

Research articleSubmitted: January 25th, 2017 - Accepted: April 28th, 2017 - Published: June 30th, 2017**Vertical stratification of selected Hymenoptera in a remnant forest of the Po Plain (Italy, Lombardy) (Hymenoptera: Ampulicidae, Crabronidae, Sphecidae)**Filippo DI GIOVANNI^{1*}, Maurizio MEI¹, Pierfilippo CERRETTI¹¹ Department of Biology and Biotechnologies "Charles Darwin", "Sapienza" University of Rome - Piazzale Aldo Moro 5, I-00185 Rome, Italy - filippo.digiovanni@uniroma1.it; maurizio.mei@uniroma1.it; pierfilippo.cerretti@uniroma1.it

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Abstract

Communities of the canopy of temperate forests are still relatively unexplored. Furthermore, very little is known on how vertical stratification for some insect groups is related to biological strategies. In this study, we investigated the community composition of both canopy and understory of the families Ampulicidae, Crabronidae and Sphecidae (Hymenoptera) of the Natural Reserve of "Bosco della Fontana", a remnant lowland forest in northeastern Italy. Observed patterns in vertical stratification have been related to species foraging habits. Our study reveals that the bulk of the community of Spheciformes of the understory consists of species preying dipterans and spiders, while species associated with the canopy are mainly predators of sap-sucking honeydew producers and epiphyte grazers, like aphids, thrips, and barkflies. Comparing the communities of canopy and understory may lead to a better understanding of species ecology and provides useful information to forest managers.

Key words: canopy, biological traits, Spheciformes, Italian fauna, lowland forest.**Introduction**

Studying the relations between biotic communities and environmental components is crucial to unveil hidden aspects of organism ecology and to provide useful information on how communities respond to management practices. Canopies of temperate forests and their communities have been nearly neglected so far in insect studies. Forest managers have often ignored the effects that certain silvicultural practices would have on the diversity of insects associated with higher strata of the forest. In recent years, improved methods to access canopies gave the opportunity to sample insects of this habitat (Basset et al. 1997, 2003; Vance et al. 2007), showing that canopies can host some rarely collected or undescribed species (Floren & Schmidl 1999, 2008; Thunes et al. 2004; Vance et al. 2007; Di Giovanni et al. 2015).

Vertical stratification has been demonstrated for many groups of insects in tropical and temperate forests (Preisser et al. 1998; Basset et al. 2003, 2012; Floren & Schmidl 2008) as a result of microclimatic variations in temperature, humidity or light exposure between canopy and understory, variation in resources availability, or as a consequence of inter-specific interactions (competition, predation) or niche-differentiation (Basset et al. 2003; Ulyshen 2011). In both tropical and temperate forests, canopies can provide resources which are seasonally unavailable in the

understory (Ulyshen et al. 2010) and can offer nesting sites for specialized saproxylic organisms (Sobek et al. 2009; Ulyshen et al. 2011b). In certain conditions, the canopy layer may also work as aggregation point for several flying insects during mating swarming (Birtele & Hardersen 2012; Stireman et al. 2012).

Yet, only few studies have focused on highly mobile (and highly diverse) insects as dipterans or hymenopterans of the canopy of temperate forests (Preisser et al. 1998; Sperber et al. 2004; Thunes et al. 2004; Vance et al. 2007; Pucci 2008; Stireman 2008; Sobek et al. 2009; Ulyshen et al. 2010, 2011a, 2011b; Birtele & Hardersen 2012; Stireman et al. 2012; Di Giovanni et al. 2015). In this study, we analyzed the community composition of solitary wasps belonging to Ampulicidae, Crabronidae and Sphecidae (the three families of Apoidea Spheciformes present in Italy) of understory and canopy of the Natural Reserve of "Bosco della Fontana", a temperate plain forest in North Italy. Spheciformes are mostly predators, although some genera are parasitoids or cleptoparasites of other insects or arachnids. Adults feed on nectar or sugary secretions, more rarely on fluids of the prey hunted as food for their larvae (Pagliano & Negrisolo 2005). So far, several surveys have been carried out in this area to provide a comprehensive framework of the arthropod fauna of this remnant forest (Mason et al. 2002; Cerretti et al. 2004; Birtele & Hardersen 2012; Hardersen et al. 2012; Stireman et al. 2012;

Di Giovanni et al. 2015). Thanks to an intensive sampling with Malaise traps, we tested for differences in community composition of Spheciformes between canopy and understory. Observed patterns in different layers were related to species biology in order to understand if species association with canopy or understory may be explained by differences in species foraging habits.

Material & Methods

Sampling

The sampling was carried out in the Natural Reserve of “Bosco della Fontana” (45°12'N, 10°44'E), a semi-natural forest of 233ha, located about 5km from the municipality of Mantua (Lombardy, Italy), at an average altitude of 25m. The forest is surrounded by intensive crops and industries. Further details on the study area are reported in Mason et al. (2002) and Mason (2004).

Fourteen Malaise traps were placed, seven in the understory and seven in the canopy (hanged on branches between 15 and 21m above the ground), in oak-hornbeam sections of the forest (*Polygonato multiflori-Quercetum roboris* Sartori 1980), which is the dominant vegetation type at “Bosco della Fontana”. The sites were chosen using a complete randomized design, with a minimum distance between traps of 70m. To minimize the edge-effect, the traps were placed at least 40m from the borders of the forest, 30m from the internal artificial clearings and 10m from the forest tracks.

The traps were activated continuously from April 1st to November 25th 2008. Collecting jars were filled with 70% ethanol and replaced every two weeks. The material collected during this study is preserved, partly pinned and partly in ethanol, in the entomological collections of the Museum of Zoology of the “Sapienza” University of Rome (MZUR). The Spheciformes wasps were identified to species level by MM by using Pagliano & Negrisola (2005), Bitsch & Leclercq (1993) and Bitsch et al. (1997, 2007).

Data Analysis

To compare the species richness and the sampling effort in the two habitats, sample-based accumulation curves and 95% confidence intervals were calculated for pooled canopy and understory traps using EstimateS 9.1.0 (Colwell 2013). Phenological patterns of Spheciformes abundance and diversity were also examined graphically.

Differences in the community composition between canopy and understory was tested using a permutation MANOVA (Anderson 2001), as implemented in the *vegan* package in R (Oksanen et al. 2013). The test employed Bray-Curtis distances and 1000 randomizations to assess significance.

To show the association between traps and species composition, a PCA analysis was carried out using CANOCO

4.5 (Lepš & Šmilauer 2003), on a $\log(x + 1)$ -transformed species abundances and scaling on interspecies correlations. Then, a RDA was performed on the same dataset to assess how much of the observed variation in species composition can be explained by trap position (canopy vs. understory). The significance of the habitat variable in the constrained analysis was previously tested using a Monte Carlo permutation with 499 randomizations (Lepš & Šmilauer 2003). In the plotted graph, species have been listed according to their predatory habits (following Pagliano & Negrisola 2005, Bitsch & Leclercq 1993; Bitsch et al. 1997, 2007 and references therein).

Results

A total of 1118 specimens were collected (983 females and 135 males), belonging to 42 species and 21 genera of Ampulicidae, Crabronidae and Sphecidae. Families Ampulicidae and Sphecidae were represented by two (*Ampulex fasciata*, *Dolichurus corniculatus*) and three species (*Ammophila sabulosa*, *Prionyx subfuscatus*, *Sceliphron curvatum*), respectively. About half of the sample (545) belonged to Crabronidae of the genus *Trypoxylon*. Eleven out of 42 species were singletons (i.e., one individual), eight in the canopy and three in the understory, respectively.

Understory traps caught more than twice the specimens collected in the canopy, 763 individuals belonging to 26 species. Canopy traps collected 355 specimens and 33 species, i.e. about 80% of the overall species diversity in this study (Table 1). At present, 52 species and 27 genera of Spheciformes have been recorded for the Natural Reserve of “Bosco della Fontana” (cf. Negrisola 2002; Mei 2008; present work).

Sample-based accumulation curves showed a clear different slope for traps in the two habitats (Fig. 1). Both curves are still far from reaching an asymptote, suggesting that a greater sampling effort in both habitats would significantly increase the number of species collected. Temporal patterns of abundance and species richness indicated a late-spring peak in May-June, followed by a second one in August with high abundance and relatively low diversity. After September, there is a general decline of abundance and species richness for both habitat types, with the canopy hosting relatively more species and individuals than the understory (Fig. 2).

The permutation MANOVA revealed that the community composition of the two habitat layers is clearly different ($F_{1,12}=9.22$, $P<0.01$). Assemblages from the two forest levels appear distinctly separated also in the two-dimensional PCA plot (Fig. 3). In the PCA analysis, the first two axes accounted for about 58% of the total variance. The RDA showed trap position explains the 54% of the observed variation in species distribution between canopy and understory (Monte Carlo test $F=7.49$, $P<0.01$).

Table 1 – Species and abundances of Ampulicidae, Crabronidae and Sphecidae collected during the Canopy project 2008. For each species, predatory habits are provided. C = canopy trap; U = understory trap.

Species	Prey	Canopy							Understory						
		C1	C2	C3	C4	C5	C6	C7	U1	U2	U3	U4	U5	U6	U7
Ampulicidae															
<i>Ampulex fasciata</i> Jurine, 1807	Blattodea	2	-	1	2	1	2	5	2	-	-	-	3	1	2
<i>Dolichurus corniculus</i> (Spinola, 1808)	Blattodea	-	-	-	-	-	-	-	-	-	-	-	1	1	1
Crabronidae															
<i>Crossocerus acanthophorus</i> (Kohl, 1892)	unknown	-	6	-	-	-	-	-	-	-	-	-	-	-	-
<i>Crossocerus annulipes</i> (Lepeletier & Brullé, 1835)	Rhynchota	-	-	-	-	-	1	-	-	-	-	-	1	1	-
<i>Crossocerus binotatus</i> Lepeletier & Brullé, 1835	Diptera	-	-	-	-	-	-	-	-	1	-	-	-	-	-
<i>Crossocerus cetratus</i> (Shuckard, 1837)	Diptera	-	-	-	-	-	-	-	-	-	-	-	2	-	-
<i>Crossocerus elongatulus</i> (van der Linden, 1829)	Diptera	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Crossocerus podagricus</i> (van der Linden, 1829)	Diptera	-	-	-	1	-	-	-	4	10	8	-	2	10	9
<i>Crossocerus quadrimaculatus</i> (Fabricius, 1793)	Diptera	-	-	-	-	-	-	-	2	10	-	1	2	1	-
<i>Crossocerus vagabundus</i> (Panzer, 1798)	Diptera	1	-	-	-	-	-	-	-	-	-	1	1	-	-
<i>Ectemnius cavifrons</i> (Thomson, 1870)	Diptera	2	1	2	-	-	3	3	2	5	5	-	-	3	1
<i>Ectemnius cephalotes</i> (Olivier, 1792)	Diptera	1	-	2	4	-	1	5	11	3	9	8	9	18	10
<i>Ectemnius continuus</i> (Fabricius, 1804)	Diptera	-	-	1	-	-	-	-	-	-	-	-	-	-	-
<i>Ectemnius lituratus</i> (Panzer, 1805)	Diptera	-	-	-	-	-	-	-	-	1	-	-	-	1	-
<i>Ectemnius nigratarsus</i> (Herrich-Schaeffer, 1840)	unknown (Diptera?)	-	-	-	-	-	-	-	-	-	1	-	-	1	3
<i>Mimumesa unicolor</i> (van der Linden, 1829)	Rhynchota Auchenorrhyncha	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Nitela borealis</i> Valkeila, 1974	Psocoptera	3	-	1	-	-	3	3	-	-	-	-	-	-	-
<i>Nitela fallax</i> Kohl, 1884	Psocoptera	2	1	-	3	-	-	1	-	-	-	-	-	-	-
<i>Nitela spinolae</i> Latreille, 1809	Psocoptera	1	-	-	-	-	-	2	-	-	-	-	-	-	-
<i>Nysson trimaculatus</i> (Rossi, 1790)	kleptoparasite	-	-	-	-	-	-	-	-	3	-	-	1	2	-
<i>Passaloecus corniger</i> Shuckard, 1837	Rhynchota Sternorrhyncha	-	-	-	-	-	-	3	-	-	-	-	-	-	-
<i>Passaloecus gracilis</i> (Curtis, 1834)	Rhynchota Sternorrhyncha	12	9	2	4	-	6	7	7	1	-	-	-	-	-
<i>Pemphredon austriaca</i> (Kohl, 1888)	Rhynchota Sternorrhyncha	-	-	-	-	-	-	1	-	-	-	-	-	-	-
<i>Pemphredon lethifer</i> (Shuckard, 1837)	Rhynchota Sternorrhyncha	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pemphredon lugubris</i> (Fabricius, 1793)	Rhynchota Sternorrhyncha	-	-	-	-	-	1	2	3	1	4	2	2	9	3
<i>Polemistus abnormis</i> (Kohl, 1888)	Rhynchota Sternorrhyncha	2	-	-	1	-	-	-	-	-	-	-	-	-	-
<i>Psen exaratus</i> (Eversmann, 1849)	unknown (Rhynchota Auchenorrhyncha?)	-	-	-	-	-	-	2	-	-	-	-	-	1	2
<i>Psenulus fuscipennis</i> (Dahlbom, 1843)	Rhynchota Sternorrhyncha	3	1	-	1	3	11	4	-	-	-	-	-	1	-
<i>Psenulus pallipes</i> (Panzer, 1798)	Rhynchota Sternorrhyncha	8	37	10	7	8	12	12	13	25	3	2	8	20	9
<i>Psenulus schencki</i> (Tournier, 1889)	Rhynchota Sternorrhyncha	1	1	-	1	1	2	3	-	-	-	-	-	1	-
<i>Rhopalum coarctatum</i> (Scopoli, 1763)	Diptera	-	-	-	-	1	1	-	1	-	2	1	-	4	8
<i>Solierella compedita</i> (Piccioli, 1869)	Rhynchota Heteroptera	-	-	-	1	-	-	-	-	-	-	-	-	-	-
<i>Spilomena troglodytes</i> (van der Linden, 1829)	Thysanoptera	3	1	-	-	-	1	-	-	-	-	-	-	-	-
<i>Stigmus solskyi</i> Morawitz, 1864	Rhynchota Sternorrhyncha	2	-	-	-	1	1	-	-	-	-	-	-	1	-
<i>Tachytes etruscus</i> (Rossi, 1790)	Orthoptera	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Trypoxylon clavicerum</i> Lepeletier & Serville, 1825	Araneae	7	13	4	9	2	12	6	48	96	51	25	14	35	26
<i>Trypoxylon deceptorium</i> Antropov, 1991	Araneae	-	-	-	-	-	-	-	-	-	-	-	-	1	-
<i>Trypoxylon figulus</i> (Linnaeus, 1758)	Araneae	-	1	2	3	1	4	2	21	34	21	3	7	22	11
<i>Trypoxylon minus</i> de Beaumont, 1945	Araneae	6	4	4	3	1	3	4	1	3	-	-	-	29	6
Sphecidae															
<i>Ammophila sabulosa</i> (Linnaeus, 1758)	Lepidoptera (larvae)	1	-	-	-	-	1	-	-	-	-	-	-	-	-
<i>Prionyx subfuscatus</i> (Dahlbom, 1845)	Orthoptera	1	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Sceliphron curvatum</i> (Smith, 1870)	Araneae	-	-	-	-	-	-	-	1	-	-	-	-	-	-

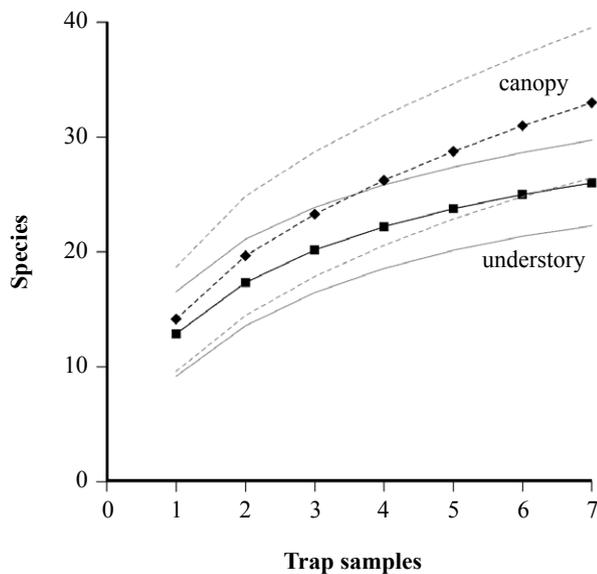


Fig. 1 – Sample-based accumulation curves and 95% confidence intervals for pooled canopy (dashed line) and understory (solid line) traps.

Wasps that prey on spiders (*Trypoxylon* spp.), cockroaches (*Dolichurus* spp.) or flies (*Crossocerus* and *Ectemnius* spp.) were strictly associated with the understory traps, while the canopy community includes species that exploit barkflies (*Nitela* spp.), thrips (*Spilomena troglodytes*) and aphids (*Passaloecus* and *Psenulus* spp.) (Fig. 3).

Discussion

As already observed in other insect groups (Birtele & Hardersen 2012; Stireman et al. 2012; Hardersen et al. 2014; Di Giovanni et al. 2015), the canopy community of Spheciformes at “Bosco della Fontana” is markedly different from that of the understory. Previous studies performed in temperate forests also showed a vertical stratification in the community composition of hymenopterans (Vance et al. 2007; Pucci 2008; Sobek et al. 2009; Ulyshen et al. 2010, 2011). Vance et al. (2007) found that, in northeastern temperate forests in Canada, Spheciformes are more common in the canopy than in the understory, suggesting that highly mobile hymenopterans may spend significant amounts of time foraging in this habitat. A similar result was found by Sobek et al. (2009), who collected more cavity-nesting bees – including Spheciformes – in the canopy of a broadleaf forest in Germany. In our study, some of the species found in the canopy, such as the crabronid *Tachytes etruscus* and the sphecids *Prionyx subfuscatus* and *Sceliphron curvatum*, prefer open habitats, and their occurrence in the canopy is likely occasional, suggesting the use of this layer as a dispersal corridor to move from one open area to another (Moran & Southwood 1982; Pucci 2008; Di Giovanni et al. 2015).

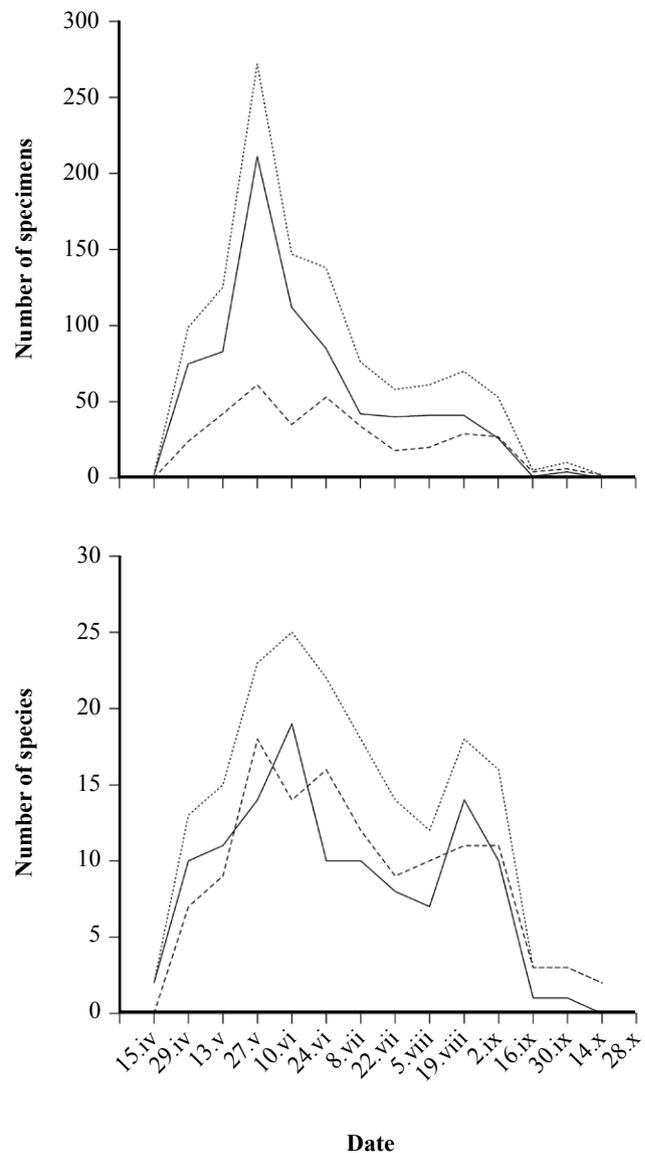


Fig. 2 – Ichneumonid abundance (top) and species richness (bottom) by sampling date over all traps. Lines indicate the number of specimens or species for canopy (dashed), understory (solid), and both habitats (dotted).

Species associated with canopy included *Passaloecus* spp. and *Psenulus* spp., predators of sap-sucking insects as aphids, *Nitela* spp., attacking epiphyte grazers such as barkflies and *Spilomena troglodytes*, preying on thrips. Previous studies showed that sap-sucking and honeydew producer insects can be abundant in the canopy of temperate forests (Moran & Southwood 1982), turning out to be an important source of non-floral sugar for bees and wasps when only few flowers are available in the understory (Ulyshen et al. 2010, 2011). Sampling the arthropod fauna of native and introduced oak species in UK and France, Southwood et al. (2005) found that moist higher strata of broadleaf forests can host a very abundant and diverse epiphyte fauna, including Psocoptera and Thysanoptera. In

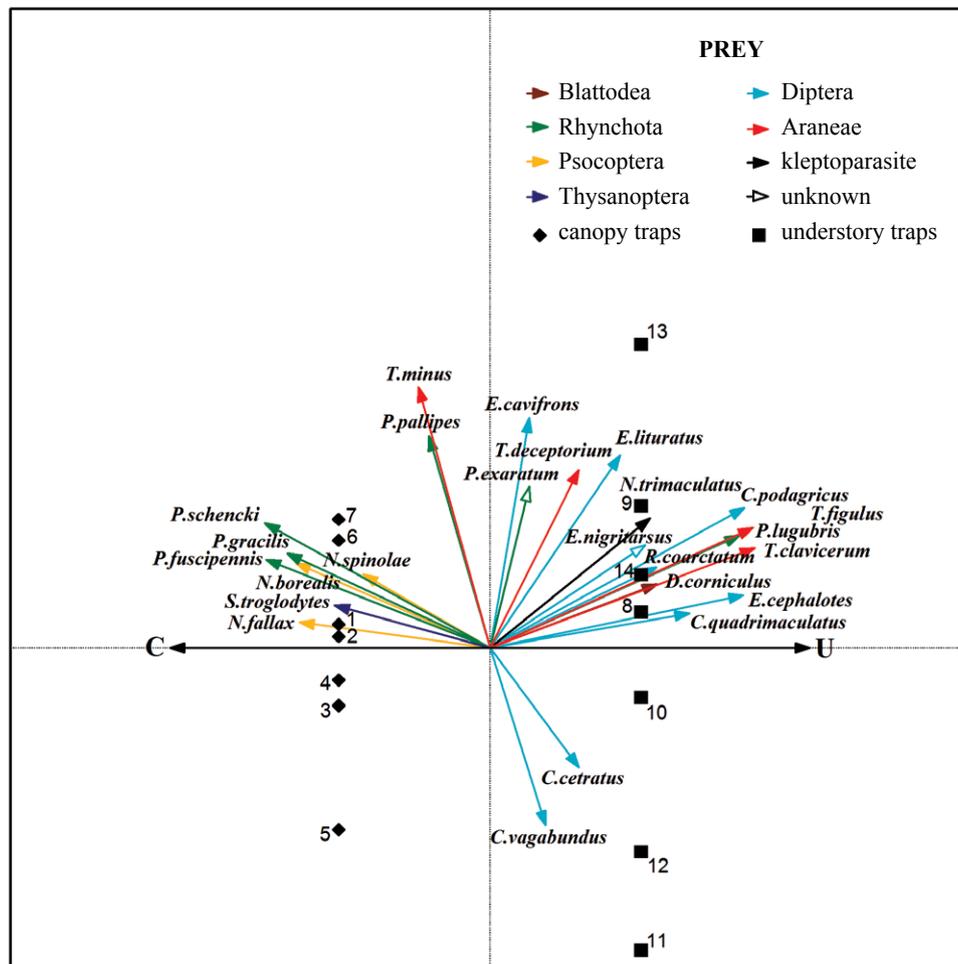


Fig. 3 – PCA ordination plot showing traps and species association for the first two axes. Species were grouped according to predatory habits. Only species with fit range 20% or more are shown. C = canopy; U = understory.

the oak-hornbeam sections of “Bosco della Fontana” the shrub layer can be very thick and often dominated by the presence of *Ruscus aculeatus*, with shrubs (*Cornus*, *Viburnum*, *Ligustrum*, *Euonymus*) often confined to forest borders (Campanaro et al. 2007). As a consequence, it is likely that sap-sucking honeydew producers like aphids, and epiphyte grazers like thrips and barkflies to be confined to the canopy level where they act as a reservoir of sugary secretions and attract predators (Moran & Southwood 1982; Southwood et al. 2005). Interestingly, phenological patterns showed relatively higher abundance and diversity of Spheciformes in the canopy from the late summer, suggesting that species may move to higher strata of the forest in search for alternative food sources when floral resources in the understory start to shrink.

The bulk of the community of Spheciformes of the understory consisted in predators of dipterans (genera *Crossocerus* and *Ectemnius*) and spiders (genus *Trypoxylon*). *Ectemnius* and *Crossocerus* species associated with ground traps prey on small Diptera Brachycera (*Ectemnius cavifrons* (Fig. 4), *E. cephalotes*, *E. lituratus* and *Crosso-*

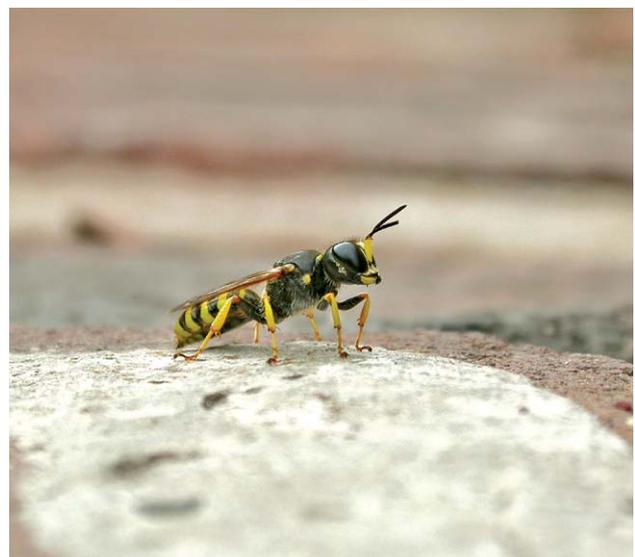


Fig. 4 – *Ectemnius cavifrons* (Thomson, 1870) (Crabronidae) from England, Nottinghamshire. Photo by Dilys and Trevor Pendleton, www.eakringbirds.com.

cerus quadrimaculatus) or Diptera Nematocera (*C. cetratus*, *C. podagricus*, *C. vagabundus*) (Schmidt 1980), which can be abundant in highly humid microhabitats like deadwood and leaf litter on the forest floor. *Ectemnius* spp. are known to nest in rotten wood or stems of herbaceous plants (Pagliano & Negrisolò 2005). *Trypoxylon* species, spider predators nesting in cavity left by wood-boring beetles or in hollow stems (Pagliano & Negrisolò 2005), have been found mostly in the understory traps. However, our results disagree with those by Sobek et al. (2009) who found specimens of *T. clavicerum* in the canopy to be almost twice those collected in the understory in a broad-leaf forest in Germany. Spider abundance in the canopy of the temperate forests is well documented (Larrivée & Buddle 2009; Otto & Floren 2010). However, as pointed out by Di Giovanni et al. (2015) for ichneumonids parasitizing spiders at “Bosco della Fontana”, different species can patrol different layers along the same tree, according to host availability. The availability of abandoned galleries of saproxylic insects in suspended deadwood may be another factor influencing vertical stratification of the species of the genus *Trypoxylon* (Sobek et al. 2009), and some of them can be found more frequently in the canopy while searching for suitable nesting-cavities.

In conclusion, it is clear that restricting any survey to the ground layer will result in a partial picture of the actual biodiversity inhabiting temperate deciduous forests (Vance et al. 2007; Stireman et al. 2012; Di Giovanni et al. 2015).

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References

- Anderson M.J. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26: 32–46.
- Basset Y., Springate N.D., Aberlenc H.-P., Delvare G. 1997. A review of methods for sampling arthropods in tree canopies, pp: 27–52. In: Stork N.E., Adis J., Didham R.K. (eds), *Canopy arthropods*. Chapman & Hall, London, xvi + 567 pp.
- Basset Y., Novotny V., Miller S.E., Kitching R.L. 2003. *Arthropod of tropical forests. Spatio-temporal dynamics and resource use in the canopy*. Cambridge University Press, Cambridge, 492 pp.
- Basset Y., Cizek L., Cuénoud P., Didham R.K., Guilhaumon F., Missa O., Novotny V., Ødegaard F., Roslin T., Schmidl J., Tishechlin A.K., Winchester N.N., Roubik D.W., Aberlenc H.-P., Bail J., Barrios H., Bridle J.R., Castaño-Meneses G., Corbara B., Curletti G., Duarte de la Rocha W., De Bakker D., Delabie J.H.C., Dejean A., Fagan L.L., Floren A., Kitching R.L., Medianero E., Miller S.E., Gama de Oliveira E., Orivel J., Pollet M., Rapp M., Ribeiro S.P., Roisin Y., Schmidt J.B., Sørensen L., Leponce M. 2012. Arthropod diversity in a tropical forest. *Science*, 338: 1481–1484.
- Birtele D., Hardersen S. 2012. Analysis of vertical stratification of Syrphidae (Diptera) in an oak-hornbeam forest in northern Italy. *Ecological Research*, 27: 755–763.
- Bitsch J., Leclercq J. 1993. *Hyménoptères Sphecidae d'Europe occidentale. Volume 1. Généralités – Crabroninae. Faune de France*, 79, 325 pp.
- Bitsch J., Barbier Y., Gayubo S. F., Schmidt K., Ohl M. 1997. *Hyménoptères Sphecidae d'Europe occidentale. Volume 2. Faune de France*, 82, 429 pp.
- Bitsch J., Dollfuss H., Bouček Z., Schmidt K., Schmid-Egger C., Gayubo S.F., Antropov A.V., Barbier Y. 2007. *Hyménoptères Sphecidae d'Europe Occidentale. Volume 3. Faune de France*, 86, 479 pp.
- Campanaro A., Hardersen S., Mason F. 2007. Piano di gestione della Riserva Naturale Statale e Sito Natura 2000 “Bosco della Fontana”. *Quaderni Conservazione Habitat*, 4. Cierre Edizioni, Verona, 221 pp.
- Cerretti P., Hardersen S., Mason F., Nardi G., Tisato M., Zapparoli M. 2004. *Invertebrati di una foresta della Pianura Padana, Bosco della Fontana. Secondo contributo. Conservazione Habitat Invertebrati*, 3. Cierre Grafica Editore, Verona, 304 pp.
- Colwell R.K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Software and user's guide available at: <http://purl.oclc.org/estimates>.
- Di Giovanni F., Cerretti P., Mason F., Minari E., Marini L. 2015. Vertical stratification of ichneumonid wasp communities: the effects of forest structure and life-history traits. *Insect Science*, 22: 688–699.
- Floren A., Schmidl J. 1999. Faunistisch-ökologische Ergebnisse eines Baumkronen-Benebelungsprojectes in einem Eichenhochwald des Steigerwaldes. *Beiträge zur bayerischen Entomofaunistik*, 3: 179–195.
- Floren A., Schmidl J. 2008. *Canopy arthropod research in Europe*. Bioform, Nuremberg, 576 pp.
- Hardersen S., Curletti G., Leseigneur L., Platia G., Liberti G., Leo P., Cornacchia P., Gatti E. 2012. Spatio-temporal analysis of beetles from the canopy and ground layer in an Italian lowland forest. *Bulletin of Insectology*, 67(1): 87–97.
- Larrivée M., Buddle C.M. 2009. Diversity of canopy and understory spiders in north-temperate hardwood forests. *Agricultural and Forest Entomology*, 11: 225–237.
- Lepš J., Šmilauer P. 2003. *Multivariate analysis of ecological data using Canoco*. Cambridge University Press, Cambridge, 376 pp.
- Mason F. 2004. *Dinamica di una foresta della Pianura Padana. Bosco della Fontana. Primo contributo, monitoraggio 1995. Seconda edizione con linee di gestione forestale. Rapporti scientifici*, 1. Gianluigi Arcari Editore, Mantova, 224 pp.
- Mason F., Cerretti P., Tagliapietra A., Speight M.C.D., Zapparoli M. 2002. *Invertebrati di una foresta della Pianura Padana, Bosco della Fontana. Primo contributo. Conservazione Habitat Invertebrati*, 1. Gianluigi Arcari Editore, Mantova, 176 pp.
- Mei M. 2008. Note faunistiche su alcuni Crabronidi della fauna italiana (Hymenoptera, Crabronidae). *Bollettino dell'Associazione Romana di Entomologia*, 63(1-4): 173–182.
- Moran V.C., Southwood T.R.E. 1982. The guild composition of arthropod communities in trees. *Journal of Animal Ecology*, 51: 289–306.
- Negrisolò E. 2002. Hymenoptera. Sphecidae, pp: 152–154. In: Mason F., Cerretti P., Tagliapietra A., Speight M.C.D., Zapparoli M. (eds), *Invertebrati di una foresta della Pianura Padana, Bosco della Fontana, Primo contributo. Conservazione*

- Habitat Invertebrati, 1. Gianluigi Arcari Editore, Mantova, 176 pp.
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Wagner H. 2013. Vegan: Community Ecology Package. Package available at <http://cran.r-project.org/web/packages/vegan>.
- Otto S., Floren A. 2010. The canopy spiders (Araneae) of the floodplain forest in Leipzig. *Arachnologische Mitteilungen*, 39: 25–38.
- Pagliano G., Negrisolò E. 2005. Hymenoptera Sphecidae. *Fauna d'Italia*, vol. XL. Edizioni Calderini, Bologna, 559 pp.
- Preisser E., Smith D.C., Lowman M.D. 1998. Canopy and ground level insect distribution in a temperate forest. *Selbyana*, 19: 141–146.
- Pucci T. 2008. A comparison of the parasitic wasps (Hymenoptera) at elevated versus ground yellow pan traps in a beech-maple forest. *Journal of Hymenoptera Research*, 17: 116–123.
- Schmidt K. 1980. Materialien zur Aufstellung einer Roten Liste der Sphecidae (Grabwespen) Baden-Württenbergs. II. Crabronini. Beihefte zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg, 51/52: 309–398.
- Sobek S., Tschamtké T., Scherber C., Schiele S., Steffan-Dewenter I. 2009. Canopy vs. understory: does tree diversity affect bee and wasp communities and their natural enemies across forest strata? *Forest Ecology and Management*, 258: 609–615.
- Southwood T.R.E., Wint G.R.W., Kennedy C.E.J., Greenwood S.R. 2005. The composition of the arthropod fauna of the canopies of some species of oak (*Quercus*). *European Journal of Entomology*, 102: 65–72.
- Sperber C.F., Nakayama K., Valverde M.J., de Siqueira Neves F. 2004. Tree species richness and density affect parasitoid diversity in cacao agroforestry. *Basic and Applied Ecology*, 5: 241–251.
- Stireman J.O. III. 2008. α and β diversity of a tachinid parasitoid community over space and time. *Annals of the Entomological Society of America*, 101(2): 362–370.
- Stireman J.O. III, Cerretti P., Whitmore D., Hardersen S., Gignelle D. 2012. Composition and stratification of a tachinid (Diptera: Tachinidae) parasitoid community in a European temperate plain forest. *Insect Conservation and Diversity*, 5: 346–357.
- Thunes K.H., Skartveit J., Gjerde I., Stary J., Solhøy T., Fjellberg A., Kobro S., Nakahara S., zur Strassen R., Vierbergen G., Szadziewski R., Hagan D.V., Grogan Jr. W.L., Jonassen T., Aakra K., Anonby J., Greve L., Aukema B., Heller K., Michelsen V., Haenni J.-P., Emeljanov A.F., Douwes P., Berggren K., Franzen J., Disney R.H.L., Prescher S., Johanson K.A., Mamaev B., Podenas S., Andersen S., Gaimari S.D., Nartshuk E., Söli G.E.E., Papp L., Midtgaard F., Andersen A., Tschirnhaus M. von, Bächli G., Olsen K.M., Olsvik H., Földvári M., Raadstad J.E., Hansen L.O., Djursvoll P. 2004. The arthropod community of Scots pine (*Pinus sylvestris* L.) canopies in Norway. *Entomologica Fennica*, 15: 65–90.
- Ulyshen M.D. 2011. Arthropod vertical stratification in temperate deciduous forests: implications for conservation-oriented management. *Forest Ecology and Management*, 261: 1479–1489.
- Ulyshen M.D., Soon V., Hanula J.L. 2010. On the vertical distribution of bees in a temperate deciduous forest. *Insect Conservation and Diversity*, 3: 222–228.
- Ulyshen M.D., Pucci T.M., Hanula J.L. 2011a. The importance of forest type, tree species and wood posture to saproxylic wasp (Hymenoptera) communities in the southeastern United States. *Journal of Insect Conservation*, 15: 539–546.
- Ulyshen M.D., Soon V., Hanula J.L. 2011b. Vertical distribution and seasonality of predatory wasps (Hymenoptera: Vespidae) in a temperate deciduous forest. *Florida Entomologist*, 94(4): 1068–1070.
- Vance C.C., Smith S.M., Malcolm J.R., Huber J., Bellocq M.I. 2007. Differences between forest type and vertical strata in the diversity and composition of hymenopteran families and mymarid genera in northeastern temperate forests. *Environmental Entomology*, 36(5): 1073–1083.