Does the shrub layer act as an intermediary? Effects on abundance of insects and abundances of particular insect orders caught flying in the canopies of deciduous forests in Central Germany

**Stephanie Stiegel, Anna Korfhage and Jasmin Mantilla-Contreras**

University of Hildesheim – Biology and Chemistry, Universitätsplatz 1, Hildesheim 31141, Germany;
e-mails: stiegel@uni-hildesheim.de, anna.korfhage@web.de, mantilla@uni-hildesheim.de

**Key words.** Insects, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera, Thysanoptera, *Fagus sylvatica*, forest, phytodiversity, plant cover, air temperature, relative air humidity, plant species richness, Germany

**Abstract.** Scientists and society are increasingly becoming aware of loss of insect biodiversity and biomass. The level of biodiversity determines the efficiency of ecological communities to capture essential resources, produce biomass, decompose and recycle nutrients. Relationships between plant and insect diversity can be modified by changes in insect abundance. This study determined the associations between microclimate and diversity of forest plants on overall insect abundance and abundances of different insect orders in the canopy of temperate deciduous forests dominated by *Fagus sylvatica* L. (European beech; Fagaceae) in Central Germany. Following model selection, a linear mixed model was used to analyse the associations between abiotic factors (air temperature and relative humidity) as well as biotic factors (species richness and cover for the ground, shrub and tree layer) and insect abundance and abundances of insect orders. Within similar strength of evidence, best models were chosen as those with a single explanatory parameter. Significant associations were recorded between abundances of Lepidoptera and Neuroptera and relative air humidity, insect abundance and species richness in the shrub layer, and between abundances of Diptera and Psocoptera and percentage cover of shrubs. Trends in associations were detected between the abundance of Hemiptera and species richness recorded in the shrub layer, and between the abundance of Thysanoptera and the species richness in the ground layer. No significant associations with single explanatory parameters were recorded for the abundances of Coleoptera and Hymenoptera. Phytodiversity, especially that in the shrub layer, were more often associated with the abundances of insect orders than microclimatic factors. The potential importance of the association between shrub layer parameters and the abundance of insects might be based on the shrub layer combining the associations with the ground layer (bottom-up processes) and canopy layer (environmental conditions). In addition, associations between phytodiversity and abundance of insects seem to vary most for Coleoptera and Hymenoptera in which there are markedly different functional groups.

**INTRODUCTION**

Biodiversity is currently an important subject for research and nature conservation mainly motivated by reports of the extinction of many species. Unfortunately, the global decline in biodiversity (e.g. Pimm & Raven, 2000; Singh, 2002), biomass of arthropods and their abundance (Hallmann et al., 2017; Vogel, 2017; Leather, 2018) is becoming increasingly evident. The loss in biodiversity results in a reduction in the efficiency of ecological communities to produce essential resources, biomass, decompose and recycle nutrients (Cardinale et al., 2012) as is reported for forests (Piotto, 2008; Zhang et al., 2012). There is evidence of an important connection between biodiversity and ecosystem functioning. Therefore, discussions about the role of biodiversity in the stability of ecosystems are frequent and ongoing (McCann, 2000) and determinants of biodiversity becomes an increasingly important field of study in ecology (Kelly & Southwood, 1999).

Several abiotic and biotic factors affect the diversity and abundance of insects (reviewed by Ulyshen, 2011). Phytodiversity, i.e. the diversity of vascular plants, is supposed to be an important factor for insect diversity in forest ecosystems (Erwin, 1982). In food chains, plants as primary producers are the basic resource for other trophic levels. In forest habitats, tree diversity is positively associated with the overall richness of species of insects (Vehviläinen et al., 2007). Models predict that the greater the number of resources (e.g. phytodiversity) the greater the number of species (Tilman, 1986; Rosenzweig, 1995). This relationship may also hold for the abundance of species of insects as well as their diversity. That is, a greater number of resources (number of plant species or plant abundance / biomass) will support a greater number of individuals of insects. For a species of insect, its abundance determines its population density and stability. Their abundance is dependent on various factors such as environmental favourability, food...
availability and shelter (Berryman, 1986). Higher population densities can be seen as either positive in terms of cooperation between individuals for mating, defence, or attack, or negative in terms of concurrence with resources, leading to population cycles. Therefore, insect abundance plays a role in population stability and loss in the richness of species. According to Schuldt et al. (2019), relations between plant and insect diversity can be modified by changes in the overall abundance of insects because the significant associations between phytophiversity and species richness of arthropods are often indirect via effects on arthropod abundances.

In regard to abiotic factors, correlations between microclimate and insect diversity or abundance are reported in numerous studies (e.g. Logan et al., 2003; Meineke et al., 2013; Mech et al., 2018). On the one hand, temperature has a positive influence on the growth, development, activity and distribution of insects (Simonet et al., 1981; Wikelius, 1981; Strathdee et al., 1993; Whittaker & Tribe, 1998; Levesque et al., 2002). On the other hand, limited and inconsistent results are reported for the direct effects of humidity (Chiarelli et al., 2011). In addition, different species of carabids distinctly differ in terms of their preferred biotic and abiotic factors (Antvogel & Bonn, 2001). Therefore, there is a need to investigate the effects for at least subgroups because they probably vary for orders and even species of insects.

Globally the greatest abundance and diversity of insects is in the canopies of forest ecosystems (Erwin, 1982; Stork, 1988; Novotny & Basset, 2005). In comparison to tropical forests, there is little research on insects in the canopies of temperate forests, but has been increasing in Europe recently (e.g. Floren & Schmidl, 2008; Sobek et al., 2009c; Bouget et al., 2011; Normann et al., 2016). For instance, the importance of the species of tree for the patterns in species richness and abundance of beetles in the canopy of a temperate forest has been demonstrated (Gering & Crist, 2000). Fagus sylvatica L. (European beech; Fagaceae) is the dominant deciduous tree in German forests. In addition, Acer pseudoplatanus L. (sycamore maple; Sapindaceae) and Carpinus betulus L. (hornbeam; Betulaceae) occurred frequently in the understorey. The criteria used in selecting forest stands were (i) a closed canopy, (ii) absence of coniferous trees and (iii) stem circumference of mature beech trees > 1 m. The altitudes of the sites sampled ranged from 140 to 444 m a.s.l. In each forest stand two sites were selected, one facing north and the other facing south (n = 20). According to the German Weather Service (reference period: 1961–1990), mean annual precipitation increased along the transect from east to west, ranging from 474 mm (Artern, Thuringia) to 874 mm (Herzberg, Lower Saxony). Mean annual temperature, which were measured hourly using data loggers (iButton, Model DS1923, Maxim Integrated, San Jose, CA, USA) from July to August 2012. At each site, a data logger was installed in the lower canopy (average height: 18 m) of a mature F. sylvatica tree. Average values for the measured period for each site were used in the statistical analyses.

This study investigates the effect of microclimate and phytophivity on overall abundance and abundances of different orders of flying insects in temperate deciduous forests in Central Germany. Canopies of F. sylvatica were surveyed at 20 sites with northern and southern exposures in ten different forest stands. The aim is to determine differences in microclimate and phytophivity and their associations with total insect abundance and abundances of particular orders of flying insects. The following hypotheses are tested: (1) insect abundance and abundances of insect orders increase with temperature, (2) insect abundance and abundances of insect orders are positively associated with phytophivity and (3) the determining factors vary for different insect orders.

MATERIAL AND METHODS

Study area

The area studied is located in Central Germany within the federal states of Thuringia, Lower Saxony and Hesse. Along a 140 km east-west transect, ten sites were selected in forest stands dominated by several deciduous species of trees (Fig. 1). These sites were dominated by F. sylvatica, the most common deciduous tree in German forests. In addition, Acer pseudoplatanus L. (sycamore maple; Sapindaceae) and Carpinus betulus L. (hornbeam; Betulaceae) occurred frequently in the understorey. The area studied is located in Central Germany within the federal states of Thuringia, Lower Saxony and Hesse. Along a 140 km east-west transect, ten sites were selected in forest stands dominated by several deciduous species of trees (Fig. 1). These sites were dominated by F. sylvatica, the most common deciduous tree in German forests. The criteria used in selecting forest stands were (i) a closed canopy, (ii) absence of coniferous trees and (iii) stem circumference of mature beech trees > 1 m. The altitudes of the sites sampled ranged from 140 to 444 m a.s.l. In each forest stand two sites were selected, one facing north and the other facing south (n = 20). According to the German Weather Service (reference period: 1961–1990), mean annual precipitation increased along the transect from east to west, ranging from 474 mm (Artern, Thuringia) to 874 mm (Herzberg, Lower Saxony). Mean annual temperatures were similar in the different forest stands in the area studied and increased from about 8°C to 9°C at the beginning of the 21st century (German Weather Service, reference period: 1961–1990 and 1981–2010). The geological substrate at the forest sites was lower Trias sandstone, except for upper Trias sandstone at one site (Bocksbühl) and middle Triassic limestone at two sites (Feuerkuppe and Heidelberg).

Data collection

The abiotic conditions were air temperature and relative air humidity, which were measured hourly using data loggers (iButton, Model DS1923, Maxim Integrated, San Jose, CA, USA) from July to August 2012. At each site, a data logger was installed in the lower canopy (average height: 18 m) of a mature F. sylvatica tree. Average values for the measured period for each site were used in the statistical analyses.

The phytophivity at each site was assessed by surveying the vegetation. Species of angiosperms were recorded in the ground (0–2 m), shrub (2–6 m) and tree layers (> 6 m). In a plot of 10 × 10 m square, abundances of the species in each layer were esti-
Average height: 18 m) of providing shelter or food for because the ground and shrub layer might be important in terms of species richness). All three forest layers were included in the analysis. The phytodiversity in each layer was recorded in terms of the number of species of plants per plot (species cover scale in percent). The phytodiversity at each of the forest sites. In addition, est stands were assessed using window traps that catch insects and / or were not present at all sites. The sampling started in June 2012 and ended at the beginning of August 2012. Each window trap was active for about three weeks and the liquid was collected and refreshed on three occasions. Storms destroyed the catches of some window traps, which resulted in a total number of 167 samples. In the laboratory, captured insects were identified to the level of the order to which they belonged. Orders that do not include flying insects and / or were not present at all sites were not included in the analyses (Collembola, Dermaptera, Ensiferida, Ephemeroptera and Mecoptera). Insect abundance and abundance of the insect orders Coleoptera, Diptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera and Thysanoptera were calculated as the average catch per window trap for each site sampled.

Data analyses

Statistical analyses were done using R version 3.4.1 (R Development Core Team, 2017). Statistical distributions of the data for microclimate, vegetation, insect abundance and abundances of insect orders were assessed using the Shapiro-Wilk test. Associations between microclimate (air temperature and relative humidity) and vegetation (species richness and cover of the ground, shrub and tree layers) and insect abundance and abundances of insect orders were determined using selected linear mixed models (LMM). Calculations were done using the R libraries `lmer` to determine suitable LMMs and `MuMln` to select the most suitable model (Bartoń, 2016; Bates et al., 2017). Abundance values for insects, Diptera, Hymenoptera and Neuroptera were log transformed and those for Lepidoptera squared to reduce the skewness of their distribution. Whether the explanatory variables were correlated with one another was determined using the R libraries `ggplot2` and `GGally`. The `ggpairs` function indicates pairs of plots including the correlation coefficients (Fig. S1). There was a strong correlation (correlation coefficient > 0.6) between species richness and cover of ground layer. Therefore, the cover of ground layer was excluded from the final model that included all explanatory variables without strong correlations. For insect abundance and abundances of insect orders, comparisons were made using the final model. All models included the forest site as a random effect. The best models were selected based on the Bayesian Information Criterion (BIC). The lowest BIC value indicated either fewer explanatory variables, better fit, or both. The strength of evidence for different models was similar based on using $\Delta$BIC = 0–2 (Kass & Raftery, 1995). The final model and model comparisons were done using the following R codes, respectively:

```
fullmod <- lmer(response variable ~ temperature + humidity + species richness of ground layer + species richness of shrub layer + species richness of tree layer + cover of shrub layer + cover of tree layer + (1|site),REML = FALSE)
mod <- dredge(update(fullmod),rank = "BIC")
```

Associations between explanatory variables and overall insect abundance and abundances of insect orders were calculated. Models with a single parameter in the range of $\Delta$BIC = 0–2 were selected for plotting. Linear regressions are graphically presented for significant relationships along with trends between explanatory and response variables, based on highest F-values and significance levels.

RESULTS

Overall, the species composition of plants and insect orders differed between the sites sampled. Eight different species of trees were recorded in the tree and shrub layer, while there were 66 species of plants in the ground layer at all the sites sampled. Fagus sylvatica was present at all the sites sampled and in all forest layers. Insect catches using window traps totalled 17,218 individuals belonging to 13 different orders of insects (with a range of 10–12 orders per site sampled): Coleoptera, Collembola, Dermaptera, Diptera, Ensiferida, Ephemeroptera, Hemiptera, Hymenoptera, Lepidoptera, Mecoptera, Neuroptera, Psocoptera and Thysanoptera. Most of the insect caught were Diptera (59%), followed by Coleoptera (17%), with the other or-

Fig. 2. Window trap (in red circle) installed in the lower canopy (average height: 18 m) of Fagus sylvatica for capturing flying insects.
Table 1. The phytodiversity (represented by species richness in the ground, shrub, and tree layer) and insect abundance (represented by the mean number of individuals per window trap) of all sample sites.

| Site | Exposition | Plant species richness | Insect abundance | \\n|------|------------|------------------------|------------------|---------|
|      |            | Ground layer | Shrub layer | Tree layer | individuals/trap | \\n| WB   | north      | 19           | 3           | 3         | 117 (7)         | \\n| TE   | north      | 7            | 1           | 1         | 92 (8)          | \\n| KVB  | north      | 5            | 1           | 3         | 91 (9)          | \\n| SS   | north      | 6            | 1           | 3         | 101 (9)         | \\n| HGB  | north      | 22           | 1           | 1         | 56 (9)          | \\n| BB   | north      | 12           | 4           | 1         | 96 (9)          | \\n| HB   | north      | 21           | 2           | 1         | 107 (8)         | \\n| FK   | north      | 8            | 4           | 1         | 136 (9)         | \\n| HDB  | north      | 26           | 3           | 1         | 58 (9)          | \\n| EL   | south      | 15           | 4           | 3         | 264 (8)         | \\n|      | south      | 4            | 2           | 2         | 122 (8)         | \\n
1 Abbreviations: WB – Winkelberg; TE – Tiefentals Ebene; KVB – Klingenberg/Vaaker Berg; SS – Schierfeinstein; HGB – Heiligenberg; BB – Bocksbühl; HB – Hubenberg; FK – Feuerkuppe; HDB – Heiligenberg; EL – Eichleite. The number of traps per sample site is given in brackets. Insects are represented by individual numbers of the following orders: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Psocoptera and Thysanoptera.

The LMM indicates that the explanatory variables for insect abundance differ from those for and abundances of insect orders (Table 1). Other models of similar robustness (ΔBIC = 0–2), indicate significant and non-significant single explanatory variables associated with abundance of insects and abundances of insect orders (Table 2). Significant effects of single explanatory variables were indicated for abundance of insects (species richness recorded in shrub layer), dipteran abundance (cover of shrub layer), lepidopteran abundance (relative air humidity), neuropteran abundance (relative air humidity) and psocopteran abundance (cover of shrub layer). Trends were found for the explanatory variable associated with hemipteran abundance (species richness recorded in the shrub layer) and thysanopteran abundance (species richness of ground layer). Associations with coleopteran and hymenopteran abundances (relative air humidity and species richness of shrub layer) were not significant.

Generally, neuropteran and lepidopteran abundances are significantly associated with relative air humidity (Fig. 3). The associations with plant species richness differed depending on the forest layer. While the overall insect and hemipteran abundances are positively and significantly associated with the species richness of the shrub layer (Fig. 4a,b), thysanopteran abundance decreased with increase in the species richness of the ground layer (Fig. 4c). In addition, dipteran and psocopteran abundances are positively and significantly associated with increase in the cover of the shrub layer (Fig. 5).

DISCUSSION

Abundance patterns of flying insects

Overall, phytodiversity is more often associated with the abundances of insect orders than microclimatic factors. Despite the positive association between temperature, growth, development, activity and distribution of insects, none were detected between insect abundance and temperature contrary to our first hypothesis. However, lepidopteran and neuropteran abundances are associated with relative air humidity and it is known that a low relative humidity adversely affects the development of some species of Neuroptera (Tauber & Tauber, 1983). This could have resulted in the decrease in neuropteran abundance associated with the increase in relative air humidity recorded in this study. The same was recorded for lepidopteran abundance, which is in accordance with the results of Jonason et al. (2014). Increase in air humidity could also be associated with high rainfall, which potentially has a negative effect on the activity of Lepidoptera. Indeed, the weather in June and July in 2012 was more humid due to high rainfall compared to the average values recorded by the German Weather Ser.

Table 2. Effects of abiotic conditions and vegetation parameters on the insect abundance and insect order abundances (linear regressions: df(numerator) = 1; df(denominator) = 18). Calculations are based on models compared by the Bayesian Information Criterion with similar strength of evidence for ΔBIC = 0–2 (Table S1). The preference was set on models containing single explanatory variables. Underlines indicate parameters with highest F-values and significances for the response variables.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Insects</th>
<th>Coleoptera</th>
<th>Diptera</th>
<th>Hemiptera</th>
<th>Hymenoptera</th>
<th>Lepidoptera</th>
<th>Neuroptera</th>
<th>Psocoptera</th>
<th>Thysanoptera</th>
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<td></td>
<td></td>
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<tr>
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<td>3.96*</td>
<td></td>
<td></td>
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<tr>
<td>CS</td>
<td>4.23*</td>
<td>6.76*</td>
<td>2.80</td>
<td></td>
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</table>

1 Abbreviations: Temp – air temperature; Humid – relative humidity; SRS – species richness recorded in ground layer; SRS – species richness recorded in shrub layer; CS – cover of shrub layer. 2 Significance codes: * – p < 0.1; ** – p < 0.05. 3 Tested model for thysanopteran abundance had a positive strength of evidence (ΔBIC = 2–6) compared to the model with the lowest BIC value.
Fig. 3. Significant relationships between the response variable and relative air humidity (n = 20; CI = 95%) based on linear regressions (Table 2): (a) abundance of Neuroptera and (b) abundance of Lepidoptera.

Fig. 4. Significant and trend relationships between response variables and plant species richness (n = 20; CI = 95%) based on linear regressions (Table 2): (a) abundance of insects and species richness of the shrub layer, (b) abundance of Hemiptera and species richness of the shrub layer and (c) abundance of Thysanoptera and species richness of the ground layer.
vice. Generally, temperature is an important determinant of flight activity in Lepidoptera as light traps catch more moths during warm than cold nights during their most active period (McGeachie, 1989; Yela & Holyoak, 1997; Johnson et al., 2014), which is because of the positive association between the activity of poikilothermic species and air temperature (Holyoak et al., 1997).

Abundances of Lepidoptera and Neuroptera are also affected by phytodiversity. Although the abundance of Lepidoptera is not associated with plant abundance there is a direct link between their abundance and the species diversity of plants (Root et al., 2017). According to the niche-partitioning hypothesis, a high phytodiversity provides a greater diversity of niches (Chesson, 2000), which could support the existence of more species of Lepidoptera. Tree species diversity also increases the diversity and abundance of dominant neopteran species, which indicates different levels of association with host trees (Gruppe & Sobek, 2011). According to the enemies hypothesis, habitats rich in species of plants offer more alternative prey, additional food and shelter for predators and parasitoids (Root, 1973). Therefore, it is hypothesized that the diversity of predators belonging to different taxa increases with increase in phytodiversity via direct (more structural and floral resources) and indirect (greater abundance and diversity of prey) pathways (Hunter & Price, 1992; Siemann et al., 1998). However, direct positive effects of phytodiversity decline with increase in trophic level and the degree of omnivory (Scherber et al., 2010). Relative abundances of predators and parasitoids are higher in plant species-rich plots (Sobek et al., 2009b). However, phytodiversity effects on species richness at higher trophic-levels are often mediated by alterations in the abundance of the consumers (Schult et al., 2019). Many species of Lepidoptera are highly specialized herbivores as their larvae feed on a single taxonomic group of plants (Miller et al., 2003). Therefore, specialist species of Lepidoptera at a low trophic level are more likely to be affected by reductions in phytodiversity than generalist predatory species of Neuroptera.

The dependence of the effect of diversity on the trophic level is in accordance with our third hypothesis that the determining parameter differs for different orders of insects. In contrast to the associations between the abundances of Neuroptera and Lepidoptera with microclimate, those of Diptera, Hemiptera, Psocoptera and overall insect abundance are positively associated with the vegetation in the shrub layer, as predicted by the second hypothesis. Overall insect and hemipteran abundances increased with increase in the species richness recorded in the shrub layer. This outcome is in line with other studies that reveal an increase in hemipteran abundance along a gradient in tree diversity (Sobek et al., 2009a) and an increase of general insect abundance with increase in phytodiversity (Schult et al., 2019). Although Sobek et al. (2009a) report positive effects of phytodiversity independent of the hemipteran trophic level (herbivores and predators), Schult et al. (2019) report that the direct effect and strength of the effect of phytodiversity vary between different functional groups (herbivores, predators and parasitoids) and between forest and grassland ecosystems.

Since there are several functional groups in Hymenoptera (herbivores, pollen feeders, parasitoids and predators) this study probably could not detect a general positive effect of phytodiversity on hymenopteran abundance. Furthermore, despite positive effects of phytodiversity on coleopteran abundance in temperate deciduous forests (Gering & Crist, 2000; Sobek et al., 2009b) none of the associations were significant. As there are also several functional groups in Coleoptera (herbivores, predators and fungivores), this might account for the absence of an overall effect of phytodiversity. Other studies report high abundance of predatory beetles in mature forests with a high species richness of herbaceous plants (Zou et al., 2019), an increase in abundance of ground dwelling beetles with forest age (Lange...
et al., 2014), an increase in the abundance of dung beetles with increase in ambient temperature and fine sand content of the soil (von Hoermann et al., 2020) and a high abundance of saproxylic species occurring at different stages in the decay of wood (Buse et al., 2008).

Other associations with vegetation recorded in this study was the increase in the abundance of Diptera and Psocoptera associated with the cover of the shrub layer. Although Psocoptera are an important component of the arthropod community in forest canopies (Thornton, 1985; Halaj et al., 2000; Thunes et al., 2004), their diversity and abundance are rarely investigated in temperate forests (Kanervo & Kozlov, 2014). Species of both orders are herbivores, with dipteran larvae being leaf-miners and gall-inducers. The association with plant cover could simply be because it is quantitative measure of the resources available for insect herbivores. Generally, there is a positive correlation between plant cover and biomass in the understoreys of forests (Muukkonen et al., 2006). While no effect of plant biomass on insect abundance has been detected in grasslands (Borer et al., 2012) the abundance of Diptera in temperate deciduous forest is positively associated with the cover of tree and ground vegetation (Scherber et al., 2014; Fuller et al., 2018). Forests are more complex than grasslands in terms of biomass and structure of the plants in the different layers. While the diversity of ground vegetation may influence insect communities by direct bottom-up processes, difference in the canopy determine environmental conditions that may affect insect communities (Scherber et al., 2014). The importance of the shrub layer in affecting insect abundances recorded in this study is potentially based on the shrub layer being between the ground and canopy layer and influencing bottom-up processes and environmental conditions.

In contrast to the positive associations with vegetation described above, the abundance of Thysanoptera decreased with increase in the species richness of ground layer. Potentially, the window traps used in this study were not suitably positioned to capture mature individuals of species of Thysanoptera because they have tiny wings and are weak fliers. However, the temperatures favourable for the pest species of Thysanoptera are well known (Ganaha-Kikumura & Kijima, 2016; e.g. Cao et al., 2018). According to the resource concentration hypothesis (Root, 1973), herbivory decreases with increase in phytodiversity, which would account for the pattern in the abundance of Thysanoptera recorded in this study.

Lastly, Diptera made up a high percentage (59%) of catches of the window traps in this study. Individual window traps caught more than 200 Diptera most of which belonged to one morph species (visual inspection). This is probably linked to swarming behaviour, a feature of mature individuals of many species of Diptera. As part of their mating behaviour, males attract females by flying in swarms. The high number of Diptera caught by particular trap could indicate a swarm passed by that trap.

Conclusions and limitations of the design of this study

As Schuldt et al. (2019) suggest by investigating the associations between changes in the abundances of species and environmental conditions, this study provides insights into the factors that influence the abundance of flying insects in a temperate forest. However, there are some limitations due to design of this study. By using window traps, the focus was on flying insects and, therefore, only their individual numbers can be compared. Window trap catches may have a limited ability to reveal more detailed information on particular insect orders. For instance, one study reports the minimum number of moths caught per night as 10–12 individuals (Infusino et al., 2017), whereas in our study not more than three Lepidoptera were caught per trap over a period of three weeks. Different types of traps, such as, coloured pan traps for Diptera and Hymenoptera and UV-light traps for Lepidoptera need to be used in future studies comparing the absolute abundance of different groups of insects.

As there are seasonal changes in the vertical stratifications and abundances of insects in temperate forests (e.g. Gruppe et al., 2008; Gößner, 2008), varying the heights of traps and the periods sampled is likely to result in different numbers of insects being caught. For instance, the numbers of phloem/wood feeding beetles caught increase with trap height; whereas the opposite is the case for ambrosia beetles (Ulyshen & Sheehan, 2019). Therefore, our results are incomplete because we did not sample insects in all the different layers in the forest, since traps were only installed in the lower canopy. In addition, the variation in mean temperature per day recorded in our study was only 17–18.6°C, which in part accounts for its low explanatory power in terms of insect abundances.

The association between insect species richness and phytodiversity has been investigated by other studies (e.g. Siemann et al., 1998; Sobek et al., 2009b). Furthermore, Scherber et al. (2014) report that phytodiversity effects on higher trophic levels depend on the identity of species. Therefore, insect orders with diverse functional feeding groups (e.g. Coleoptera, Diptera, and Hymenoptera) need to be investigated in greater detail than in this study. However, insect abundance plays an important role in plant-insect-interactions concerning changes in biodiversity and associated ecosystem functions. Therefore, future investigations on insect diversity need to include insect abundance as it is important to combine it with species richness, because a species can be abundant (as observed in monocultures) and negatively affect biodiversity and functioning of ecosystems. Therefore, other aspects of biodiversity, such as number of families, species richness and insect biomass, need to be considered as they may reveal different results in terms of associations with phytodiversity.

Finally, the robustness of the BIC models used in this study is relatively low and statistical analyses of the results for the abundances of Psocoptera, Lepidoptera, Hymenoptera and Hemiptera also reveal suitable models without
significant explanatory variables. Therefore, it can be assumed that either there was no effect, or other important factors affecting insect abundances were not measured (e.g. forest size, adjacent land use and age structure of the forest). In addition, the potential associations between insect abundance and phytdiversity, microclimate, stand structure and age can be altered by forest management. Consequently, forestry practices play an important role in determining the abundance of insects and conservation of insect diversity.

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**Fig. S1.** Pairs plot for the explanatory variables. Values indicate the Pearson correlation coefficients. Abbreviations: temp – air temperature; humid – relative humidity; SRG – species richness recorded in the ground layer; SRS – species richness recorded in the shrub layer; SRT – species richness recorded in the tree layer; CG – cover of the ground layer; CS – cover of the shrub layer; CT – cover of the tree layer.
Table S1. Selection of models for comparing\(^1\) the associations between abiotic conditions and vegetation and the abundance of insects and abundances of particular insect orders (individuals per window trap). Based on the Bayesian Information Criterion (BIC), models with similar strength of evidence, compared to the model with the lowest BIC (ΔBIC = 0–2), are displayed. Linear regressions for models containing one explanatory variable are shaded grey.

<table>
<thead>
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<th>Insect abundance</th>
<th>#</th>
<th>Intercept</th>
<th>Temp</th>
<th>Humid</th>
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<th>SRS</th>
<th>SRT</th>
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\(^1\) Models are ordered with those with the lowest BIC at the top (specified by rank). Positive and negative values for model variables indicate positive and negative associations with insect abundance, respectively. Temp – air temperature; Humid – relative humidity; SRG – species richness recorded in ground layer; SRS – species richness recorded in shrub layer; SRT – species richness recorded in tree layer; CS – cover of shrub layer; CT – cover of tree layer; logLik – log-likelihood; Delta – delta-BIC; Weight – Akaike weight.