads, the leaves were taken off one by one and searched until the inner stalk or scape was reached. Bromeliads growing above head height were sampled where it was possible to reach them by climbing trees up to 3 m in height. Tree holes, sap runs, and bamboo stems were searched for larvae that were transferred to a plastic container with mesh on the top and including part of the material for allowing continuation of the rearing process. Decomposing tree ferns, palm stems and leaves, fallen fruits, and decaying tree logs were opened using a machete or a penknife and the larvae searched for manually, checking crevices, decaying pockets and galleries, and the larvae transferred, along with part of the substrate, to a plastic container with mesh on the top.

3) Malaise Traps (MT). For this study, Malaise traps (Townes 1972) were made of white netting at the top and black netting on the sides and 80% ethanol was used as the killing and preserving agent. Traps were located in a natural clearing or corridor for three consecutive days each month. We placed two Malaise traps on Buenavista, Cabanga, and Tenorio 1 sites for 11 mo (Table 1). Tenorio sites 1–4 were sampled with one Malaise trap per site for 16 mo (Table 1).

Rearing Immature Stages. Larvae and pupae were reared in plastic containers with small quantities of water and debris from the water pocket or decaying medium from which they were collected. Containers were covered with gauze to ensure exchange of air and they were stored in outdoor shaded conditions at the Tenorio field station (780 m) (Fig. 1c). Every 2 d, containers were examined for puparia, which usually were found on dry parts of the decaying material or on the container. To ensure association with the correct adult, puparia were removed and placed individually in separate petri dishes until adult emergence. Petri dishes were examined every day to avoid damage in the wings of the emerging adults. The puparia was preserved in a small vial pinned together with the adult. Predatory species were reared by providing them with suitable prey until pupation and puparia similarly were reared individually.

Identification of Adults. Adults were pin mounted and where necessary, male genitalia dissected. They were identified using Rotheray et al. 2000, 2005, 2007, 2009b; Pérez-Bañón et al. 2003; Thompson et al. 2010. In addition, material was compared with named specimens in the Natural History Museum, London, United Kingdom; Smithsonian Institution, Washington, DC; and Entomological Collection of the Instituto Nacional de la Biodiversidad (INBio), Santo Domingo de Heredia, Costa Rica. All specimens have been identified by M. A. Marcos, G. E. Rotheray, and M. A. Zumbado. Institutions where specimens are deposited are the Centro Iberoamericano de la Biodiversidad (CIBIO), University of Alicante, Spain; the INBio, Santo Domingo de Heredia, Costa Rica; and the National Museums of Scotland, Edinburgh (United Kingdom). All specimens are bar-code labeled according to a Global Biodiversity Information Facility protocol.

Data Analysis. To assess differences in species richness among methods, rarefaction curves, with 95% confidence intervals, were generated. Estimation of curves and confidence intervals were conducted with the Species Diversity and Richness 3.02 software (Henderson and Seaby 2002). The software calculates the curves and associated confidence limits and provides estimates for the confidence limits at the top of the curves (Colwell et al. 2004). Significant differences were defined when both curves were situated outside the others' confidence limits at the point of the curve where the least sampled community ends.

To test the consistence of the effectiveness pattern found, data of the species richness and abundance obtained by each sampling method at each forest site were examined. In the same way, the possibility of variation in effectiveness of the three methods depending on the species functional groups and annual season was assessed using the diversity data of predators and saprophagous species separately and those from the rainy and dry seasons separately. Rainy and dry seasons run from May to December and from January to April, respectively (Janzen 1991).

To test whether the pattern found was shared among the different sampling sites, the effectiveness of the three methods also was compared by calculating the percentages of species richness and abundance made up at each site by each one of them totalled over the whole sampling at this site. In the same way, the possibility of variation in effectiveness of the three methods depending on the species functional groups, and annual season was assessed by calculating the percentages of captures made up by each method for predators and saprophagous species separately, and for the rainy and dry season catches separately. Rainy and dry seasons run from May to December, and from January to April, respectively (Janzen 1991).

Variation in abundance among the three sampling methods was measured using a multifactor analysis of variance (ANOVA) and Bonferroni posthoc tests by using STATISTICA (StatSoft Inc. 2007). The null hypothesis tested was that the three sampling methods were equally effective to capture the studied group.

Complementarity between sampling methods was investigated by calculating the variation in species composition between the three methods by using the Sorensen similarity measure of presence and absence matrices (Sorensen 1948). This analysis calculates the proportion of all species collected by two methods that were captured by only one method. This value varies from 100 (both methods share all species) to 0 (methods have no species in common). An analysis of similarity (ANOSIM; Faith et al. 1987) was performed to test the significance of these differences by using PRIMER software (Clarke and Gorley 2006).

The three methods catches also were compared by analyzing the distribution of unique and shared species for and between methods.

Results

Combining results from the three methods, 494 individuals in total belonging to 74 syrphid species and 15 genera were obtained during this study, of which 45 species are new to science (Supp. Table S1). Only nine species were represented in catches by >10 adult specimens, whereas a third of the species were represented by single individuals (Supp. Table S1). The nine species with >10 individuals were all reared specimens. Development sites were discovered for 42 saprophagous and one zoophagous species.

Differences in the cumulative species richness were observed among methods (Fig. 2). Comparing the species rarefaction curves at the lowest abundance value (14 individuals), the MT showed the lowest value of richness (Fig. 2). HCA and HCI species richness showed no differences at this point, although when the number of individuals was increased they differed, with HCI being the method with the highest species richness value.

This pattern of differing effectiveness of sampling method was maintained at the different sampling sites, for each functional group and for the two analyzed seasons.

The data of species richness and abundance obtained by each method revealed that the Malaise trap was the method with the lowest effectiveness in the capture of the study group (Table 3), whereas HCI

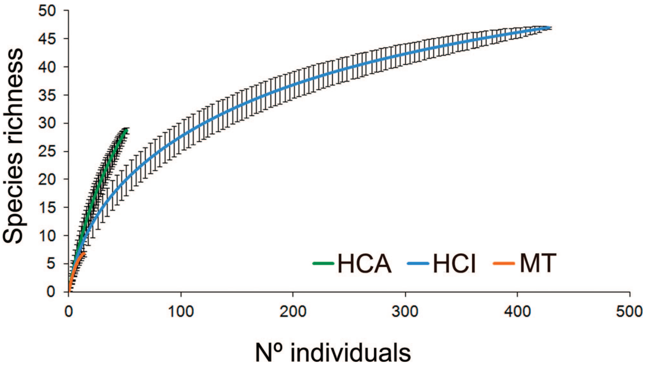

Fig. 2. Rarefaction curves (with 95% confidence intervals) for the estimated richness of species sampled by the three sampling methods. HCA: hand collection of adults; HCI: hand collection of immatures; MT: Malaise trap. (Online figure in color.)

was in all the cases the method obtaining the highest number of species and individuals, except for the species richness at Tenorio 3 and 4, where HCA was the most effective method (Table 3).

The relationship between abundance of individuals and sampling method was significantly different (ANOVA ($H = 15.9$, df = 2, $P < 0.001$). Posthoc tests showed that catches from the HCI were significantly higher ($P < 0.01$), whereas there were no significant differences between the effectiveness of HCA and MT.

Species composition also varied according to sampling method (ANOSIM, $R = 0.299$, $P < 0.001$). The composition similarity analysis, based on a Sorensen index, emphasizes the differences in species sampled by each method with no species shared among methods at most of the sites (0% of similarity). HCI and MT had no shared species across all sites, whereas similarity levels were highest between HCA and MT (Table 4).

The distribution of unique and shared species was variable according to capture method. There were no species obtained across all three sampling methods. Both HCA and the HCI obtained a high proportion of unique species and together, they obtained 97.3% of the total species collected. Only two species were uniquely obtained by MT (Fig. 3).

Discussion

The results presented here reveal that none of the survey methods tested obtained 100% of the species surveyed across all methods, although HCI came closest to it (Supp. Table S1). Species richness results demonstrate the poverty of MT and success of HCI as sampling techniques (Fig. 2; Table 3). Furthermore, the three methods varied not only in effectiveness but also in levels of biological data acquired. They also varied in fieldwork and processing costs that must also be taken into account. Hence, for each type of habitat, analysis of all these factors is required to make informed choices about the appropriate sampling regime for minimizing effort and optimizing results.

Although HCI was the most effective method in terms of species richness and abundance, high complementarity was found between it and HCA (i.e., both had high numbers of species not obtained by other methods (Fig. 2; Table 4) and together, they

Table 2. Functional groups of the genera analyzed according to Thompson et al. (2010)

Genus	Functional group	Microhabitat	Species no.	Collecting method
Aristosyrphus	Unknown	Unknown	1	HCA
Cacoceria	Unknown	Unknown	1	HCA
Chalcosyrphus	Saprophagous	Under tree bark	3	HCA
Copestylum	Saprophagous	Wide variety of decaying plant and phytotelmata[a]	46	HAC, HCI, MT
Habromyia	Saprophagous	Tree holes[a]	1	HCI
Lycopale	Saprophagous	Tree holes[a]	1	HCI
Mallota	Saprophagous	Tree holes and decaying stems of tree ferns[a]	3	HCA, HCI
Microdon	Zoophagous	Ant colonies	1	HCA
Ocyptamus	Zoophagous	Predators of insects living on phytotelmata	1	HCI
Ornidia	Saprophagous	Wide variety of decaying plant and animal	2	HCA, HCI
Palpada	Saprophagous	Decaying plant	8	HCA, MT
Quichuana	Saprophagous	Pockets of wet decay	1	HCI
Rhingia	Saprophagous	Animal dung	1	HCA
Sterphus	Unknown	Unknown	1	HCA
Xylota	Saprophagous	Tree sap and wet decaying wood	3	HCA, HCI, MT

[a] Denotes phytotelmata.

Table 3. Species richness and abundance obtained by each sampling method at each sampling site, for each functional group and during each annual season

	Species richness and abundance			
	HCA	HCI	MT	Total
Site				
Buenavista	8/13	9/105	2/5	19/123
Cabanga	2/2	14/92	0/0	16/94
Tenorio 1	5/5	20/100	2/2	27/107
Tenorio 2	4/4	11/32	1/1	16/37
Tenorio 3	10/17	4/32	0/0	14/49
Tenorio 4	10/11	9/67	3/6	22/84
Total	29/52	47/428	7/14	74/494
Functional group				
Predators	1/1	1/3	0/0	2/4
Saprophagous	25/39	46/425	14/7	69/478
Season				
Dry	7/10	22/177	2/5	29/192
Rainy	23/42	37/251	6/9	62/302

HCA: hand collection of adults, HCI: hand collection of immatures, MT: Malaise trap.

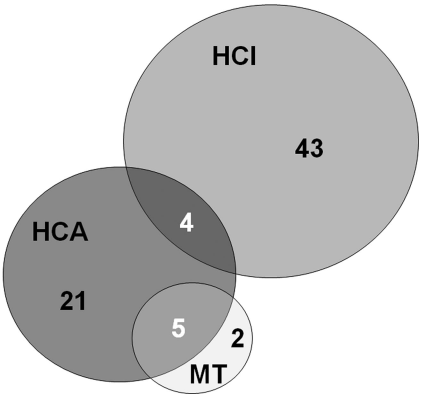

Fig. 3. Venn diagram showing syrphid species caught in the three sampling methods. HCA: hand collection of adults; HCI: hand collection of immatures; MT: Malaise trap.

accounted for 97.3% of the total species collected. Hence, in Neotropical forests, the most complete species inventory will be obtained only when both these methods are used together.

The pattern of effectiveness we obtained was independent of functional group and season (Table 3), but more adults were captured by HCA and MT in the rainy than the dry season. This probably is explained by differences in patterns of adult emergence. Adults time their emergence to coincide with the higher availability of food resources such as nectar and pollen (Bawa et al. 2003) and development sites in the rainy season.

In addition to the high values of effectiveness found for HCI, collection of immatures obtained a higher number of undescribed species (32) than the other two methods (Supp. Table S1). A result, we also have found using HCI to sample bromeliads alone (Rotheray et al. 2007) and demonstrating that syrphids are poorly sampled in tropical forests. Moreover, HCI allows simultaneous collection of data on breeding sites, microhabitat preferences, and larval development. These data can be critical for syrphid habitat and species conservation (Ricarte et al. 2009, Rotheray et al. 2009a). In addition to these advantages, HCI provides material for the study of early stages that in syrphids, are a valuable source of taxonomic and phylogenetic data (Rotheray and Gilbert 1999). Levels of associated data may also be high using HCA (e.g., data on adult behavior, plant associations, flight periods, oviposition sites). However, this classic method has high fieldwork and processing costs and is affected by the relative experience of individual workers (Westphal et al. 2008).

Table 4. Percentages of similarity of sampled species among the three sampling methods analyzed

Site	Percentage of similarity (Sorensen Index)		
	HCA-HCI	HCA-MT	HCI-MT
Total	10.5	27.8	0
Buenavista	0	40	0
Cabanga	0	–	–
Tenorio 1	0	0	0
Tenorio 2	0	0	0
Tenorio 3	0	–	–
Tenorio 4	10.5	30.8	0

HCA: hand collection of adults; HCI: hand collection of immatures; MT: Malaise trap. Dash indicates the sites where MT did not capture any species.

Malaise traps collect continuously, passively, and indiscriminately, and fieldwork costs of time and effort are low (Pompe′ and Cölln 1993). However, processing costs are high as target and nontarget material is collected together and must be separated. In our study, MT was the least effective sampling method (Fig. 2; Table 3). These poor results could be explained by a vertical stratification of syrphids in which individuals tend to aggregate in the canopy for mating, dispersal, and feeding (M.A.M.-G. and A.G.-L., personal observations). The existence of vertical stratification by syrphids in temperate forests already is known (Grimbacher and Stork 2007, Birtele and Hardersen 2012) with males more numerous in the canopy and females only descending to search for breeding sites (Birtele and Hardersen 2012; G.E.R., unpublished observations). This probably explains our results where only one of the 14 individuals captured by MT was a male. Campbell and Hanula (2007) also recorded low catches of hoverflies with MT versus other types of traps in temperate forests. These results contrast with those obtained in Mediterranean areas where high numbers of syrphid species were captured exclusively only with MT as opposed to HCA or HCI (Ricarte and Marcos-García 2008). This higher effectiveness of MT could be a consequence of vegetation structure. In open habitats, such as typify Mediterranean ecosystems, the chances of syrphid flight paths being intercepted by MT are probably higher than in closed habitats like tropical forests (Vockeroth and Thompson 1987, Owen 1991, Marinoni et al. 2004, Céuli and Marinoni 2007, Mazón and Bordera 2008) where MT is often ineffective (Gittings et al. 2006) which apart from flying in the canopy, in temperate regions, additionally may be explained by syrphids avoiding cool, shaded conditions in the under-storey (Fayt et al. 2006).

Regarding functional groups, saprophages were most frequently encountered in our study, both at generic (66.6%) and species (93.2%) levels (Table 2; Supp. Table S1). This result is consistent with the high proportion of saprophages within the known syrphid fauna of Costa Rica, 49.1%, (Thompson et al. 2010). Most saprophages (46) belonged to the genus *Copestylum* (Table 2; Supp. Table S1). Of these, 35 species were only collected by HCI, 28 being new species. With over 400 species, *Copestylum* is one of the most speciose syrphid genera known (Thompson 1981) and most of this diversity occurs within tropical forests, corresponding probably, to the high frequency of wet and moist development sites in these habitats, particularly phytotelmata (Table 2) (Rotheray et al. 2007). Such a pattern is also known for other macroinvertebrate groups (Montero et al. 2010).

Zoophages were the second most frequently sampled functional group. One zoophagous species each of *Microdon* Meigen, 1803 and *Ocyptamus* Macquart, 1834 was new to science. Adults of *Microdon* were caught using HCA near the breeding site (ant nests), and larvae of *Ocyptamus* species have been found preying on other insect larvae inside water tanks of bromeliads (Rotheray at al. 2000).

Independent of functional group, in general, a low number of individuals per species were obtained. These results are consistent with those of Meyer et al. (2007), who found a negative response of hoverfly density to landscape diversity. However, the low abundance found in our results could be because of sampling method: numerous species had few individuals sampled by HCA or MT, but higher abundances sampled by HCI (Supp. Table S1).

Despite the effectiveness of HCI in Costa Rica, our results should not be generalized to other habitats. In places where larval development sites are patchy and overdispersed or difficult of access, then levels of effort required to sample them may not be cost effective relative to MT or HCA. For example, in Mediterranean forests, HCI may not be as effective as MT or HCA because of the time it takes to find and search the development sites of saproxylic syrphids, such as tree holes and decaying plant tissues (Ricarte and Marcos-García 2008).

This study provides a measurement of sampling method effectiveness for monitoring and inventorying the diversity of syrphids in tropical forests. Given the importance of tropical ecosystems for biodiversity and the potential of tropical syrphids for recognizing biodiversity hotspots, centers of endemism and particularly, for monitoring environmental change, this study contributes to a better understanding of the costs and benefits of realizing this potential through appropriate choice of sampling technique.

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