Functional groups of hoverflies in Southeast Europe across different vegetation types

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Abstract:	To better understand the relationship between biodiversity and ecosystem functioning, it is increasingly accepted that the focus of study needs to shift from taxonomic identity to the diversity of functional traits displayed by species within a community. Such an approach allows species to be grouped according to particular functional characteristics. Increasingly viewed as an extremely important group of model organisms, hoverflies have been the focus of a variety of ecological studies. Based on data regarding selected functional traits of hoverflies registered in Southeast Europe, the main aims of our study were to define hoverfly functional groups according to the similarity of these traits, as well as to compare the representation of delineated hoverfly functional groups among these vegetation types. We used fuzzy clustering to classify 568 SE European hoverfly species into five functional groups. The principle trait separating these functional groups was larval feeding type, followed by size of species range, flight ability, number of generations, inundation tolerance, and tolerance to human impact. For 9 of 11 vegetation types, the dominant functional group was characterized by species with good flight ability, having high human impact tolerance and more annual generations. The remaining two vegetation types, South-west Balkan sub-Mediterranean mixed oak

	forests and Mediterranean mixed forests, showed disparate dominance patterns, indicating that richness of functional groups is dependent on vegetation. Further investigation of whether and how established conservation measures enable recovery of the functional richness affected by habitat disturbance would help elucidate the importance of functional diversity in preserving biodiversity.

Functional groups of hoverflies in Southeast Europe across different vegetation types

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Abstract

To better understand the relationship between biodiversity and ecosystem functioning, it is increasingly accepted that the focus of study needs to shift from taxonomic identity to the diversity of functional traits displayed by species within a community. Such an approach allows species to be grouped according to particular functional characteristics. Increasingly viewed as an extremely important group of model organisms, hoverflies have been the focus of a variety of ecological studies. Based on data regarding selected functional traits of hoverflies registered in Southeast Europe, the main aims of our study were to define hoverfly functional groups according to the similarity of these traits, as well as to compare the representation of delineated hoverfly functional groups among these vegetation types. We used fuzzy clustering to classify 568 SE European hoverfly species into five functional groups. The principle trait separating these functional groups was larval feeding type, followed by size of species range, flight ability, number of generations, inundation tolerance, and tolerance to human impact. For 9 of 11 vegetation types, the dominant functional group was characterized by species with good flight ability, having high human impact tolerance and more annual generations. The remaining two vegetation types, South-west Balkan sub-Mediterranean mixed oak forests and Mediterranean mixed forests, showed disparate dominance patterns, indicating that richness of functional groups is dependent on vegetation. Further investigation of whether and how established conservation measures enable recovery of the functional richness affected by habitat disturbance would help elucidate the importance of functional diversity in preserving biodiversity.

Key words: Diptera, functional classification, insects, plant cover, richness, Syrphidae, traits

INTRODUCTION

Species richness and abundance have commonly been used as indicators to evaluate the state of a given ecosystem or ecosystem process (Medellín *et al*. 2000; Peters *et al*. 2016). However, a diverse and species-rich community does not necessarily mean that ecosystem functions or services are intact and function properly (Winsa *et al.* 2017). To better understand the relationship between biodiversity and (ecosystem) functioning, it is increasingly accepted that our focus needs to shift from taxonomic identity to the diversity of functional traits exhibited by species within a community (Díaz & Cabido 2001; Cadotte *et al*. 2011; Cardinale *et al*. 2012).

A functional group can be defined as a set of species displaying a similar response to the environment or having similar effects on ecosystem processes (Gitay & Noble 1997). Functional classification often has two objectives, one being to investigate the effects of species on ecosystem characteristics (Cornwell & Ackerly 2009), and the other to explore the type of response to environmental changes (functional response groups), such as habitat loss or degradation (Craven *et al*. 2016), availability of resources (Perkins *et al*. 2018), or climate change (Ooi *et al*. 2014). Identification of functional response groups may help to understand and predict how certain aspects of the community and ecosystem can be affected by environmental changes (Hooper *et al*. 2002).

Hoverflies are increasingly viewed as an extremely important group of model organisms with remarkable ecological and cultural value as pollinators (Jauker & Wolters 2008; Doyle *et al.* 2020) and biological control agents (Grosskopf 2005; Day *et al*. 2015), and they have been the focus of diverse ecological studies. Considerable effort has been devoted to investigating how hoverflies respond to the biggest environmental challenges worldwide, such as intensive agriculture (Li *et al*. 2020), urbanization (Persson *et al*. 2020), climate change (Miličić *et al.* 2018), and invasive species (Davis *et al*. 2018; Szigeti *et al*. 2020). However, the majority of past research has explored links between hoverfly species richness, abundance and/or distribution patterns, and environmental conditions, but very few studies have considered evaluating hoverfly functional groups (Schweiger *et al.* 2007; Keil *et al*. 2008).

Southeast Europe (SE Europe: Balkan Peninsula and the Aegean islands) is a region rich in flora (Sabovljević *et al*. 2008) and fauna (Crnobrnja-Isailović 2007; Poulakakis *et al*. 2015). Its geographical position at a crossroad of biogeographic influences, reliefs, climatic types and underlying bedrock preconditions it for high biodiversity within a relatively small area (Sabovljević *et al*. 2008). This region has been designated as one of the world's hotspots for hoverflies, harboring a great number of endemic and rare species (Vujić *et al*. 2001, Radenković *et al*. 2011). Such a rich and diverse environment makes it particularly suitable for examining not only taxonomic but also functional diversity, as different types of habitat support different ecological functions (Gibb & Hochuli 2002). These habitats can be found in various vegetation types across SE Europe, and they display the dominant natural plant communities in accordance with current edaphic and climatic conditions (Bohn *et al.* 2007).

Based on data pertaining to selected functional traits of hoverflies in SE Europe, we aimed to define hoverfly functional groups in this region based on the similarity of these traits, as well as to compare the representation of delineated hoverfly functional groups among different vegetation types.

MATERIAL AND METHODS

A list of all hoverflies in SE Europe and their representation in different vegetation types was created based on data from the existing literature, personal observations (resulting from more than 50 years of collecting hoverflies in the region; dataset deposited in the Database of Department of Biology and Ecology, Faculty of Sciences, University of Novi Sad, Serbia), and expert opinion.

Classification of hoverflies into functional groups was conducted based on 11 functional traits relating to the biological and ecological characteristics of each species, which together encompassed 46 trait categories. . Information on larval microhabitat, larval feeding type, duration of larval development, inundation tolerance, number of generations and period of flight was directly extracted from existing literature (Speight 2018; Speight *et al*. 2020). Area of species range was inferred based on the available distribution data of analyzed species. Flight ability was partly based on field observations and partly on data available in Speight *et al*. 2020, from which information about the migratory status of species was extracted. Species was categorized as being a good or bad flier based on its ability to fly longer distances; species lingering around the feeding place, flying slowly and heavily were categorized as having bad flight ability, opposed to species crossing longer distances, flying fast and briskly, which were categorized as having good flight ability. Height at which species fly was scored solely on field observations. Species observed flying at height below 1m above the ground were classified as flying near the ground, while species flying above 1.5 m above the ground were scored as arboreal. Human impact tolerance was scored based on expert opinion. As data on body size was not available in the literature, we obtained these measures in the laboratory (details in Miličić *et al*. 2020). There were several possible states for each defined trait. To avoid bias for traits having multiple trait states, we applied a weighted average, whereby the weight of each trait state was divided by the number of trait states for that particular trait. In several cases where the trait state for a particular species was unknown, the species was assigned the most common trait state found among other species from the same genus. A list of the functional traits and corresponding trait states we considered is presented in Table S1.

As a preliminary analysis to categorize species into functional groups, we conducted a Principal Component Analysis (PCA). PCA was carried out by applying a normal varimax rotation of factor loadings (Dennis & Hellberg, 2010; Livshultz *et al*. 2011). Only factors with an eigenvalue greater than one were considered significant. Functional traits with a factor loading greater than 0.6 were considered relevant. To classify species into functional groups, we applied fuzzy clustering in the R package cluster (Maechler *et al*. 2019). In fuzzy clustering, each observation can potentially belong to a larger number of clusters and thereby be "scattered" across a number of clusters (Podani 1994). To determine the optimal number of clusters, the Dunn partition coefficient was used, which varies between one for "hard" clusters and 1 / k (where k is the number of clusters) for fully dispersed datasets (Trauwaert 1988). We used silhouette width to determine the separation distance between clusters. Silhouette coefficients close to +1 indicate that a sample (species) is distant from neighboring clusters, a value of 0 indicates that a species is close to the boundaries of two clusters, and negative values indicate that a species is potentially included in the wrong cluster (Maechler *et al*. 2019). Allocation of species to one "hard cluster" was based on the highest percentage of attribution to some of the fuzzy clusters. After classification of the functional groups, the correlation of allocated variability with defined clusters was tested using analysis of variance (ANOVA). To examine the significance of the differences between clusters, a Tukey's HSD test was used. The degree to which individual species belonged to defined clusters (functional groups) was tested by Discriminant Function Analysis. Based on the square of the Mahalanobis distance, the UPGMA (Unweighted Pair-Group Method using Arithmetic Averages) method was applied to construct a dendrogram describing the distance between different functional groups.

In order to estimate the representation of functional groups of hoverflies in different vegetation types represented in SE Europe, we used the map of natural vegetation of Europe published in Miličić *et al*. (2020) (Fig. 1), which was based on a previously published map of natural vegetation in Europe (Bohn *et al.* 2000). Details on map conversion are reported in Miličić *et al.* (2020). A Chi-squared test was used to determine if there were significant differences between the frequencies of the different functional groups across 11 vegetation types in SE Europe.

RESULTS

In total, 568 species registered in SE Europe were included in the analyses. The first 5 PCA axes were kept in further analyses based on the results of the Scree test, explaining 39.9% of the variability (10.9%, 10.1%, 7.3%, 6.1% and 5.5%, respectively). The eigenvalues for axes 1-5 were 5.12, 4.77, 3.44, 2.85 and 2.60, respectively.

Division into functional groups

The fuzzy cluster analysis applied to the factor scores of first five PC axes resulted in five clearly separated functional groups (FGs) of hoverflies. Dunn's partitioning coefficient was 0.78 with a membership exponent set to 1.5. The average silhouette width for the total dataset was 0.52, with widths per cluster (FG) of 0.53, 0.29, 0.53, 0.62 and 0.70, respectively. Of the 568 analyzed species, 56 exhibited 100% affiliation to one FG, and a further 460 species were classified into an FG based on >70% affiliation. These parameters indicate that overall separation of species into FGs was good. There were 68 species in the first FG, 165 in the second, 78 in the third, 128 in the fourth, and 129 species in the fifth (Table S1).

The ANOVA showed that all five PCA axes describe differences among the defined FGs (Table S2). This outcome was further confirmed by the Tukey's HSD test, which identified significant differences ($p < 0.05$) and confirmed separation of the FGs based on all PCA axes (Table S3).

Table 1 shows functional traits of hoverflies that were significant for the separation of species into functional groups. FG1 consisted mainly of species with saprophagous larvae that develop in submerged sediment. These traits were negatively correlated with axis PC1, which clearly separated the first cluster (Fig. 2A). FG2 encloses widely distributed species (based on PC5, Fig. 2C) whose larvae are not tolerant to inundation, as defined by axes PC1 and PC4 (Fig. 2A). Axis PC2 can partly be used for the description of FG2, albeit cautiously, as it predominantly (but not exclusively) encompasses traits negatively correlated with PC2, designating species with very good flight ability that can migrate, have a high tolerance to human impact, and have more generations during the year to this group (Fig. 2B). However, FG3 is clearly separated from other functional groups based on axis PC4 (Fig. 2C) It consisted mainly of species with saproxylic larvae, protracted larval development, and having less than one generation per year. FG4 was defined based on axis PC3 (Fig. 2B). It includes species whose larvae develop in plant roots, stems and leaves and with a low tolerance to human impact. FG5 consists of a high proportion of endemic and relict species with phytophagous larvae that develop in plant bulbs, as defined by axis PC5 (Fig. 2C). Additionally, axis PC4 revealed that the larvae of FG5 species are not tolerant to inundation (Table 1).

Discriminant analysis conducted on PC1-PC5 factor scores separated all hoverfly FGs with high significance based on the functional traits we considered (Table S4). Species were correctly classified into *a priori*-defined FGs with an overall accuracy of 92.79%: 97.06% of species within FG1, 92.73% in FG2, 98.72% in FG3, 88.29% in FG4, and 91.47% in FG5 were correctly classified.

The dendrogram based on the square of Mahalanobis distances revealed that species classified in FG2 and FG4 exhibited the greatest similarity, whereas species in FG1 were the most distinct based on the functional traits we used for classification (Fig. 3).

Functional groups and vegetation types

Relative frequency of the different FGs varied significantly across SE Europe ($\chi^2(4) = 56.63$, $p = 0.00$), as well as across different vegetation types (Table 2). Species within FG2 dominated both among SE European hoverflies and in the majority of vegetation types (9 of 11). The least represented species in the majority of vegetation types (6 of 11) were species within FG3, followed by FG1 and FG5, respectively (Table 2).

Interestingly, two vegetation types, south-west Balkan sub-Mediterranean mixed oak forests (H) and Mediterranean mixed forests (J), did not follow this trend. With regard to the former, species from FG4 were dominant ($\chi^2(4)= 50.64$, $p=0.00$), whereas the latter contained the highest percentage of species classified in FG5. South-west Balkan sub-Mediterranean mixed oak forests are particularly interesting since they harbour the smallest percentages of species from both FG1 and FG3 (Fig. 4).

DISCUSSION

Our multivariate classification of the functional traits of hoverflies identified five ecologically interpretable FGs. The significance of functional classification is that functional affiliation does not have to coincide with taxonomic similarities among species (Grime 1988). Thus, relationships between species can be revealed that could otherwise remain hidden if only a taxonomic classification is used.

None of the defined FGs is genus-specific. Furthermore, although they dominated some of the FGs, the genera with the largest numbers of species (i.e., *Cheilosia* Meigen, 1838, *Merodon* Meigen, 1803, and *Eumerus* Meigen, 1822) were not exclusively grouped together in a single cluster. This arrangement of species within FGs confirms the notion that species may exhibit functional similarities, even though they exhibit significant differences in morphology and, moreover, that morphologically similar species may have different functions in the ecosystem (Young *et al*. 2007).

Very few studies of the functional grouping of hoverflies have been conducted previously. Schweiger *et al.* (2007) analyzed 133 hoverfly species registered on agricultural land and the impact of intensive land use on the richness of functional groups. Keil *et al.* (2008) grouped 641 species of hoverflies recorded in Europe and then examined how richness of the groupings changed in relation to latitudinal variations, as well as the effect of selected environmental factors on functional richness. These studies have also revealed the importance of larval feeding type and larval inundation tolerance to delineating functional groups, though the relevance of some other traits differed from the results of our study. In both Schweiger *et al*. (2007) and Keil et *al.* (2008), traits that proved to be significant for functional categorization were larval microhabitat, number of generations per year, length of larval development, and body size. However, here, we also considered functional traits not assessed in those previous studies. Newly analyzed traits, such as flight ability and tolerance to human impact, had a great contribution to separating our functional groups. This outcome confirms that by considering a larger number of relevant characters, more comprehensive results can be obtained (Petchey & Gaston 2006).

Although our study was focused on hoverfly species in SE Europe, we hypothesize that this functional grouping could be applied to other regions as well. The reason lies in the fact that the traits that have proven to be most significant for the separation of the species into functional groups do not exhibit geographical variation, i.e. species would have the same state of a particular trait (e. g. larval feeding mode or extent of species range) in another region as well. Traits that vary across different geographical ranges, such as period of flight, were not marked as significant in defining hoverfly functional groups.

Most significant traits for the separation of hoverfly functional groups

The trait that proved dominant in distinguishing hoverfly FGs in our study is larval feeding type. Indeed, as for the extraordinary variability among adults, hoverfly larvae also display equally diverse feeding modes (Doyle *et al.* 2020). Considering the broad variation in this functional trait, which largely determines other biological and ecological characteristics of hoverfly species (Rotheray & Gilbert 2011), it is perhaps no surprise that we found this trait in particular to be the most significantly informative in terms of functional groups. For example, larval feeding type is directly related to the level of species specialization (Bonelli *et al*. 2011; Orsucci *et al.* 2018). Species having phytophagous larvae, which develop in roots and bulbs, are considered specialists, as are species with saproxylic larvae. This dependency on a host plant or, in the case of saproxylic species, a specific phase of tree decay has a considerable limiting effect on the possibility for a species to expand its range. Larvae of the saproxylic species *Blera fallax* (of FG3 herein) develop almost exclusively in rot holes of *Pinus sylvestris* (Rotheray *et al*. 2016). Species from the *Cheilosia canicularis* taxonomic group (which includes *C. canicularis, C. hymantopus* and *C. ortotricha*, and all classified within FG4) are even more specialized, with the larvae of these three species being exclusively associated with the plant *Petasites hybridus*, but each one develops in a different part of the plant, from root to leaf (Stuke & Claussen 2000).

We also found extent of species range to be an important parameter for defining functional groups, particularly FG5. Endemic or relict species are highly adapted to their particular niches (Harrison & Noss 2017), which limits their potential spread into new areas, as exemplified by the assignment to FG5 of many *Merodon* species restricted to specific Aegean islands (Radenković *et al.* 2011, Vujić *et al*. 2016).

Ability to fly determines the dispersal capability of hoverfly species; if a species is a good flyer it can migrate and expand the area of occupancy, whereas species that are poor flyers and only travel short distances have very limited distributions. Numerous studies have confirmed the significance of flight ability to resilience to extinction (Osborne *et al*. 2002; Chapman *et al*. 2015; Dällenbach *et al*. 2018, Chichorro *et al*. 2020).

Number of generations in a year can reflect the survival strategies of hoverfly species. Hoverflies that produce multiple generations annually usually produce large numbers of eggs (Zheng *et al.* 2019) and are considered less specific in terms of microhabitat selection (Speight *et al.* 2020).

However, species having fewer generations within a year are more likely to efficiently use necessary resources compared to those having shorter generation timespans (Aguirre-Gutiérrez *et al*. 2016).

Inundation tolerance provides hoverflies with a superior survival kit upon exposure to wet conditions (Brust *et al.* 2007). Indeed, saprophagous hoverfly larvae that have breeding tubes enable them to survive in moist areas and more easily overcome challenging environmental conditions (Moquet *et al*. 2018).

Species tolerance to human impact has proved significant in defining the functional groups, revealing a link between the ability to resist changes in the environment caused by anthropogenic pressures and species functions in ecosystems (Samia *et al*. 2015).

Based on our results, the most functionally similar hoverfly species among those we considered are those of FG2 and FG4, with the most divergent being those in FG1. This similarity can be epitomized in the direct and indirect links between FG2, FG4 and FG5 and herbaceous plants. Larval development of species in FG4 and FG5 is related to different plant parts, and the hosts of larvae from FG2 species develop strictly within plant tissues, as many species from this group are aphidophagous. Species in FG3, characterized by having saproxylic larvae, are the second most divergent group. Unlike FG2, species in FG3 depend on dead plant matter, as these species are wood decomposers (Soszyńska-Maj *et al*. 2009). The reason why FG1 is the most divergent group is likely to the saprophagous nature of the larvae, which can be linked to extremely wet and, in many cases aquatic habitats, unlike for all other functional groups.

Functional groups and vegetation types

Species within FG4, dominant in south-west Balkan sub-Mediterranean mixed oak forests, mostly belong to the genus *Cheilosia,* whose larvae develop in roots, stems and leaves of host plants and that are particularly sensitive to anthropogenic impact. This high percentage of species directly dependent on specific vegetation types supports the notion that south-west Balkan sub-Mediterranean mixed oak forests represent an ecologically unique ecosystem, the high conservation value of which is often neglected (Mansourian *et al.* 2013). The diverse shrub understorey within these forests, intermixed with grasslands, increases habitat heterogeneity (Bugalho *et al.* 2011), supporting the macrohabitat requirements of these FG4 species. Notably, this vegetation type hosts the smallest percentage of species belonging to the functional groups FG1 and FG3, which mainly comprise saprophagous and saproxylic species, respectively. This pattern of FG representation may be attributable to climate change and inappropriate forest management. Indeed, climate change might have a particularly negative impact on species from FG1 in mixed oak forests, as these species are highly dependent on wet microhabitats (Speight 2018), which are severely affected by global warming (Papadopoulos & Pantera 2016). The second threat to forest health and condition is intensive forest management (whereby old oak trees and dead wood are removed from ecosystems), or even sometimes a lack of management

(Stojanović *et al*. 2015). It is important to highlight the fact that this vegetation type exhibits the highest dark diversity of hoverflies in SE Europe (Miličić *et al*. 2020), which reflects reduced local biodiversity relative to potential richness. Therefore, it is likely that changes in management of such oak forests, such as retention of habitat trees (Mölder *et al*. 2020) and creating stepping-stones between veteran tree sites (Mestre *et al.* 2018), could potentially restore damaged ecosystems. In such circumstances, occurrence of a greater proportion of hoverflies dependent on dead or dying wood for some part of their lifecycle could be expected at such localities.

Mediterranean mixed forests were found to host a significant proportion of species within FG5, a group rich in endemic and relict species with phytophagous larvae that develop in bulbs. Mediterranean islands are characterized by high plant diversity and endemism (Georghiou & Delipetrou 2010), so a particular functional profile for species detected in Mediterranean mixed forests was somewhat anticipated. The long-lasting influence of human impacts in this region (Thompson 2005) has resulted in peculiar landscape patterns that have shaped distinctive species compositions. In particular, large and highly connected areas of this vegetation type, together with interspersed open habitats and the high diversity of bulbous plants (Petanidou *et al*. 2013), contribute to the maintenance of *Merodon* species that constitute a considerable proportion of the species in FG5.

CONCLUSION

We found that larval feeding type is the most dominant trait responsible for the categorization of 568 hoverfly species registered in SE Europe into five functional groups. The influence of different environmental pressures defines the richness of functional groups in specific vegetation types in this region. Further study is needed to investigate how established conservation measures can enable recovery of the functional richness affected by habitat disturbance, which would help us to further understand the importance of functional diversity to the preservation of biodiversity.

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Figure legends:

Figure 1. Map of vegetation types in Southeast Europe. A - Alpine; subalpine and oro-Mediterranean vegetation; B - montane spruce and mixed spruce forests; C - montane pine forests; D - acidophilous oak and mixed oak–hornbeam forests; E - beech and mixed beech forests; F - thermophilous mixed bitter, pedunculate or sessile oak forests; G - south-east Balkan sub-Mediterranean mixed oak forests; H - south-west Balkan sub-Mediterranean mixed oak forests; I - Pannonian lowland mixed oak forests and steppes; J - Mediterranean mixed forests; K - hardwood alluvial forests, wet lowland forests and swamps. Map is published in Miličić *et al*. (2020), available at: https://onlinelibrary.wiley.com/doi/full/10.1111/een.12788.

Figure 2. The distribution of clusters of functional groups, as defined by PCA axes. a) Axis PC1 clearly separates FG1 from other functional groups, whereas axis PC4 differentiates FG2 and FG3. b) Axis PC2 displays the variability between FG1 and FG2, whereas axis PC3 differentiates FG2 and FG4. c) Axis PC4 clearly separates FG3 from other functional groups, and axis PC5 differentiates FG5.

Figure 3. The UPGMA dendrogram constructed based on the square of the Mahalanobis distances depicts the similarity among the defined functional groups.

Figure 4. A comparison of the number of hoverfly species present in the different functional groups across 11 vegetation types in Southeast Europe. A - Alpine; subalpine and oro-Mediterranean vegetation; B - montane spruce and mixed spruce forests; C - montane pine forests; D - acidophilous oak and mixed oak–hornbeam forests; E - beech and mixed beech forests; F - thermophilous mixed bitter, pedunculate or sessile oak forests; G - south-east Balkan sub-Mediterranean mixed oak forests; H - south-west Balkan sub-Mediterranean mixed oak forests; I - Pannonian lowland mixed oak forests and steppes; J - Mediterranean mixed forests; K - hardwood alluvial forests, wet lowland forests and swamps.

Table legends:Table 1. Results of PCA analysis of traits used for functional classification of hoverflies. Factor loading values greater than ± 0.6 are bolded and underlined.

Table 2. Functional group composition (relative frequency percentage of hoverfly species) of the hoverfly community across different vegetation types in South East Europe. A - Alpine; subalpine and oro-Mediterranean vegetation; B - montane spruce and mixed spruce forests; C - montane pine forests; D - acidophilous oak and mixed oak–hornbeam forests; E - beech and mixed beech forests; F - thermophilous mixed bitter, pedunculate or sessile oak forests; G - south-east Balkan sub-Mediterranean mixed oak forests; H - south-west Balkan sub-Mediterranean mixed oak forests; I - Pannonian lowland mixed oak forests and steppes; J - Mediterranean mixed forests; K - hardwood alluvial forests, wet lowland forests and swamps.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1. List of all analyzed hoverfly species with its attribution to functional groups (FGs), percentage of belonging to each of the clusters and silhouette width.

Table S2. Analysis of variance of defined functional groups.

Table S3. Results of Tuckey HSD test for PC1-PC5.

Table S4. Statistical significance of the difference between defined functional groups based on discriminant analysis. p values - below the diagonal; F values - above the diagonal; df = 5.56

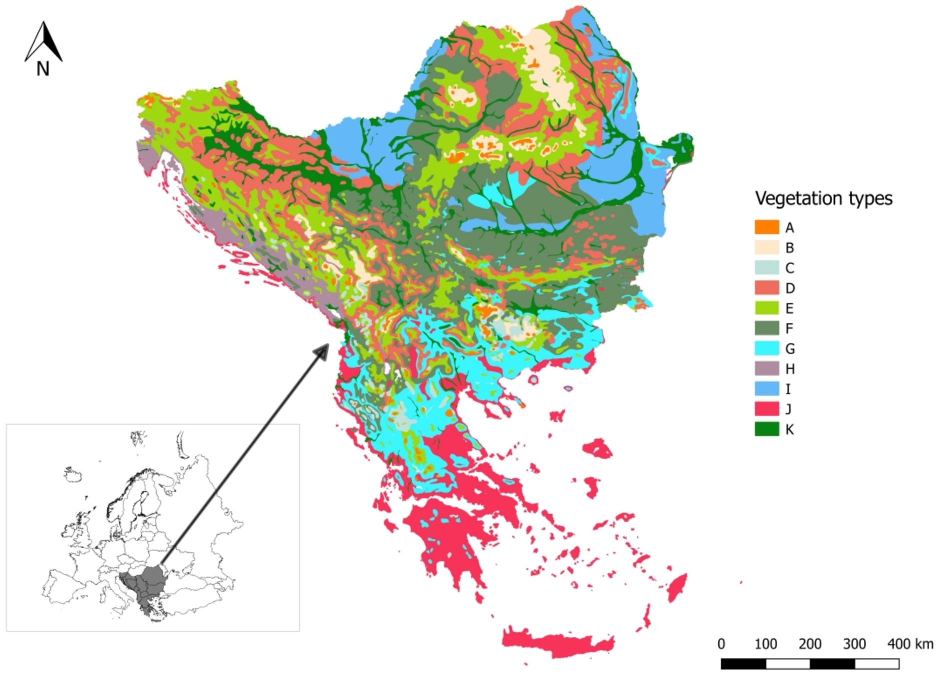

Figure 1. Map of vegetation types in Southeast Europe. A - Alpine; subalpine and oro-Mediterranean vegetation; B - montane spruce and mixed spruce forests; C - montane pine forests; D - acidophilous oak and mixed oak–hornbeam forests; E - beech and mixed beech forests; F - thermophilous mixed bitter, pedunculate or sessile oak forests; G - south-east Balkan sub-Mediterranean mixed oak forests; H - south-west Balkan sub-Mediterranean mixed oak forests; I - Pannonian lowland mixed oak forests and steppes; J - Mediterranean mixed forests; K - hardwood alluvial forests, wet lowland forests and swamps. Map is published in Miličić et al. (2020), available at: https://onlinelibrary.wiley.com/doi/full/10.1111/een.12788.

297x210mm (598 x 598 DPI)

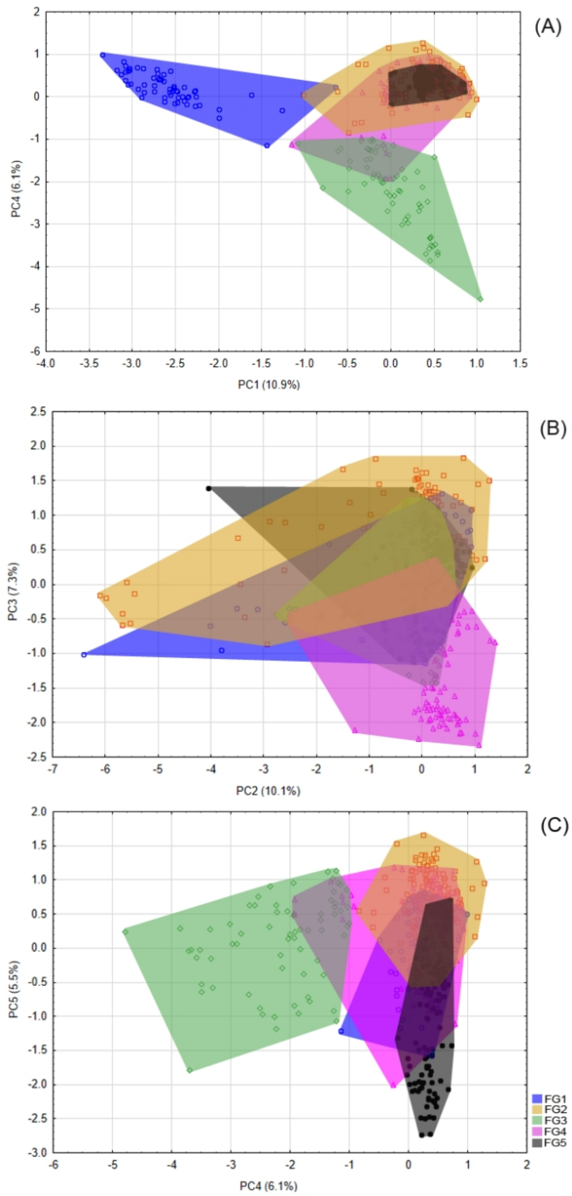

Figure 2. The distribution of clusters of functional groups, as defined by PCA axes. A) Axis PC1 clearly separates FG1 from other functional groups, whereas axis PC4 differentiates FG2 and FG3. B) Axis PC2 displays the variability between FG1 and FG2, whereas axis PC3 differentiates FG2 and FG4. C) Axis PC4 clearly separates FG3 from other functional groups, and axis PC5 differentiates FG5.

177x371mm (96 x 96 DPI)

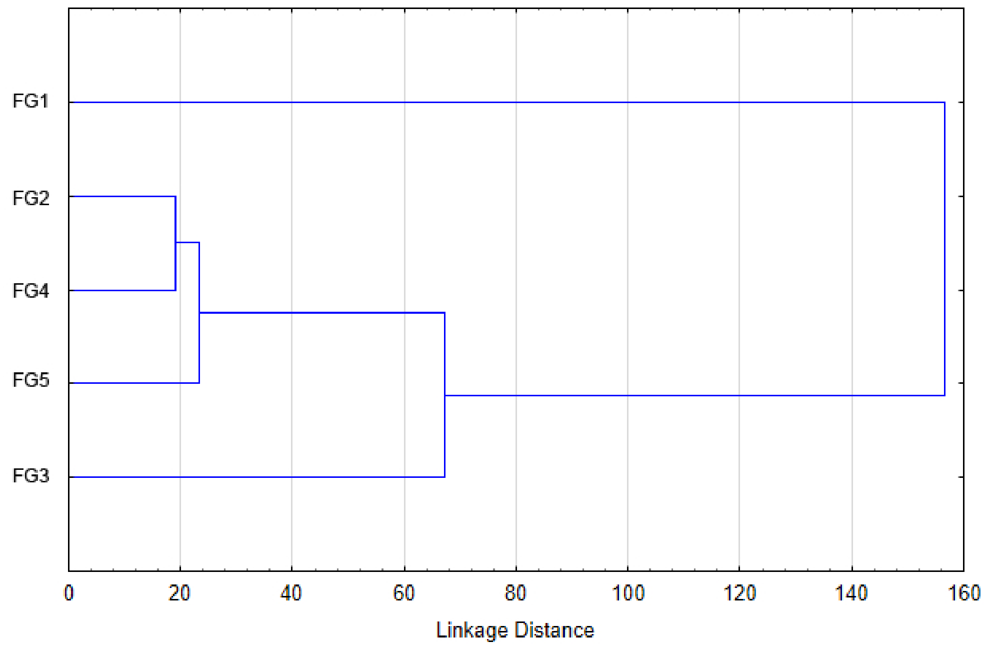

Figure 3. The UPGMA dendrogram constructed based on the square of the Mahalanobis distances depicts the similarity among the defined functional groups.

166x109mm (96 x 96 DPI)

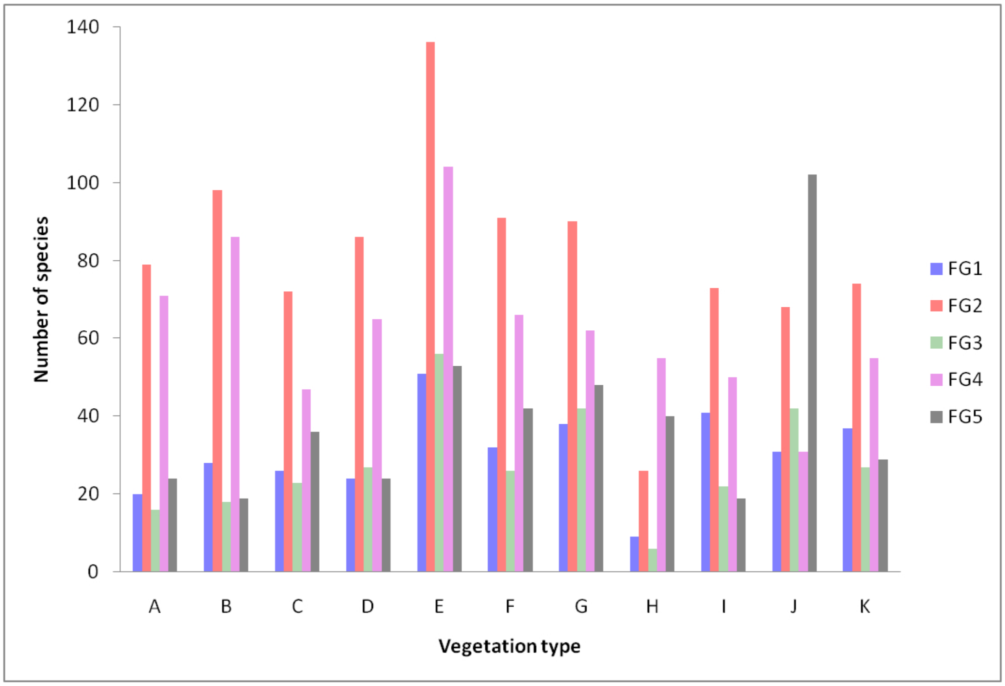

Figure 4. A comparison of the number of hoverfly species present in the different functional groups across 11 vegetation types in Southeast Europe. A - Alpine; subalpine and oro-Mediterranean vegetation; B - montane spruce and mixed spruce forests; C - montane pine forests; D - acidophilous oak and mixed oak–hornbeam forests; E - beech and mixed beech forests; F - thermophilous mixed bitter, pedunculate or sessile oak forests; G - south-east Balkan sub-Mediterranean mixed oak forests; H - south-west Balkan sub-Mediterranean mixed oak forests; I - Pannonian lowland mixed oak forests and steppes; J - Mediterranean mixed forests; K - hardwood alluvial forests, wet lowland forests and swamps.

196x133mm (149 x 149 DPI)

Table 1. Results of PCA analysis of traits used for functional classification of hoverflies. Factor loading values greater than ± 0.6 are bolded and underlined.

Trait	Trait state	PC1	PC2	PC3	PC4	PC5
Larval microhabitat	trees	0.18	-0.10	0.37	-0.48	0.38
	upward climbing lianas	0.07	-0.38	0.12	0.03	0.04
	herb layer	0.43	-0.01	-0.31	0.39	-0.20
	timber	0.02	0.05	-0.11	-0.57	0.03
	dung	-0.28	-0.23	-0.02	0.00	0.01
	litter	0.02	-0.09	0.05	0.02	0.13
	stones	0.01	0.03	0.03	-0.01	0.05
	nests of social insects	0.04	0.05	0.15	0.10	0.08
	root zone	0.28	0.29	-0.21	0.26	-0.38
	water plants	-0.45	0.07	0.14	0.08	0.05
	submerged sediment/debris	**-0.87**	-0.05	-0.04	0.05	0.01
Larval feeding mode	saprophagous	**-0.94**	-0.08	0.01	0.08	0.02
	saproxylic	-0.01	0.06	0.03	**-0.89**	0.08
	phytophagous-bulbs	0.19	0.14	0.09	0.19	**-0.74**
	phytophagous-roots	0.16	0.17	**-0.68**	0.22	0.14
	zoophagous	0.36	-0.26	0.42	0.29	0.46
Duration of larval development	less than 2 months	-0.08	-0.59	0.04	0.03	0.08
	2-6 months	-0.08	-0.12	0.02	0.18	0.02
	7-12 months	0.04	0.26	-0.08	0.28	-0.02
	more than a year	0.10	0.03	0.07	**-0.77**	-0.03
Inundation tolerance	intolerant	**0.65**	-0.07	0.03	**0.61**	-0.15
	tolerant (short breathing tube)	-0.01	0.16	-0.1	-0.09	0.16
	tolerant (medium breathing tube)	-0.4	0.09	-0.02	-0.49	0.08
	tolerant (long breathing tube)	-0.52	-0.13	0.08	-0.28	0.00
Number of generations	less than one generation	0.08	0.03	0.10	**-0.67**	-0.02
	one generation	0.03	0.23	-0.07	0.08	-0.11
	two generations	-0.02	0.05	0.03	0.17	0.1
	more than two generations	-0.1	**-0.64**	0.00	0.07	0.06
Period of flight	early spring	0.03	-0.14	0.01	0.03	-0.05
	spring	0.02	0.07	-0.07	-0.03	-0.02
	early summer	-0.06	0.06	-0.18	-0.06	0.28
	summer	0.01	0.02	0.09	0.05	0.05
	autumn	0.01	-0.09	0.16	0.02	-0.27
Body size	small	0.03	0.01	-0.05	0.06	0.24
	medium	0.01	-0.07	0.01	0.14	-0.24
	large	-0.05	0.07	0.05	-0.23	0.05
Area of species range	endemic and/or relict	0.06	0.03	-0.02	-0.01	**-0.82**
	widely distributed	-0.06	-0.03	0.02	0.01	**0.82**

Flight ability	very good-migrants	0.03	**-0.76**	-0.04	0.03	0.04
	good	-0.04	**0.70**	0.05	0.00	0.00
	bad	0.04	-0.07	-0.01	-0.03	-0.05
Height at which species fly	arboreal	0.12	0.00	-0.23	-0.19	0.43
	near the ground	-0.12	0.00	0.23	0.19	-0.43
	low	0.11	0.10	**-0.79**	-0.02	-0.03
Human impact tolerance	medium	0.04	0.26	**0.82**	-0.03	-0.01
	high	-0.24	-0.08	-0.07	0.11	0.07
	very high	-0.10	**-0.8**	-0.08	0.01	0.02

Table 2. Functional group composition of the hoverfly community across different vegetation types in South East Europe. A - Alpine; subalpine and oro-Mediterranean vegetation; B - montane spruce and mixed spruce forests; C -montane pine forests; D - acidophilous oak and mixed oak–hornbeam forests; E - beech and mixed beech forests; F - thermophilous mixed bitter, pedunculate or sessile oak forests; G - south-east Balkan sub-Mediterranean mixed oak forests; H - south-west Balkan sub-Mediterranean mixed oak forests; I - Pannonian lowland mixed oak forests and steppes; J - Mediterranean mixed forests; K - hardwood alluvial forests, wet lowland forests and swamps; No. species - number of species per functional group.

Vegetation type		FG1	FG2	FG3	FG4	FG5	Total	χ^2 value
A	No. species	20	79	16	71	24	210	
	% within A	9.52	37.62	7.62	33.81	11.43	100	$\chi^2(4)$= 56.62755, p=.00000
	% within total sample	3.52	13.91	2.82	12.5	4.23	36.97	
B	No. species	28	98	18	86	19	249	
	% within B	11.24	39.36	7.23	34.54	7.63	100	$\chi^2(4)$= 102.8108, p=.00000
	% within total sample	4.93	17.25	3.17	15.14	3.35	43.84	
C	No. species	26	72	23	47	36	204	
	% within C	12.75	35.29	11.27	23.04	17.65	100	$\chi^2(4)$= 9.463429, p=.05050
	% within total sample	4.58	12.68	4.05	8.27	6.34	35.92	
D	No. species	24	86	27	65	24	226	
	% within D	10.62	38.05	11.95	28.76	10.62	100	$\chi^2(4)$= 42.53976, p=.00000
	% within total sample	4.23	15.14	4.75	11.44	4.23	39.79	
E	No. species	51	136	56	104	53	400	
	% within E	12.75	34.00	14.00	26.00	13.25	100	$\chi^2(4)$= 72.67274, p=.00000
	% within total sample	8.98	23.94	9.86	18.31	9.33	70.42	
F	No. species	32	91	26	66	42	257	
	% within F	12.45	35.41	10.12	25.68	16.34	100	$\chi^2(4)$= 21.53701, p=.00025
	% within total sample	5.63	16.02	4.58	11.62	7.39	45.24	
G	No. species	38	90	42	62	48	280	
	% within G	13.57	32.14	15.00	22.14	17.14	100	$\chi^2(4)$= 11.22276, p=.02417
	% within total sample	6.69	15.85	7.39	10.92	8.45	49.3	
H	No. species	9	26	6	55	40	136	
	% within H	6.62	19.12	4.41	40.44	29.41	100	$\chi^2(4)$= 50.64183, p=.00000
	% within total sample	1.58	4.58	1.06	9.68	7.04	23.94	
I	No. species	41	73	22	50	19	205	
	% within I	20.00	35.61	10.73	24.39	9.27	100	$\chi^2(4)$= 50.13845, p=.00000
	% within total sample	7.22	12.85	3.87	8.8	3.35	36.09	
J	No. species	31	68	42	31	102	274	
	% within J	11.31	24.82	15.33	11.31	37.23	100	$\chi^2(4)$= 83.12266, p=.00000
	% within total sample	5.46	11.97	7.39	5.46	17.96	48.24	
K	No. species	37	74	27	55	29	222	
	% within K	16.67	33.33	12.16	24.77	13.06	100	$\chi^2(4)$= 25.41516, p=.00004
	% within total sample	6.51	13.03	4.75	9.68	5.11	39.08	