Vertical stratification of Diptera abundance and species richness in an Amazonian tropical forest

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Abstract

Measuring species richness of tropical forests is a major challenge. Such measurement is a key information in many senses, from an evolutionary perspective to conservation of threatened, fragile habitats. Data has gradually shown that the canopy of tropical forest is a hugely complex component of the forest, but a precise assessment of the diversity of megadiverse groups in the canopy is still wanting. We collected large samples of insects were along a period of two weeks using 6-meter Gressitt-style Malaise traps set at five heights on a metal tower in a tropical forest north of Manaus—one trap at the ground level, one trap above the canopy (32 m) and three traps at intermediate levels (8, 16 and 24 m). The samples contained 37,778 specimens belonging to 18 order of insects. Fifty-seven families of flies (Diptera) were found, 39 of which were identified to 368 genera and 856 species. The species of these 39 families of flies fit into eight patterns of vertical distribution of abundance and species richness of the fauna, with patterns of one or two peaks of species at different levels. A total of 527 (61.6%) of the 856 fly species recognized in the samples were not collected at the ground level. The canopy-associated species of Diptera showed a high species richness and a relatively low abundance indicating that they represent vulnerable components of tropical diversity. The biology of the flies families and genera we collected in the canopy suggest that the evolution of flies went through a unique process: independent clades of Diptera explored in different ways the resources originated along the very evolution of the angiosperm forest canopy along the early Cenozoic. Unlike other primarily phytophagous groups of insects, flies radiated into a large array of biologies associated with the canopies: parasitoids, hematophagous, phytosaprophagous, kleptoparasites, sap feeders, gall-makers etc. The results only stress the need of additional strategies to protect this diversity.

Introduction

Measuring the species richness of tropical forests, particularly when insects are involved, is a challenging but key step to properly understand these hugely complex environments. Such measuring is also a fundamental step to estimate in a precise way the biodiversity loss due to anthropogenic pressure on these vital natural habitats.

Canopies have been described as vertically stratified ecosystems interconnected with other strata of the forests[1]. Different aspects of canopy ecology have been studied to date, including climatic gradients within the forest[2], biomass[3,4], abundance[5], alpha diversity[6], beta diversity[7], species interactions[8], biogeochemical cycles[9], guild structure[10], long-term succession[11], community organization[12], human impact[13] and other parameters.

To understand the vertical stratification of abundance and species richness of flies (Insecta: Diptera) in a tropical forest, we studied the collections from a novel sampling protocol using the 53 m high tower of the ZF2 biological reserve (2°35’21”S, 60°06’55”W) belonging to the Instituto Nacional de Pesquisas da Amazônia (INPA), in Manaus, Brazil. Six-meter long Gressitt-style Malaise traps were used to sample insects at every eight meters of the tower's height (Fig. 1), from the ground level to slightly above the canopy top, at 32 m.

Diptera are the least-studied of the megadiverse insect orders and much remains to be discovered about the diversity of the fly fauna in tropical forests. Aside from the heavily-researched disease vectors of medical importance (mosquitoes and phlebotomine sand flies), this group receives much less attention from tropical biologists than other, more charismatic groups of insects. The number of described species of flies worldwide is about 160,000, comprising about 10% of all known species of organisms. The real number of existing Diptera species, however, is much higher than this, based on projections from mass-sampling projects[14, 15, 16].

Results

Insect order and Diptera family vertical abundance patterns

We identified and counted 37,778 insect specimens belonging to 18 orders at the five sampling levels, with special attention given to the Diptera (Fig. 2). The most abundant order of insects were the flies (16,600 specimens in the samples), followed by hymenopterans (wasps, bees and ants, 7,279 specimens), moths and butterflies (6,899), true bugs (3,939) and beetles (2,670). The 16,600 specimens of flies were further identified as belonging to 57 families, of which the most abundant was the family Phoridae (3,843 specimens in the samples), followed by Sciaridae (2,066), Cecidomyiidae (1,977) Psychodidae (1,178), Dolichopodidae (935), Chironomidae (880), Tachinidae (833) and Mycetophilidae (797). A total of 8,809 fly specimens belonging to 39 of the families were identified to species (or to genus in the hyperdiverse family Phoridae), belonging to 856 species of 368 genera. Of the families identified to species, the most species-rich was Tachinidae (166 species), followed by Mycetophilidae (101), Dolichopodidae (71), Limoniidae (60), and Drosophilidae (51). The Supplementary Material has the complete dataset of insects identified at each level of the tower (Supplementary Tables I–IV).

Vertical patterns of abundance in the samples reflect how different insect groups explore resources available in the vertical structure of the forest. The ground level individually has the highest insect abundance, which is expected since the resources typically available at the ground includes what falls to the ground from higher levels of the forest (leaves, fruits, dead animals, dung etc.). Over two thirds of the insect abundance, however, was found above the ground level. This suggests that the amount of food and other kinds of resources at the ground level is individually larger than any other individual level, but the overall amount and types of resources above the ground is higher than that at the ground itself. This cannot be overestimated while understanding tropical forest dynamics, since it has been argued that the main driver for spatial and temporal distribution patterns is largely the availability of resources[18].

The vertical distribution of abundance is not the same across the 18 sampled insect orders (Supplementary Table I). Of 11 orders with more than 10 sampled specimens (Fig. 2), three have the highest abundance at the ground level, with the abundance decreasing towards the canopy—termites, collembolans and psocopterans. Four orders have a peak of abundance at the ground level, with a second peak at 24 m—orthopterans, beetles, hymenopterans, and flies. True bugs (hemipterans) and neuropterans have a 2-peak abundance pattern (with peaks at 8 m and 24 m), while cockroaches and lepidopterans have a 1-peak abundance pattern at the canopy (16 m or 24 m). Trichopterans (which have aquatic larvae) were the only group to have a peak of abundance at 32 m. These insects are probably using the open area above the canopy as an avenue for dispersal above the forest.

The heterogeneity of abundance patterns in different insect orders (Supplementary Table I) and different fly families (Supplementary Table II) in our study support the idea that the vertical distribution of different kinds of resources in the forest affects the abundance of insects belonging to different guilds. A study in Borneo[5] demonstrated that 85% of the variability in arthropod abundance is explained by variability in total leaf area—hence, understory and canopy contributing more to the bulk of abundance. A 2-peak 0/24m pattern was found in Panama[10], with most adult arthropods collected from the soil/litter and from the upper canopy.

Diptera vertical abundance patterns

The abundance particularly of flies at the four higher tower levels in relation to the ground level—1.88— is smaller than the overall proportion of insects between the same levels—2.23. This means that the canopy is slightly more relevant in terms of abundance for some insect orders (such as the largely herbivorous moth and butterfly fauna, as well as for the cockroaches, bugs, the neuropteran predator fauna etc.) than it is for flies. The fact that Blattaria, Hemiptera, Neuroptera, Trichoptera and Lepidoptera have over 80% of their abundance above the ground level is particularly remarkable.

The patterns of vertical abundance of different Diptera families in the various levels of the forest are far more complex (Supplementary Table II, Figs. 3A-H). Only eight among 57 families of flies have a single peak of abundance at the ground level—including, e.g., fungus-gnat families (Mycetophilidae), groups with larvae that predate other organisms in the mud (Tabanidae), insect predator adults (Asilidae) or groups with saprophagous larvae (Micropezidae). Two-peak patterns including the ground level and either the 16 m, 24 m or 32 m levels are seen in 16 other fly families, including groups exploring very different kinds of resources, such as hematophagous flies (Culicidae and Ceratopogonidae), predators (Empididae and Dolichopodidae), and groups with kleptoparasitic flies (Milichiidae). A single peak of abundance at 8 meters or a 2-peak pattern involving the 8 m level was found in four families. These are possibly flies associated with wood holes and tree trunks or flies that use the area between the understory and the canopy to move around in the forest (which may be the case of the fly parasitoid family Tachinidae). Overall, the summed abundance of flies at levels 16 m and 24 m (the body of the canopy) is only slightly smaller (33.3%) than the abundance of flies at the ground level (34.7%).

The abundance patterns of the various insect orders and of the fly families sampled at the ZF2 tower in general agrees with what is known about the biology of these groups. Our study, however, formally measured for each family the relative importance of the canopy fauna at different levels in relation to the ground level fauna, an information not available in previous studies. Additionally, there were some surprises: over half of the abundance of crane flies and over one third of the abundance of fungus-gnats, for example (families largely connected to resources present at the ground level) were found at levels above the ground. The astonishing 90.0% of abundance of clusiids, 92.6% of lauxaniids, 94.1% of tachinids and 100% of syrphids at the four higher strata at the forest depicts a much larger canopy fauna of the family than ever shown before.

Diptera vertical species-richness patterns

Of the 856 species of flies of 39 families identified to the species level in our study, 329 (38.4%) occurred at the ground level, 188 (22.0%) of which were exclusive to the ground level (Supplementary Table II, Figs. 4A-K). Similar numbers were obtained in Panama[10], which also compared beta-diversity and found it to be much less significant. One major implication of these numbers is that, if insect sampling took place only at ground level, 61.6% of the fauna would be missed. This means that collecting only at the ground level leads to a significant underestimation of the species diversity of a megadiverse order of insects in the Amazon forest.
The rarefaction curves show (Fig. 5) that, for the same number of sampled individuals of all tower strata, there would be a higher number of species for any stratum above the ground than at the ground level, but probably with a lower abundance for each additional species to be found. Our results also show a large species turnover within the vertical structure of the forest (Fig. 6). Only 20 species of flies were collected at all five levels (2.3%) and 46 other species were collected from the ground level to the 24 m canopy level (5.4%). Out of the 855 identified species of flies, 277 species are shared between any pair of levels and 577 species are exclusive of some level. The sum of species exclusive to levels 16 m and 24 m alone (corresponding to the bulk of the canopy) was 197 species, slightly higher than the number of species exclusive to the ground level—188.

The total species richness projected through the rarefaction curves with pseudoreplicas for our samples (Fig. 5) reached 1,489 species of flies (of the 39 families identified down to species) for a sampling period of two weeks, with a standard error of about 6%—a number 1.75· that of recognized species. Considering the different levels, the rarefaction curve of fly species richness at the ground level is an estimated 609 species, based on 330 observed species. The ground level has a larger number of individuals and produces the most complete rarefaction curve. The measured and inferred species richness of the higher levels decrease, until only 180 observed species were observed for the level above the canopy (32 m), leading to an estimated 364 species for that level.

The mean difference between the number of species in each family in the ZF2 samples with 10 or more species identified and the number of species of the same families in the recent all-Diptera survey of a Costa Rican site (ZADBI) study[14,15] in Costa Rica is 0.656. We can use this proportion to make a general estimation of the species-richness also of the families not identified down to species in our study (i.e., Cecidomyiidae, Sciaridae, Psychodidae etc.) based on the Zurquí fauna. This suggests another 2,741 species of flies, raising the total number of species of Diptera in the five levels of the ZF2 tower altogether to about 3,600 in a 2-weeks collecting effort. Rarefaction accumulation curves for the ZADBI study projects over 7,300 species for 4,332 species actually counted in their 1-year study[14, 15].

The similarity analysis (Figs. 7A–C) for species composition in the five strata indicates a total dissimilarity of 0.7524414 among all traps, with the effect of turnover (0.7891015) about twenty times stronger than that of nestedness (0.03666009), which is a too weak of an effect to be considered[17]. The same pattern was found for the turnover component of these communities (Fig. 7). The turnover dissimilarity analysis shows objectively how the communities change along the forest structure. We recognize (1) distinctiveness of the five levels, forming a turnover gradient from the ground to the canopy; (2) a distinct ground level fauna; (3) reasonable similarity of the two middle levels (8 and 16 m); and (4) the canopy level and above (24 m and 32 m levels) standing as a community largely different from the other three.

There are some additional patterns—such as the 2-peak 8/24 m pattern in Chloropidae and the Clusiidae or the 2-peak 0/32 m pattern of the well-known hill-toppers of the family Sarcophagidae, that mate at high places in the landscape. The families Sciaridae and Cecidomyiidae do not show a clear pattern and have a more or less regular distribution along the five levels.

Discussion

There is a different set of vertical distribution patterns of species-richness (Fig. 4A-G). Only two out of 21 families of flies identified to species and with over five sampled specimens have a single highest peak of species-richness at the level of the ground level—Mycetophilidae (fungus-gnats) and Micropezidae (the micropezid species in our samples basically with phytosaprophagous larvae) (Fig. 4A). An additional eight families have a species-richness peak at the ground level and a second peak at the 16 m or 24 m levels or above the canopy (Fig. 4G)—three of which with the larger peak at the canopy. Fourteen out of these 21 families do not have a peak of species diversity at the ground level.

This contrasts with the abundance patterns of these same families seen above. Of the 19 fly families that have either a single high peak of abundance at the ground or a 2-peak pattern including the ground level (Supplementary Table II), only ten also have a peak of species diversity at the ground level (Supplementary Table III). This means that many families have high abundance at the ground level but with a lower diversity, while the 8 m or higher levels have higher diversity but lower abundance. The rarefaction curves of the tower strata indicate that the extension of the sampling would increase the number of species in higher strata in relation to the ground-level (Fig. 5). This suggests that the canopy would harbor a larger number of species with smaller abundance, something to be tested in a study with extended temporal sampling.

In a large study of canopy insects in Panama[10], a broad range of methods were used to ascertain large patterns of species distribution and turnover in the canopy. That study was designed to uncover the most generalized factors that affected diversity, which they found to be seasonality and vertical stratification, whereas distance between sites was shown to be less important. In order to reach these broad conclusions, based on a large number of insect groups and sampling methods, they were understandably forced to sacrifice some detail that could be studied in less comprehensive projects. They were only able to address seven families of Diptera (true flies) and considered the understory to encompass the entire range of 3–35 m in the forest, a range in which we found possible stratification.

Our study differs from that of Basset *et al.*[10] in Panama most notably by our limited sampling period and by the narrower range of sampling methods and taxonomic groups considered. The novel use of the 6m Gressitt traps, however, was amazingly productive for Diptera specimens, catching a large number of incredibly rare and new flies—such as the odiniids, possibly many new genera of phorids, large number of species of lauxaniids etc. The efficiency of the traps used in our study (as compared to the uninspiring catch from canopy Malaise traps in the ZADBI project) is due to the much larger interception surface in the 6m traps with two collector vials, and to the fact that the tower platforms provide a floor for the traps, preventing flies from escaping through the bottom.

Even more importantly, our sampling approach allows discriminating the fauna of different levels and a more precise modeling of the vertical distribution of Diptera abundance and species richness in a forest than in previous studies. In Panama[10], ground level ("understory") samples were collected at 0 to 3 m above the forest floor, while canopy ("lower canopy") combined the results of the samples from 3 to 35 m above the ground—a space subdivided and showing notable differences in our study. Finally, their data for Diptera covers just seven families, of which only four had more than 10 specimens. Of 188 species of flies identified in the tropical forest in Panama, 92 (49%) occur at the ground level, while 120 (64%) occur at the canopy and 50 (27%) above the canopy, results that are in large terms concordant with our findings. Moreover, our results show that a diversity of patterns of abundance and species-richness can be detected using a more precise sampling protocol, with discrimination of the fauna at different strata.

It was recently shown that, at least for the Neotropical forests, the closed multistratal canopies with biomass dominated by angiosperms and similar plant family correspond to a post-Cretaceous evolutionary development[19]. Our overall data shows a high level of specialization of the fly fauna at the species level of different groups to given strata of the forest, i.e., Diptera species of independent clades explore in different ways resources made available along the evolution of tropical forest canopies. It also shows that the canopy is more relevant for flies in terms of species richness than in terms of abundance. This is in agreement with prior studies that show that the main driver for most spatial and temporal distribution patterns is resource availability[18]. Unlike other groups of insects in the canopy that are largely phytophagous—such as the "Phytophaga" Coleoptera and Lepidoptera—, flies evolved into a large array of biologies associated with the canopy: parasitoids, hematophagous, kleptoparasites, sap feeders, gallers, miners etc. In other words, the very evolution of the angiosperm tropical forest canopy generated a new environment that was extremely important for the radiation of lineages of Diptera with different biologies.

This distinctness of the canopy fauna means that it vulnerable to an additional set of disturbance by human activities. Climate change has different impacts on the canopy and its fauna, including loss of biodiversity[1]. An assumption that the faunal composition of large blocks of the canopy, however, would be relatively homogenous is incorrect[10], as our data also show. Selective logging, which may disrupt the connections between upper and lower canopy levels, or even eliminate entire faunas, must be rethought as a biodiversity-friendly approach. For the large-scale protection of tropical diversity, there must be a core area of intact forest[20,21] with all canopy strata conserved.

Considering the huge pressure on the Amazon primary forest in recent years[22], in some cases even with government support, the understanding of its species diversity becomes an urgent priority, which cannot be achieved in a "vacuum of data"[23]. This paper fill in part of the gap, clarifying that flies have a much more complex role in the canopy community, in terms of number of species and guilds occupied, than understood before—but also raise an array of unanswered questions. A concerted action must be made to protect tropical ecosystems, including all levels of the canopy, against pervasive stressors, such as deforestation, climate change, and pesticide use—and this largely depends on a better understanding seasonality, phylogeography, abundance, species-richness, and guild evolution of the organisms that inhabit them.

Declarations

Competing interests statement The authors declare that they have no competing financial interests.

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Author Contributions

Conceived and designed the experiments: JAR. Identified insect orders, Diptera families, and genera/species within the families: DSA, BVB, RAR, DMAG, MIPAB, AMB, RSC, CJBC, MSC, RVPD, DAF, GBF, HFF, LMF, FMG, MH, CJEL, KL, MATM, *DWAM, MAM,* MNM, SAM, CMP, SSN, SSO, GP, GCR, PRR, MDS, DS, JRS, VCS, JAR. All authors contributed in the manuscript. Analyzed the data: DSA DB JAR. Wrote the paper: DSA BVB DB JAR. Contributed to analysis and interpretation of overall data: DSA DB BVB JAR.

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Figures

Figure 1

Some of the researchers working on the project, at the 40 m stage of the ZF2 biological reserve tower, above the canopy (from right to left, Daniel Bickel, José Albertino Rafael and Dalton de Souza Amorim).

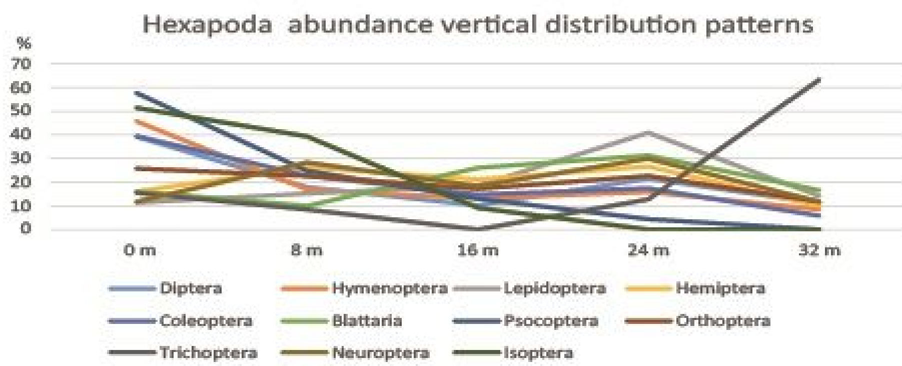

Figure 2

Vertical distribution of abundance of different hexapod orders.

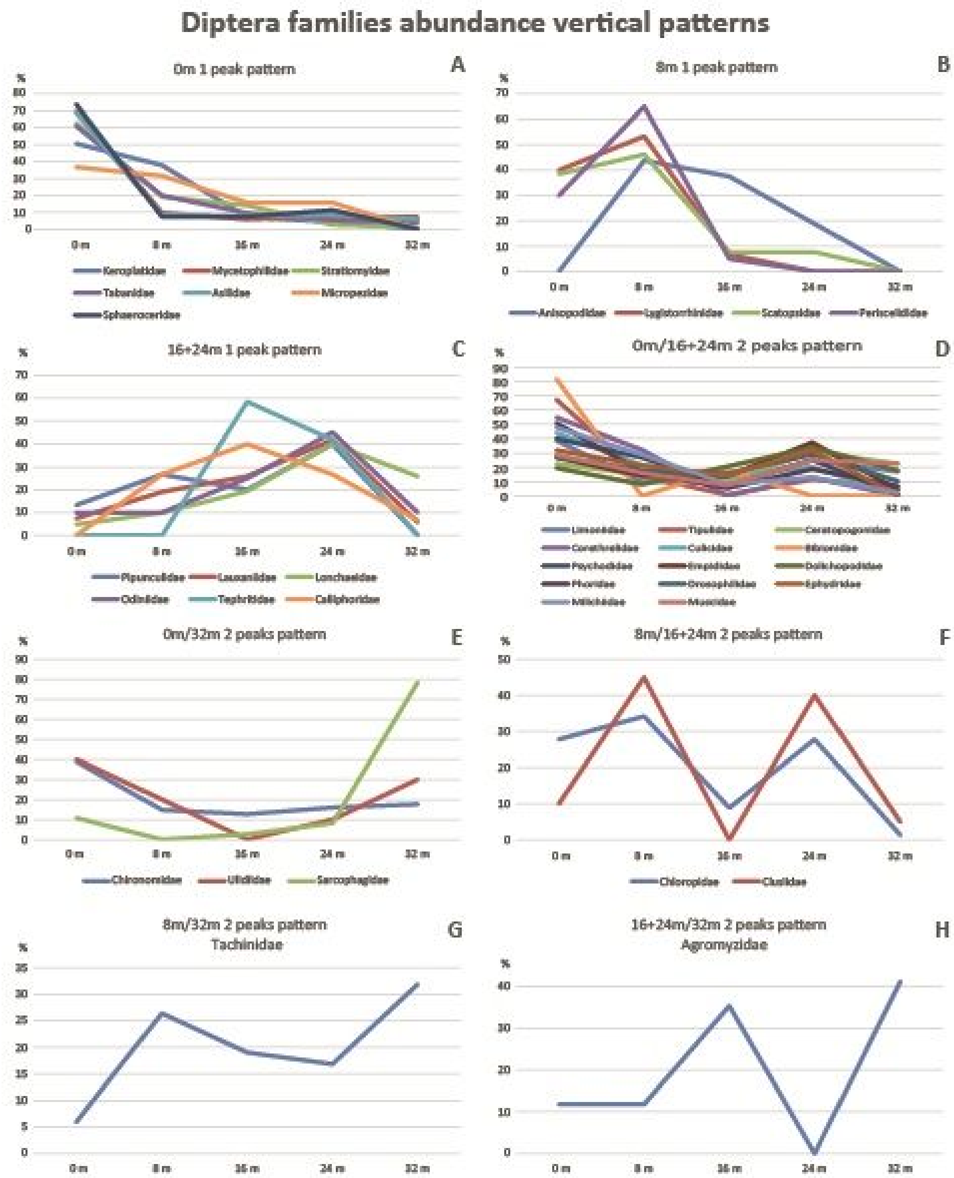

Figure 3

A-H. Vertical distribution patterns of abundance of Diptera families. A. 1-peak pattern at the ground-level. B. 1-peak pattern at 8m. C. 1-peak pattern either at 16m or at 24m. D. 2-peak pattern, with peaks at the ground-level and at 16m or 24m. E. 2-peak pattern, with peaks at the ground level and at 32m. F. 2-peak pattern, with peaks at 8m and 24m. G. 2-peak pattern, with peaks at 8m and at 32m. H. 2-peak pattern, with peaks at 16m and 32m.

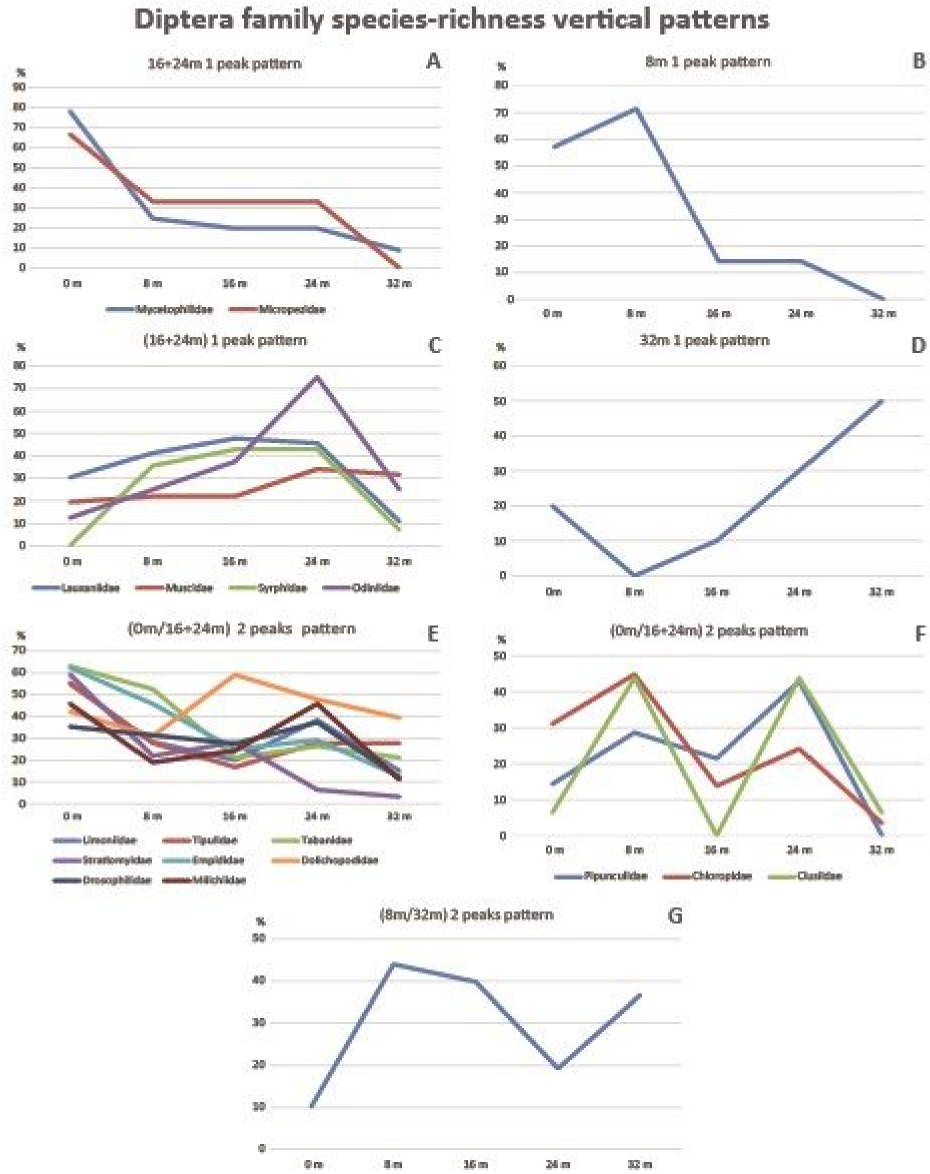

Figure 4

A-G. Vertical distribution patterns of species richness of Diptera families. A. 1-peak pattern at the ground-level. B. 1-peak pattern at 8m. C. 1-peak pattern either at 24m. D. 2-peak pattern, with peaks at the ground level and at 32m. E. 2-peak pattern, with peaks at the ground-level and at 16m or 24m. F. 2-peak pattern, with peaks at 8m and 24m. G. 2-peak pattern, with peaks at 8m and at 32m.

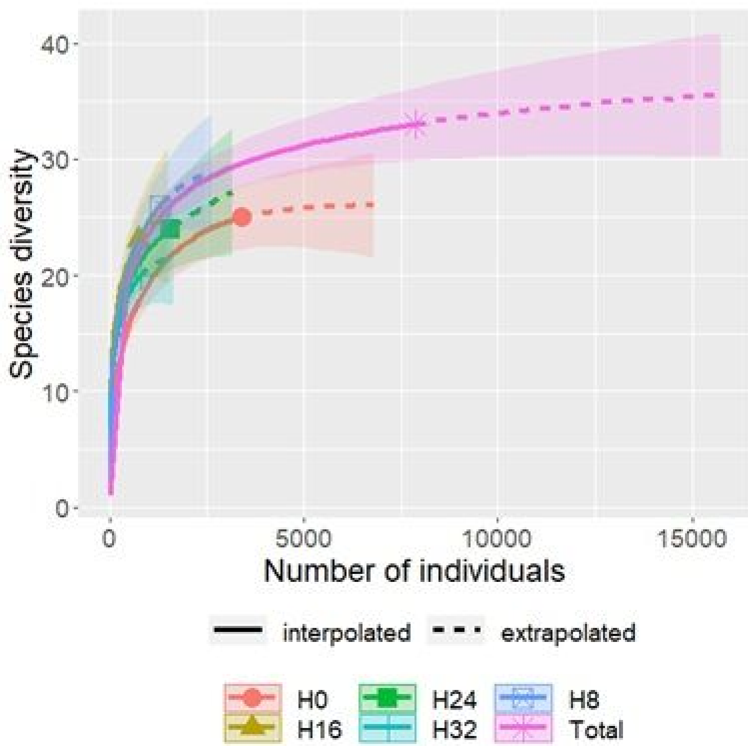

Figure 5

Rarefaction curves based on pseudoreplicas of all five sampling levels of the ZF2 biological reserve tower.

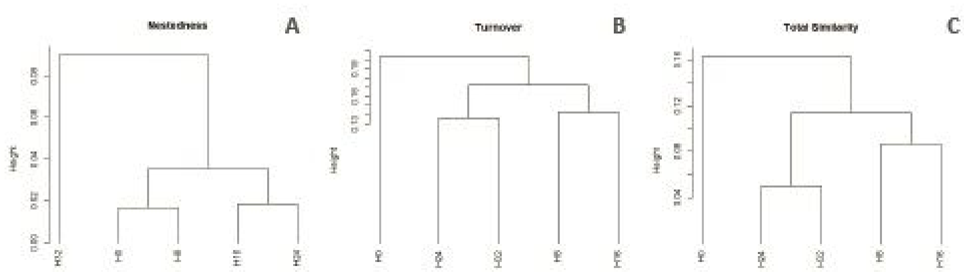

Figure 6

A-C. Similarity between species composition of the ZF2 tower five levels. A. Total similarity. B. Nestedness. C. Turnover.

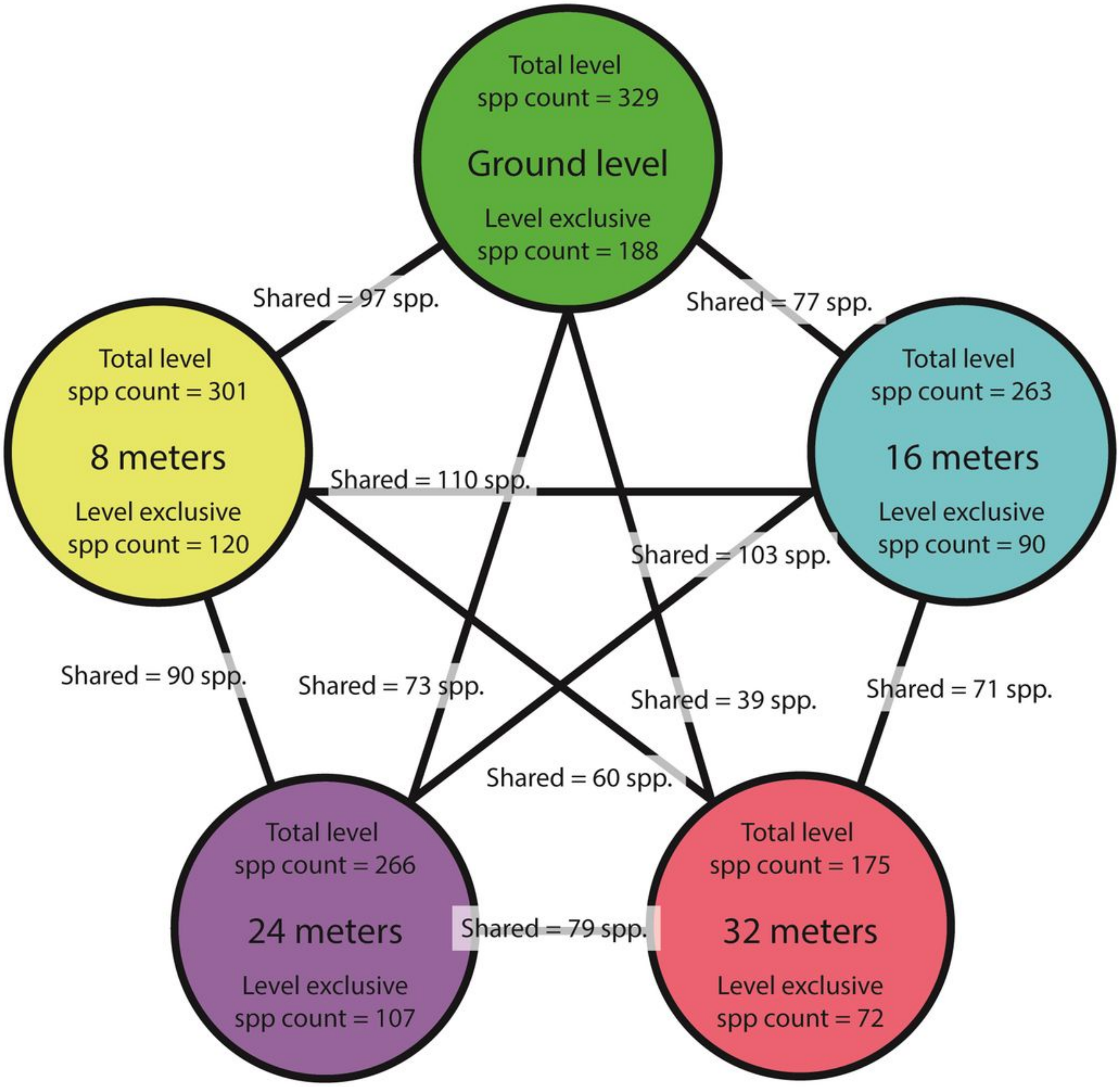

Figure 7

Shared species between all five sampling levels of the ZF2 biological reserve tower, indicating level of turnover between levels.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- ZF2SuppplementaryMaterialTableIIDipteraabundance.xlsx

- ZF2SuppplementaryMaterialTableIIIDipteraspeciesrichness.xlsx
- ZF2SuppplementaryMaterialTableIVGuildspeciesrichness.xlsx
- ZF2SuppplementaryMaterialTableVDipteraGeneraldata.xlsx