

Insect attraction to herbivore-induced beech volatiles under different forest management regimes

Martin M. Gossner · Wolfgang W. Weisser ·
Jonathan Gershenson · Sybille B. Unsicker

Received: 16 November 2013 / Accepted: 9 July 2014 / Published online: 31 July 2014
© Springer-Verlag Berlin Heidelberg 2014

Abstract Insect herbivore enemies such as parasitoids and predators are important in controlling herbivore pests. From agricultural systems we know that land-use intensification can negatively impact biological control as an important ecosystem service. The aim of our study was to investigate the importance of management regime for natural enemy pressure and biological control possibilities in forests dominated by European beech. We hypothesize that the volatile blend released from herbivore-infested beech trees functions as a signal, attracting parasitoids and herbivore enemies. Furthermore, we hypothesize that forest management regime influences the composition of species attracted by these herbivore-induced beech volatiles. We installed flight-interception traps next to *Lymantria dispar* caterpillar-infested young beech trees releasing herbivore-induced volatiles and next to non-infested control trees. Significantly more parasitoids were captured next to

caterpillar-infested trees compared to non-infested controls, irrespective of forest type. However, the composition of the trophic guilds in the traps did vary in response to forest management regime. While the proportion of chewing insects was highest in non-managed forests, the proportion of sucking insects peaked in forests with low management and of parasitoids in young, highly managed, forest stands. Neither the number of naturally occurring beech saplings nor herbivory levels in the proximity of our experiment affected the abundance and diversity of parasitoids caught. Our data show that herbivore-induced beech volatiles attract herbivore enemies under field conditions. They further suggest that differences in the structural complexity of forests as a consequence of management regime only play a minor role in parasitoid activity and thus in indirect tree defense.

Keywords *Fagus sylvatica* · Indirect defense · *Lymantria dispar* · Parasitoid · Predator

Communicated by Ingolf Steffan-Dewenter.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-014-3025-4) contains supplementary material, which is available to authorized users.

M. M. Gossner · W. W. Weisser
Institute of Ecology, Friedrich-Schiller-University, Dornburger
Strasse 159, 07745 Jena, Germany

M. M. Gossner · W. W. Weisser
Terrestrial Ecology Research Group, Department
of Ecology and Ecosystem Management, Technische
Universität München, Hans-Carl-von-Carlowitz-Platz 2,
85354 Freising-Weihenstephan, Germany

J. Gershenson · S. B. Unsicker (✉)
Department of Biochemistry, Max Planck Institute for Chemical
Ecology, Hans-Knöll-Strasse 8, 07745 Jena, Germany
e-mail: sunsicker@ice.mpg.de

Introduction

Changes in land-use systems and increasing land-use intensity have been identified as main drivers of biodiversity loss in all types of terrestrial habitats, from agricultural landscapes to forests (Dormann 2007; Lambin et al. 2001; Sala et al. 2000). The consequences of management regimes for interaction-based ecosystem processes and services are fairly well studied in agricultural cropping systems (Chaplin-Kramer et al. 2011; Letourneau et al. 2012; Rand et al. 2012). Thus, we know that anthropogenic intensification in agriculture can strongly impact species interactions and ecosystem services such as biological control (reviewed by Tschardt et al. 2005). Herbivore parasitoids

and predators have important functions in controlling insect herbivore outbreaks, but with increasing land-use intensity, the abundance and diversity of the herbivores' natural enemies decreases (reviewed by Bianchi et al. 2006; Jonsson et al. 2012).

In forest ecosystems, biological control mechanisms are not well studied overall and thus our knowledge of the role of forest management regimes on this important ecosystem service is weak (Didham et al. 1996). Forest management might influence arthropod communities either directly by mechanically reducing population size during harvest activities or indirectly by, e.g., affecting habitat availability (shelter, overwintering structures, etc.), habitat complexity and heterogeneity, tree species composition or prey availability (e.g., Brunet et al. 2010; Lange et al. 2011; Paillet et al. 2010). Structural simplification as well as the substantial reduction of plant species richness might be the consequences of converting structurally highly complex natural forests into one-layered plantations of a single tree species. As structural complexity and plant architecture of habitats has been described as one main factor influencing movement and host finding of herbivores as well as their antagonists (Goodwin and Fahrig 2002; Hannunen 2002; Obermaier et al. 2008), forest management intensification might highly affect interactions between plants, herbivores and insect predators and parasitoids. Additionally vegetation structure might be important as shelter, etc. for herbivore antagonists. Only a few studies, however, have investigated the role of forest management regime on higher trophic level insects such as parasitoids and predators and even less on interactions between trophic levels (e.g., Dodd et al. 2012). In boreal forests of Sweden, Hilszczanski et al. (2005) showed that at the species level the assemblages of saproxylic ichneumonid parasitoids are significantly affected by the forest management regime. For temperate beech forests, Sobek et al. (2009) concluded from their study on herbivory and relative abundance of predators across a tree diversity gradient in the Hainich National Park in central Germany that beech herbivory is mediated bottom-up by resource concentration as well as regulated top-down by natural enemies.

In the past, numerous laboratory and greenhouse experiments showed that parasitoids and predators use volatiles released from herbivore-damaged plants as major cues in finding their hosts/prey (reviewed by Dicke 2009; Heil 2008; Unsicker et al. 2009). However, experimental evidence for the role of herbivore-induced volatiles in indirect defense under field conditions is scant (Hare 2011). Very few studies document the effect of specific volatiles or volatile blends for insect attraction under field conditions, but almost all of these were performed in agricultural systems (i.e., Bernasconi Ockroy et al. 2001; Degen et al. 2012;

Simpson et al. 2011). Klemola et al. (2012) investigated rates of caterpillar parasitism in herbivore-infested versus almost non-infested birch stands. In this study caterpillars on herbivore-infested birch trees were significantly more frequently parasitized than caterpillars on control trees. The authors argue that this difference is due to an attraction of parasitoids to herbivore-induced volatiles released from birch (Klemola et al. 2012).

The aim of our study was to investigate how the abundance of insect herbivore enemies is influenced by management practices in forests dominated by the European beech (*Fagus sylvatica*). We assessed enemy abundance by determining their attraction to herbivore-induced volatiles. Therefore we first investigated the role of tree volatile emission in mediating natural enemy attraction in beech forests. We hypothesize that young beech trees infested with *Lymantria dispar* caterpillars will release a quantitatively and qualitatively different odor blend compared to non-infested control trees and thus attract more parasitoids and herbivore enemies than the controls. Furthermore, we hypothesize that the composition of species attracted to the herbivore-induced beech odor will differ with respect to forest management regime due to differences in the population densities of insects and varying host-finding success. Studies in agricultural systems and grasslands have already shown that higher trophic-level predators and parasitoids can be strongly affected by land-use intensification (e.g., Tylianakis et al. 2007; Herbst et al. 2013) and concurrent changes in plant species richness and structural vegetation complexity (Randlkofer et al. 2010; Meiners and Obermaier 2004). For forest ecosystems, these relationships are poorly studied.

We selected European beech (*F. sylvatica*) for our experimental approach as it is the most dominant deciduous tree species in Central European forests (Brunet et al. 2010) and occurs across various forest management regimes. European beech is a late successional species and has significant economic value for timber production. Apart from the numerous studies on the role of European beech volatiles in atmospheric chemistry (i.e., Dindorf et al. 2006; Holzke et al. 2006; Tollsten and Müller 1996), there is virtually only one study documenting the release of herbivore-induced volatiles by beech (Joó et al. 2010).

We carried out laboratory and field experiments to address the following questions:

1. What is the herbivore-induced volatile blend released by *F. sylvatica*?
2. Is there differential attraction of forest insects, in particular natural enemies, to herbivore-infested versus control trees in the field?
3. Is there an effect of forest management on the attraction of forest insects to herbivore-infested beech trees?

Table 1 Number of experimental plots in forest types of different management intensity and the corresponding number of beech phytometers [beech phytometers infested with *Lymantria dispar* cater-pillars (*Herbivory*), non-infested phytometers (*Control*)] and flight-interception traps installed in these plots, respectively

Forest type	Number of experimental plots	Number of beech phytometers and traps		Herbivory in natural beech regrowth around the phytometers Leaf no. [leaf area consumed (cm ²)]	
		Herbivory	Control	Herbivory	Control
No management	5	5	5	36 (30.6)	36 (28.0)
Low management	4	4	4	36 (30.0)	36 (31.7)
High management					
Thicket	3	3	3	36 (50.8)	36 (55.4)
Pole wood	3	3	3	36 (35.5)	36 (30.0)
Old timber	3	3	3	36 (32.5)	36 (30.9)
Total	18	18	18	648 (615.4)	648 (629.9)

The last two columns of the table display the number of leaves collected in natural beech regrowth in a radius of 2 m around the phytometer beech trees and the corresponding leaf area loss (cm²) in these leaves

Materials and methods

Study region and sites

The study was conducted in the Hainich-Dün region within the German Biodiversity Exploratories Project (Fischer et al. 2010). This region comprises a range of hills in north-west Thuringia, Germany (10°10'24"–10°46'45"E, 50°56'15"–51°22'43"N). Altitude ranges between 285 and 550 m a.s.l. (Fischer et al. 2010), whilst the mean annual temperature range is 6.5–8 °C, and the mean annual precipitation is between 500 and 800 mm. The region consists of a large closed forest area of 16,000 ha dominated by broad-leaved trees. The forests are managed with varying intensity ranging from unmanaged forests within the National Park Hainich to intensively managed age-class forests.

We performed our study at 18 forest sites of different forest management regimes that were dominated by European beech (*F. sylvatica* L.) (Table 1). Unmanaged forests (no-management sites, $n = 5$ sites) exclusively occur within the national park. They are characterized by uneven-aged (up to 250 years) mixed deciduous forest (*Fagus sylvatica*, with *Fraxinus excelsior* L., *Acer pseudoplatanus* L. and others). The core area of the national park, where there was no forest management for at least 40 years, comprises 261 ha and is unique for Germany in terms of its age, structure and extent. In the selection-cutting beech forests (low-management sites, $n = 4$) only selected trees are harvested and trees in the gaps recruit from seed fall. This type of management creates a permanent forest of uneven-aged stands of different tree species of different age. Age-class beech forests (high-management sites, $n = 9$) are characterized by homogeneous even-aged stands of different developmental stages (age classes); we studied thickets ($n = 3$) characterized by trees of a diameter at breast height (DBH) <7 cm

which corresponds to a tree age of <30 years, pole wood ($n = 3$; 7–15 cm DBH; 30–50 years), and old timber ($n = 3$; >30 cm DBH; >90 years) (Table 1). The rotation for high-management beech forests is around 160 (± 30) years. Because of a change in management practices, the younger high-management forests did not originate from clear-cuts with subsequent planting, but included both natural seedling recruitment and the preservation of some mature trees (120–180 years old) that were cut only once the young cohort reached an age of somewhere between 10 and 20 years. Both the no-management forests and the high-management forests are characterized by a closed canopy without big gaps. These shady conditions result in a low cover of the shrub layer, in particular in the studied young age-class beech stands (4 ± 3 SE %). The cover of the shrub layer increased from old age-class timber stands (22 ± 6 %) to unmanaged forests (26 ± 5 %), to the uneven-aged (selective cutting) stands (38 ± 10 %). Age-class thicket stands had by definition (woody species <5 m) a relatively high shrub layer (47 ± 14 %) [data from vegetation relevés, see Boch et al. (2013); Boch, personal communication].

Plant and insect material

We decided to use transplants instead of naturally occurring beech trees in order to avoid confounding factors that we could not control for in the field (e.g., different soil properties at the sites, different damage levels by herbivores and plant pathogens). The *F. sylvatica* trees were all around 1.50 m high and were purchased from a tree nursery, grown from regional seeds (Müller-Münchehof, Seesen-Münchehof, Germany). Twelve trees were used for the laboratory and 54 for the field experiment.

Gypsy moth (*L. dispar*) caterpillars originated from a culture at the Max Planck Institute (MPI) for Chemical

Ecology and were grown on artificial wheat germ diet (gypsy moth diet; MP Biomedicals, Illkirch, France).

Attraction of insects to beech trees

We performed our field experiment for a period of 36 days between 29 May and 3 July 2008 on all plots in parallel. In each of the 18 plots two beech phytometers were installed (total 36 trees, plus 18 trees that were exchanged during the experiment) where one was infested with caterpillars (herbivory treatment, 15 third-instar caterpillars per tree), and the other functioned as a ‘control’ tree. In each plot the distance between the two phytometers was 100 m. To prevent caterpillars in the herbivory treatment from escaping and to avoid predation by birds and ground-living predators, all phytometers were caged (for a detailed description of the experimental set up, see Fig. S1).

Composite flight-interception traps (Fig. S1) were used to catch insects that might be attracted to the beech phytometers. This trap type has been shown to representatively assess activity densities of flying insects of different trophic levels including parasitoid communities in forests (Springate and Basset 1996; Jäkel and Roth 2004). At the top of each beech phytometer (treatment and control) one trap was installed (n total = 36 traps). The traps consisted of a crossed pair of gauze (50 cm × 50 cm) with a funnel of tough material attached to the bottom and to the top; at the end of both funnels sampling jars were mounted filled with killing and preserving agent (3 % copper sulphate solution) and a drop of detergent to reduce surface tension. The traps were emptied three times at 12-day intervals and all arthropods were transferred to 70 % ethanol in the field. Insects were sorted into taxonomic orders in the laboratory. Determination of Coleoptera, Diptera (only parasitoids), Hemiptera, Hymenoptera, Neuroptera and Thysanoptera was performed to a level at which feeding guild (herbivores, suckers–chewers; predators, parasitoids) could be classified. Hemiptera and Thysanoptera were classified as suckers and Coleoptera, Hymenoptera, and Neuroptera as chewers. Among Hemiptera all Heteroptera were identified to species level (by M. M. G.) and classified as herbivores and predators according to Wachmann et al. (2004–2012). All Homoptera and Thysanoptera were classified as herbivores. Coleoptera were identified to a level at which classification into herbivores and predators according to Böhme (2005) was possible (e.g., all specimens of the family Curculionidae were classified as herbivores, whereas in Staphylinidae genus-level determination was necessary). All Hymenoptera were sent to specialists for further identification and classification. Only parasitic Diptera (Tachinidae and Pipunculidae) were identified and integrated in statistical analysis as the other, more than 2,000, trapped Diptera could not be assigned to a specific trophic level

(the diversity of trophic levels within families is high and ecological knowledge is not sufficient for a reliable classification). Only flight-capable individuals (no larvae or nymphs) were used for further analysis of abundances as with flight-interception traps only activity densities of these insects can be estimated. Thus all non-winged insects and mites (mostly phoretic species) were excluded. Furthermore, more than 1,300 holometabolic larvae and all Collembola were ignored, as well as around 300 spiders that might have tried to use the traps to build webs.

Herbivory of all phytometers (gypsy moth treatments and control) was measured at the end of the experiment (in the herbivory treatment additionally mid experiment) by visually estimating the percent leaf area loss (caused by *L. dispar* caterpillars and others). Phytometers of the herbivory treatment were exchanged mid experiment, to avoid complete defoliation, which would have resulted in a drastically reduced emission of herbivore-induced volatiles.

To test if density and herbivory of surrounding trees (up to 10 m height) of the natural vegetation affected the trap catches, number of trees were counted and herbivory was measured in a circle of 2-m radius around each phytometer. These variables were considered as covariates in the analyses. Herbivory was assessed along four 2-m radial transects (north-east, south-east, north-west, south-west direction) at three locations (next to the cage, 1- and 2-m distance). At each location one leaf at three heights (lowest, middle, uppermost part of the regeneration up to 2 m height) was collected haphazardly by blindly pointing with a stick to the respective foliage in the tree. Herbivory was measured as average percentage of leaves damaged and as average leaf area consumed. For the calculation of leaf area consumed all leaves were spread on a white board containing a reference square and covered with non-reflecting Plexiglas before they were photographed with a digital camera. Digital photographs were analyzed with the graphics software Adobe Photoshop 8.0. Total remaining leaf area was determined by using the pixel number of the reference square as a template. Herbivore-related missing leaf area was then reconstructed. Leaf area was then determined again for the reconstructed leaves and leaf damage was quantified using the differences in pixel number between the reconstructed and the damaged leaves.

Release of herbivore-induced volatiles by beech trees

To investigate the emission of volatiles from young *F. sylvatica* trees after *L. dispar* feeding, 12 trees (~150 cm in height) from the same nursery as those for the field experiment were selected. Six of these entered the caterpillar-herbivory treatment, and six functioned as non-infested control trees. For experimental herbivory and following volatile collections, all trees were transferred to a shaded

area outside the MPI-ICE greenhouse in Jena. The trees were completely enclosed with mesh bags and 15 caterpillars in fourth and fifth instar were released on the herbivore-treated individuals. Twenty-two hours after the onset of gypsy moth caterpillar feeding, the volatile collections started. The mesh bags were exchanged by PET foil bags (Toppits Bratschlauch, Minden, Germany). Volatiles were collected for 4 h around noon with 20 mg Super-Q filters using a push–pull system supported by a compressor. Air was purified through a charcoal filter before it entered the headspace of the respective tree at a flow rate of 1 l min^{-1} . Simultaneously air was sucked out of the bags through the Super-Q filter at a rate of 0.5 l min^{-1} . Slight overpressure in the bags was deliberate during volatile collection to avoid contamination from the outside. After the collection the volatile compounds were desorbed by eluting the filter twice with $100 \mu\text{l}$ dichloromethane containing nonyl acetate as an internal standard (concentration $10 \text{ ng } \mu\text{l}^{-1}$). Samples were stored at $-20 \text{ }^\circ\text{C}$ until further analysis.

To relate volatile emission to the actual leaf biomass on the tree, all leaves were harvested right after volatile collections, dried at $80 \text{ }^\circ\text{C}$ in a drying oven and then weighed.

Qualitative and quantitative determination of the volatiles emitted from *F. sylvatica* was conducted using a Agilent 6890 series gas chromatograph coupled to a Agilent 5973 quadrupole mass selective detector (interface temperature $270 \text{ }^\circ\text{C}$, quadrupole temperature $150 \text{ }^\circ\text{C}$, source temperature $230 \text{ }^\circ\text{C}$, electron energy 70 eV) and a flame ionization detector operated at $300 \text{ }^\circ\text{C}$. The constituents of the volatile bouquet were separated with a DB-5MS column (Agilent, Santa Clara, CA; $30 \text{ m} \times 0.25 \text{ mm} \times 0.25 \mu\text{m}$) and He (mass spectrometer) or H_2 (flame ionization detector; FID) as carrier gas. One microliter of the sample was injected splitless at an initial oven temperature of $40 \text{ }^\circ\text{C}$. The temperature was held for 2 min and then increased to $155 \text{ }^\circ\text{C}$ with a gradient of $7 \text{ }^\circ\text{C min}^{-1}$, followed by a further increase to $300 \text{ }^\circ\text{C}$ with $60 \text{ }^\circ\text{C min}^{-1}$ and a hold for 3 min.

Compounds were identified by comparison of retention times and mass spectra to those of authentic standards obtained from Fluka (Seelze, Germany), Roth (Karlsruhe, Germany), Sigma (St. Louis, MO) or Bedoukian (Danbury, CT), or by reference spectra in the Wiley and National Institute of Standards and Technology libraries and in the literature (Joulain and König 1998). The absolute amount of all compounds was determined based on their FID peak area in relation to the area of the internal standard using the effective carbon number concept (Scanion and Willis 1985).

Data analysis

We used generalized linear mixed-effects models (GLMM) to test for effects of forest type and treatment (herbivory/

control) on: (1) the herbivory of beech trees in the surroundings (proportion of leaves damaged/proportion of leaf area consumed) of the cages; and (2) the abundance of herbivores (chewers/suckers), predators and parasitoids sampled by composite flight-interception traps next to the cages. In both GLMMs, forest site was used as random factor and forest type and treatment as fixed factors. Additionally an interaction term between main factors (treatment, forest type) was considered. In (1) a binomial error distribution with logit link-function was specified. In (2) density of regeneration and herbivory in the surrounding (mean percentage of leaf area consumed) were used as covariates. Here a Poisson error distribution with log link-function was specified. To test for overdispersion we calculated the ratio of sum of squared Pearson residuals and the residual *df*. In all cases, the ratio was between 0.98 and 1, except for the model regarding suckers where we specified a quasi-Poisson error distribution. Experimental caterpillar herbivory is shown as % leaf area loss. Because of the unbalanced design regarding forest types we additionally tested if results are consistent when using the recently published quantitative silvicultural management intensity index (SMI) (Schall and Ammer 2013). Analyses were performed with the package lme4 within R 3.0.2 (R Development Team 2013).

Non-metric multidimensional scaling (NMDS) was used to test whether communities of parasitoids differ between treatment and forest type. The analysis was based on Bray–Curtis dissimilarities using the package vegan in R. As a measure of variance, we provide SEs throughout the manuscript.

Results

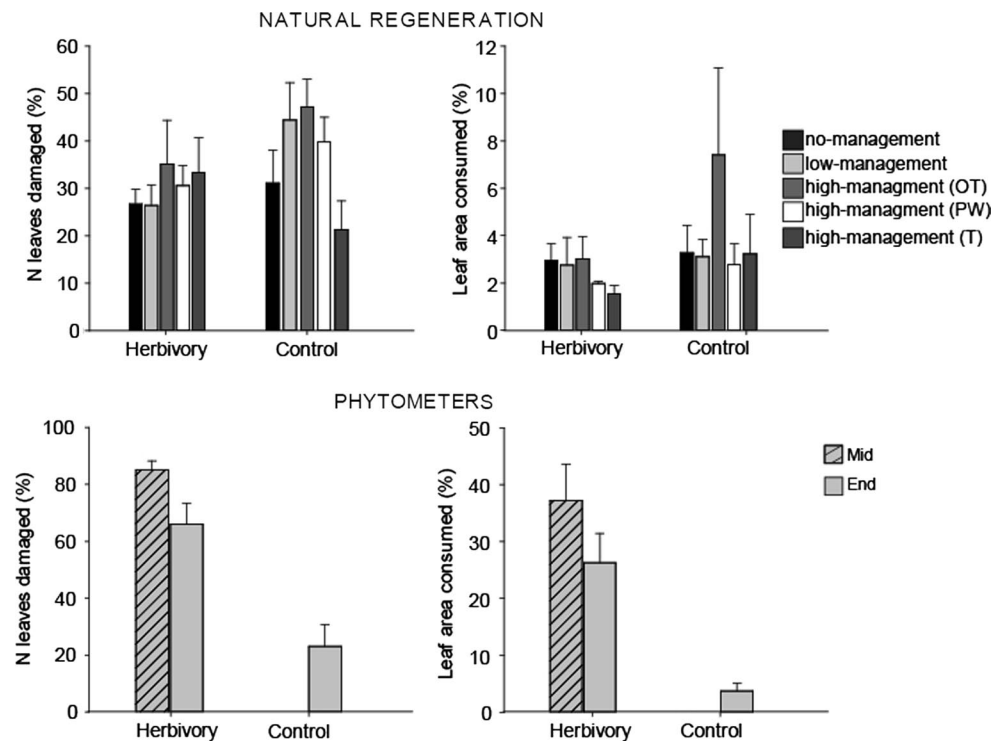
Natural herbivory in young beech regrowth

Leaf herbivory in naturally occurring young beech regrowth surrounding the beech phytometers showed high variability among forest sites (Fig. 1). However, natural herbivory was neither significantly different between forest types nor between the beech regrowth surrounding the phytometers experimentally infested with gypsy moth caterpillars ($30 \pm 2 \%$ of all leaves were damaged, $3 \pm 0.3 \%$ leaf area loss) and the control phytometers (37 ± 3 , $4 \pm 0.8 \%$) plots (Fig. 1; GLMM; $p > 0.10$ in all cases).

Experimental herbivory in beech phytometers

Aphid infestation by *Phyllaphis fagi* was already detected in all phytometers before the beginning of the experiment. Experimentally exposed caterpillars significantly increased the level of foliar herbivory of beech phytometers compared

Fig. 1 Herbivory (mean and SEs) of beech natural regeneration in the surroundings of the experiment separated by forest type (*top panel*) and beech phytometers (*bottom panel*) of herbivory treatment ($n = 18$) and control ($n = 18$). *Left* Average percentage of leaves damaged, *right* average percentage of leaf area consumed. Note that herbivory of control phytometers was measured only once, at the end of the experiment. Phytometers of the herbivory treatment were exchanged mid experiment



to the control trees, where herbivory was negligible (Fig. 1). Two weeks after introducing *L. dispar* caterpillars, 10–90 % of all leaves of the trees in the herbivory treatment were damaged (mean 85 ± 3 %). Average herbivory was 37 ± 6 % leaf area loss (in 30 % of all leaves >50 % of leaf area was consumed). Experimental herbivory in the second cohort of beech phytometers installed half-way through the experiment was also high (leaves damaged 66 ± 7 %; leaf area loss 26 ± 5 %), with often only the leaf veins left by the end of the experiment. In the control trees herbivory was much lower, showing 23 ± 7 % leaves damaged with an average of 4 ± 1 % leaf area loss observed at the end of the experiment, but there was also a high variation in herbivory among forest sites (Fig. 1).

Attraction of insects to beech phytometers

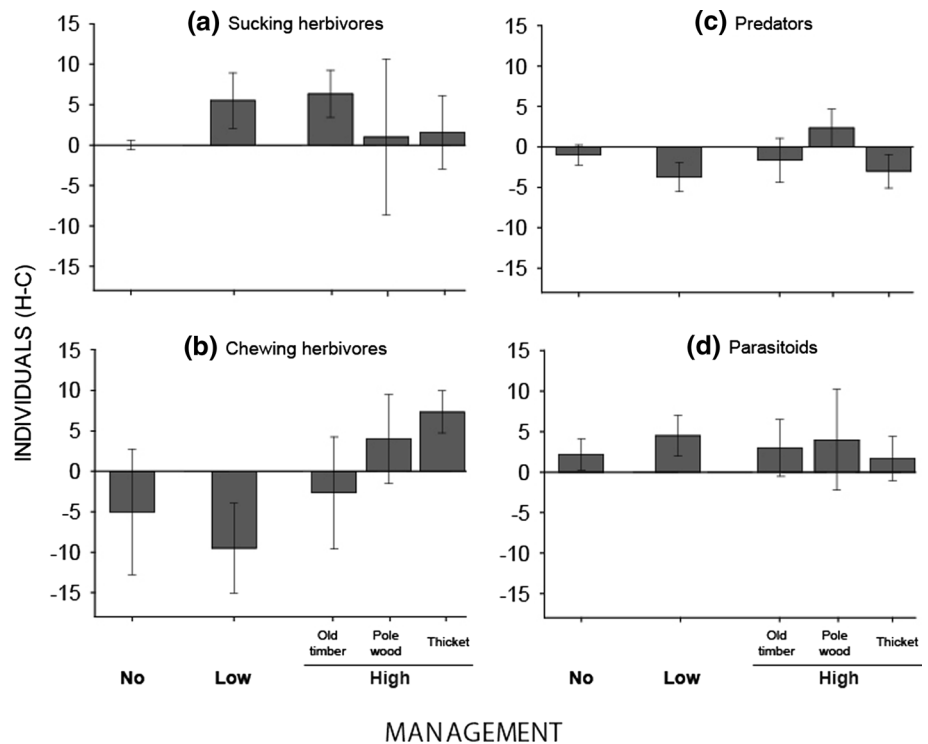
We sampled a total of 7,684 arthropods during the 36 days of the experiments. More individuals were caught next to the herbivory treatment (4,271; mean 237 ± 43) compared to the control plots (3,413, mean 190 ± 23 ; GLMM, $z = 9.77$, $p < 0.001$). Of these we assigned the 1,497 individuals with wings to trophic guilds (see Materials and methods). Chewing herbivores showed highest numbers (585), followed by sucking herbivores (452), parasitoids (269) and predators (191). Among parasitoids we observed 83 (morpho-) species of 21 families (see Table S1).

Experimental caterpillar herbivory in the beech phytometers significantly affected insects caught with the

flight-interception traps. The most conspicuous effect was observed in parasitoids. The abundance of parasitoids was significantly positively affected by experimental herbivory (Fig. 2; Table 2) and this was independent of the management regime in the different forest sites. Results were consistent when using SMI as a quantitative measure of land-use intensity measure (GLMM, SMI, $z = 0.54$, $p > 0.5$; treatment, $z = 3.0$, $p < 0.01$). No significant interaction was observed between treatment and forest type ($p > 0.05$). When only using the data of the first 2 weeks (before exchanging phytometers in the herbivory treatment) the treatment effect on the abundance of parasitoids was still significant (GLMM, $z = 2.0$, $p < 0.05$). Parasitoid abundance was neither influenced by the density of natural beech regrowth nor herbivory in these trees. Additionally, parasitoid species richness was positively affected by experimental herbivory (z -value 2.0, $p = 0.042$). Most of the caught parasitoids (>90 %) are known to parasitize herbivorous insects (see Table S1). By focusing on known parasitoids of herbivores only, the effect of treatment remained consistent, but was marginally non-significant (z -value 1.7, $p = 0.098$). When the number of parasitoid individuals was additionally fitted to the model, no additional effect of treatment on parasitoid species richness was observed (GLMM, $p > 0.10$). Moreover, parasitoid community composition did not differ between herbivory treatment and control plots (NMDS based on Bray–Curtis dissimilarities; Fig. S2).

In contrast, the abundance of predators was not affected by treatment (Fig. 2; Table 2). This effect was independent

Fig. 2 Average difference between herbivore treatment and control separated by forest type in abundance of herbivores (**a** sucking, **b** chewing), predators (**c**) and parasitoids (**d**). Positive values indicate higher abundance in herbivore treatment, negative values indicate higher abundance in control treatment



of forest type, as including an interaction term treatment \times forest type in the model revealed no significant interaction ($p > 0.05$). Furthermore, management did not significantly affect predator abundance when using forest type (Table 2) nor when using SMI (GLMM, $z = -1.8$, $p = 0.11$).

Among the herbivores caught in the traps next to the phytometers, only sucking insects were positively affected by experimental herbivory, independent of forest management type (interaction treatment \times forest type, $p > 0.05$). In contrast, chewing insect abundance was negatively affected by experimental herbivory in old stands, but positively in young high-management forest stands (Fig. 2). When an interaction term treatment \times forest type was included in the model, this was significant (Table 2). Moreover, both abundance of sucking and chewing insects was significantly affected by management type (Fig. 2; Table 2) and SMI (GLMM, suckers, $z = -2.8$, $p < 0.01$; chewers, $z = -2.9$, $p < 0.01$). Sucking insect abundance was higher in old stands, in particular in the low-management sites (no management 12 ± 2.9 , low management 21 ± 5.3 , high-management old timber 14 ± 3.6), than in young stands (high-management pole wood 9.5 ± 2.3 , high-management thicket 3.3 ± 0.67). Chewing insects showed highest abundance in no-management forests (31.90 ± 8.63 SE) followed by low-management (14 ± 3.9) and high-management sites (old timber 9 ± 2.4 , pole wood 8.3 ± 2.9 , thicket 7.3 ± 2).

All trophic guilds showed high variation in the number of sampled individuals among forest sites in herbivory treatment as well as in control plots (Fig. S3). Forest type significantly affected the abundances of herbivores, but not of predators and parasitoids, resulting in a substantial difference in guild composition among forest types (Table 2): herbivores generally showed low abundances in high-management thickets; sucking insects among them were most abundant in low-management sites and chewing insects in no-management forests.

Constitutive and herbivore-induced volatile emission from beech phytometers

We identified over 20 volatile compounds belonging to five major groups, namely monoterpenoids, sesquiterpenoids, homoterpenoids, green leaf volatiles and aromatics, in the volatile blend of young *F. sylvatica* trees (Table 3; Fig. S5). Sesquiterpenes and the homoterpene 4,8-dimethyl-1,3,7-nonatriene (DMNT) were significantly induced by experimental herbivory of gypsy moth caterpillars by showing up to 30-fold increased concentrations, whereas herbivory had no significant effect on the emission of other major groups of volatiles (Fig. 3). Among individual compounds, the highest increase in emission due to herbivory was observed in the sesquiterpene germacrene D (160-fold) followed by β -bourbonene (91-fold), another sesquiterpene, and the monoterpene α -terpinolene (55-fold). The most abundant

Table 2 Effects of treatment and forest type on the abundance of flight-capable insect herbivores (sucker, chewer), predators and parasitoids assessed by composite flight-interception traps next to the phytometers established in each forest plot

	Herbivores: sucking			Herbivores: chewing			Predators			Parasitoids						
	Estimate	SE	<i>z</i>	<i>p</i>	Estimate	SE	<i>z</i>	<i>p</i>	Estimate	SE	<i>z</i>	<i>p</i>				
Intercept	2.3	0.43	5.4	<0.001	2.2	0.39	5.8	<0.001	1.9	0.34	5.7	<0.001	2.2	0.4	5.5	<0.001
Herbivory	0.026	0.036	0.71	0.48	-4.4	4	-1.1	0.27	0.001	0.038	0.016	0.989	-0.03	0.043	-0.68	0.49
<i>n</i> Saplings	-0.001	0.002	-0.29	0.77	0.005	0.002	2	0.046	0	0.002	0.2	0.84	-0.004	0.002	-1.6	0.1
Treatment (Herbivory vs. Control)	0.27	0.11	2.5	0.013	-0.7	0.38	-1.8	0.065	-0.29	0.16	-1.8	0.069	0.4	0.14	3	0.003
Forest type																
High-management thicket	-1.4	0.56	-2.5	0.011	-1.1	0.55	-2	0.046	-0.7	0.39	-1.8	0.068	-0.27	0.41	-0.65	0.52
High-management pole wood	-0.37	0.55	-0.68	0.5	-0.42	0.52	-0.8	0.42	-0.32	0.39	-0.82	0.41	0.001	0.44	0.002	1
No management	-0.18	0.48	-0.38	0.71	1.1	0.42	2.5	0.012	-0.11	0.32	-0.35	0.73	-0.51	0.39	-1.3	0.19
Low management	0.28	0.49	0.58	0.57	0.6	0.45	1.3	0.19	-0.056	0.33	-0.17	0.87	-0.26	0.4	-0.66	0.51
Treatment × high thicket					1.8	0.5	3.6	<0.001								
Treatment × high pole wood					1.2	0.47	2.5	0.013								
Treatment × no management					0.52	0.36	1.4	0.15								
Treatment × low management					0.032	0.42	0.076	0.94								

Results of a generalized linear mixed effects model considering density of regenerating beech trees within a 2-m radius around the phytometers (= *n* saplings) and the percent leaf area loss measured in these (herbivory) as covariates and forest site as random factor. Interactions were only included in the model when they were significant (chewers only)

Table 3 Volatile compounds of *Fagus sylvatica* released from undamaged leaves (Control) and leaves damaged by gypsy moth caterpillars for 24 h (Herbivory)

Compound	Control	Herbivory	<i>p</i> -value
Aromatics			
Methyl-salicylate	152 ± 39	211 ± 85	NS
Green leaf volatiles			
(<i>Z</i>)-3-Hexenyl acetate	14 ± 5.6	36 ± 10	NS
Homoterpenoids			
DMNT	4.7 ± 1.5	128 ± 17	0.004
Monoterpenoids			
Sabinene	589 ± 349	735 ± 431	NS
α-Terpinolene	6.6 ± 4.1	14 ± 5.4	NS
γ-Terpinene	20 ± 11	26 ± 14	NS
α-Terpinene	11 ± 7.2	15 ± 8.5	NS
Linalool	1.8 ± 0.92	102 ± 37	0.004
β-Myrcene	16 ± 8.9	21 ± 10	NS
α-Pinene	9 ± 6	12 ± 6.8	NS
(<i>E</i>)-β-Ocimene	1 ± 0.36	12 ± 7.4	0.025
α-Thujene	7.5 ± 4.2	9 ± 5	NS
β-Thujene	7.9 ± 2.7	10 ± 5	NS
Sesquiterpenoids			
(<i>E,E</i>)-α-Farnesene	50 ± 16	369 ± 116	0.025
(<i>Z,E</i>)-α-Farnesene	11 ± 4	116 ± 38	0.036
(<i>E</i>)-β-Caryophyllene	7.4 ± 6.4	78 ± 38	0.014
Germacrene D	0.14 ± 0.14	23 ± 6.8	0.013
β-Bourbonene	0.1 ± 0.1	8.8 ± 2.5	0.003
α-Humulene	0 ± 0	3.8 ± 1.5	0.022
Others			
Non-analyzed	24 ± 6.4	31 ± 2.4	NS

Emission rates are displayed as mean ± SE (ng g⁻¹ dry weight h⁻¹) (*n* = 6). *p*-values are based on the results from Mann–Whitney *U*-tests between control and herbivore treatments. The compounds were identified by authentic standards and mass spectra

DMNT 4,8-Dimethyl-1,3,7-nonatriene, NS non-significant

compound in the herbivore-induced and the constitutive volatile blend of the beech trees was the monoterpene sabinene. The monoterpenes, α-pinene, trans-β ocimene and α-terpinolene, were also significantly induced by caterpillar feeding (Table 3). The only detectable green leaf volatile was (*Z*)-3-hexenyl-acetate, and methyl-salicylate was the only aromatic compound that was measured. Both occurred in similar concentrations in control and herbivory treatment.

Discussion

In this study we investigated the effects of herbivore-induced volatiles released from beech trees on the attraction of herbivores and their predators and parasitoids in

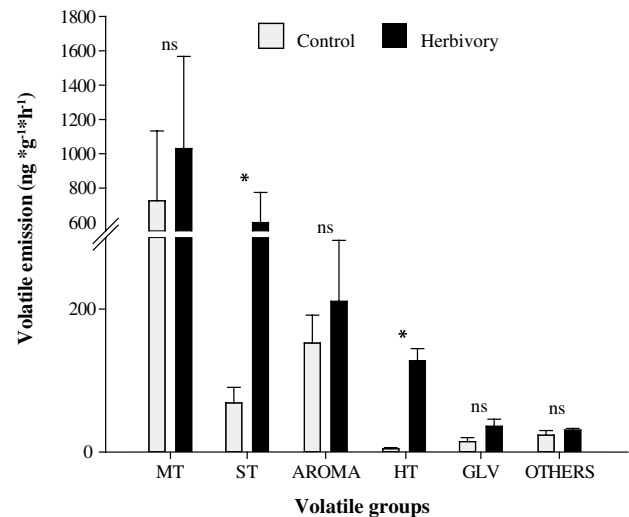


Fig. 3 Emission of major groups of volatiles from young *Fagus sylvatica* trees infested locally with *Lymantria dispar* caterpillars as compared to non-infested control trees. Mean ± SE, sample sizes *n* = 6. Asterisks indicate significant differences between controls and herbivore-infested trees (**p* < 0.05; Mann–Whitney *U*-tests). MT Monoterpenes, ST sesquiterpenes, AROMA aromatic compound (methyl salicylate), HT homoterpene (4,8-dimethyl-1,3,7-nonatriene), GLV green leaf volatile [(*Z*)-3-hexenyl acetate], OTHERS non-analyzed, ns non-significant

forest stands of differing management intensities. Next to caterpillar-infested beech phytometers significantly more parasitoids were caught as compared to non-infested control trees. This pattern was observed irrespective of forest type (from unmanaged to intensively managed) although the composition of trophic guilds in the traps did vary in response to forest management regime. Neither the number of naturally occurring beech saplings in the proximity of our experiment nor the herbivory levels in these explained the abundance and diversity of parasitoids caught. Our results suggest that differences in the structural complexity of forests as a consequence of management regime only play a minor role for parasitoid activity. An alternative explanation could, however, also be that the attraction to herbivore-induced volatiles has overcome any difference that there may have been in terms of forest structure effects on parasitoid abundance. Despite the change in abundance, no change in parasitoid community composition across management regimes could be detected.

When young beech trees in our experiment were attacked by *L. dispar* caterpillars they emitted significantly more volatiles than the non-infested control trees. The headspace consisted of around 21 compounds from within five major groups of volatiles (monoterpenes, sesquiterpenes, green leaf volatiles, aromatic compounds and the homoterpene DMNT). While individual compounds emitted from European beech such as the green leaf volatile

(*Z*)-3-hexenyl-acetate, the homoterpene DMNT and the sesquiterpenes (*E*)- β -caryophyllene and germacrene D have already been reported for other, taxonomically unrelated plant species, such as maize, lima bean, poplar, plantain, clover, oak and many others (Turlings and Tumlinson 1992; Heil and Silva Bueno 2007; Fontana et al. 2009; Kigathi et al. 2013; Danner et al. 2011; Ghirardo et al. 2012), the volatile blend of *F. sylvatica* shows some unique features: the bouquet is overall dominated by the monoterpene sabinene and the aromatic compound methyl-salicylate, both present constitutively. A number of mono- and sesquiterpenes are significantly induced by caterpillar feeding and green leaf volatiles are only present in minor amounts. Qualitatively, the volatile blend in this study was very similar to the aphid-induced bouquet measured by Joó et al. (2010). These similarities are likely due to an infestation of our beech phytometers with the same aphid species *P. fagi* as in the study by Joó et al. (2010). Although aphid infestation might have slightly leveled volatile emission from control trees and caterpillar-infested beech trees, the relative proportions of volatiles measured in our study are very different. Thus the pronounced differences in volatile emission between caterpillar-infested and control tree were certainly brought about by experimental caterpillar herbivory.

The pronounced difference in volatile emission between caterpillar-infested and control trees that we measured in a subset of beech phytometers under comparable abiotic conditions outside the MPI-ICE greenhouse in Jena shows that our experimentally induced herbivory was efficient and most likely accounts for the differences in total numbers of herbivores, predators, and parasitoids caught in the experiment. As *L. dispar* caterpillars were continuously present in the herbivore-treated beech phytometers, we cannot exclude specific volatiles emitted from the caterpillars and the frass to attract herbivore natural enemies. Yet a study by Clavijo McCormick et al. (2014) revealed that only very low amounts of volatiles are detected in the headspace of caterpillars and feces when measured alone. In laboratory studies some of the major herbivore-induced volatile compounds released from beech, such as germacrene D, DMNT and ocimene, have already been shown to attract parasitoids [Mumm and Dicke (2010) and references therein]. When autumnal and winter moth caterpillars were exposed in birch trees previously defoliated by caterpillars the rate of parasitization was more than twice as high as in caterpillars exposed on control trees (Klemola et al. 2012). The authors argue that herbivore-induced volatiles released from birch account for this parasitization pattern. Although we did not investigate in situ parasitization in our experiment, we are convinced that the differences in herbivores, parasitoids, and predators trapped in our experiment are also due to the differences in volatile emission between the caterpillar-infested and the control trees.

The parasitoid species attracted to the herbivore-infested beech trees in our experiment are neither known specialists of *L. dispar* caterpillars nor have they been documented to be restricted to the parasitization of beech herbivores. Thus we speculate that long-distance attraction of parasitoids towards herbivore-infested beech trees is rather species unspecific. It is conceivable that long-distance signaling is mediated by the most abundant herbivore-induced volatile compounds, which are in fact the ones that generally occur in the blends of most herbivore-induced plant species investigated so far (Clavijo McCormick et al. 2012).

Plant-induced attraction of herbivore antagonists is a well-known phenomenon (Dicke 2009; Heil 2008; Unsicker et al. 2009), but has rarely been shown under field conditions. A few studies performed in agricultural systems and in trees could show that herbivore-induced volatiles can attract parasitoids under field conditions (Braasch et al. 2012; Büchel et al. 2011, 2013; Clavijo McCormick et al. 2014; Degen et al. 2012; Simpson et al. 2011). Our study, with the study of Klemola et al. (2012), is one of the first to show the possible existence of this mechanistic link in forests. Surprisingly, predaceous insects were not significantly attracted by herbivore-induced beech volatiles. Flight-interception traps are not adequate to capture mostly flightless herbivore enemies such as ground beetles or ants.

We sampled a high number of insects of all trophic guilds and we were able to detect differences among forest types and between herbivory treatment and the control. Adult herbivores showed the most conspicuous response to forest type. While chewing insects showed highest abundance in no-management forests, sucking insects were most abundant in low-management forests. This could not be explained by differences in plant diversity (Boch et al., unpublished data; Fig. S2), but might be due to structural differences between forest types, i.e., high sucking insect diversity in low-management forests might be caused by the more open structure of these forests (Gossner 2009).

It is conceivable that more intensive management might disconnect the tri-trophic interaction between herbivores, plants and parasitoids resulting in less effective pest control in these forests (e.g., Klein et al. 2002). We, however, could not find a strong indication for this as the main effect of herbivory-induced attraction of parasitoids occurred independently of forest type. The difference in attraction of parasitoids between experimental and control trees was, however, stronger in unmanaged forests and forests with low (i.e., selection-cutting) compared to forests with high management intensity (i.e., age-class forests) (error bars crossed the zero line only in high-management forests; Fig. 2). One might speculate that this suggests a more effective pest control of herbivores in less intensively managed forests, which might have higher structural diversity and thus enable higher population densities of natural enemies.

Surprisingly, sucking herbivores were also attracted to herbivore-induced phytometers, although this effect was much less pronounced than in parasitoids. Certainly insect herbivores can deploy plant volatiles to find adequate host plants. There are examples for this phenomenon in the recent literature (e.g., Carroll et al. 2006; Halitschke et al. 2008; Robert et al. 2013).

Several studies have shown that land use might affect trophic interactions which are important for ecosystem processes (Gladbach et al. 2011; Mulder et al. 2011; Tylianakis et al. 2008). For example it has been shown that plant diversity can stabilize food webs (Haddad et al. 2011) and in heterogeneous landscapes an increase in natural enemy diversity benefit pest control (Tylianakis and Romo 2010). Our mechanistic understanding of these links is, however, still rudimentary.

Although we know from numerous laboratory and field studies with short-lived herbaceous plant species that herbivore-induced plant volatiles attract natural enemies and parasitoids of herbivores, our study is among the first to demonstrate that this phenomenon also occurs in long-lived deciduous tree species such as *F. sylvatica*. Our data also suggest that indirect beech defense is independent of forest management type but further experiments with, for example in situ parasitization as a response tree volatile emission have to be conducted to confirm our findings.

Acknowledgments We thank Sonja Gockel, Simone Pfeiffer, Markus Fischer, Elisabeth Kalko, Eduard Linsenmair, Dominik Hesenmöller, Jens Nieschulze, Daniel Prati, Ingo Schöning, François Buscot, and Ernst-Detlef Schulze for their role in setting up the Biodiversity Exploratories project. We are grateful to Matthias Gross, Norbert Leber, Maria Lorenz, Britt Farquharson and Rebecca Wagner for field assistance and C. van Achterberg (Leiden, the Netherlands), Wolfgang Adaschkiewitz (Jena), Eric Anton (Jena), Norman F. Johnson (Ohio), Ljubodrag Mihajlovic, Milka Glavendekic (Belgrad), Martin Schwarz (Linz), and Helmut Sebald (Munich) for species identification. We also thank Fanny Maunz and Franziska Unsicker for their help with building the flight-interception traps, and Agnes Fastnacht and the MPI-ICE greenhouse team. The work was funded by the DFG program 1374 Infrastructure-Biodiversity-Exploratories (WE 2618/9-1) and by the Max Planck Society. Fieldwork permits were issued by the responsible state environmental office of Thüringen. All experiments comply with current German law.

References

- Bernasconi Ockroy ML et al (2001) Response of natural populations of predators and parasitoids to artificially induced volatile emissions in maize plants (*Zea mays* L.). *Agric For Entomol* 3:201–209
- Bianchi FJ, Booij CJ, Tschamtké T (2006) Sustainable pest regulation in agricultural landscapes: a review on landscape composition, biodiversity and natural pest control. *Proc Biol Sci* 273:1715–1727
- Boch S et al (2013) High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic Appl Ecol* 14:496–505
- Böhme J (2005) Die Käfer Mitteleuropas, Band K-Katalog: Faunistische Übersicht. Elsevier, Spektrum, Heroldsberg
- Braasch J, Wimp GM, Kaplan I (2012) Testing for phytochemical synergism: arthropod community responses to induced plant volatile blends across crops. *J Chem Ecol* 38:1264–1275
- Brunet J, Fritz Ö, Richnau G (2010) Biodiversity in European beech forests—a review with recommendations for sustainable forest management. *Ecol Bull* 53:77–94
- Büchel K, Austel N, Mayer M, Gershenson J, Fenning TM, Meiners T (2013) Smelling the tree and the forest: elm background odours affect egg parasitoid orientation to herbivore induced terpenoids. *BioControl* 59:29–43
- Büchel K et al (2011) How plants give early herbivore alert: Volatile terpenoids attract parasitoids to egg-infested elms. *Basic Appl Ecol* 12:403–412
- Carroll MJ, Schmelz EA, Meagher RL, Teal PEA (2006) Attraction of *Spodoptera frugiperda* larvae to volatiles from herbivore-damaged maize seedlings. *J Chem Ecol* 32:1911–1924
- Chaplin-Kramer R, O'Rourke ME, Blitzer EJ, Kremen C (2011) A meta-analysis of crop pest and natural enemy response to landscape complexity. *Ecol Lett* 14:922–932
- Clavijo McCormick A, Unsicker SB, Gershenson J (2012) The specificity of herbivore-induced plant volatiles in attracting herbivore enemies. *Trends Plant Sci* 17:303–310
- Clavijo McCormick A et al (2014) Herbivore-induced volatile emission in black poplar: regulation and role in attracting herbivore enemies. *Plant Cell Environ* 37:1909–1923
- Danner H et al (2011) Four terpene synthases produce major compounds of the gypsy moth feeding-induced volatile blend of *Populus trichocarpa*. *Phytochemistry* 72:897–908
- Degen T, Bakalovic N, Bergvinson D, Turlings TC (2012) Differential performance and parasitism of caterpillars on maize inbred lines with distinctly different herbivore-induced volatile emissions. *PLoS ONE* 7:e47589
- Dicke M (2009) Behavioural and community ecology of plants that cry for help. *Plant, Cell Environ* 32:654–665
- Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. *Trends Ecol Evol* 11:255–260
- Dindorf T et al (2006) Significant light and temperature dependent monoterpene emissions from European beech (*Fagus sylvatica* L.) and their potential impact on the European volatile organic compound budget. *J Geophys Res Atmos* 111:D16305
- Dodd LE et al (2012) Forest structure affects trophic linkages: how silvicultural disturbance impacts bats and their insect prey. *For Ecol Manage* 267:262–270
- Dormann CF (2007) Promising the future? Global change projections of species distributions. *Basic Appl Ecol* 8:387–397
- Fischer M et al (2010) Implementing large-scale and long-term functional biodiversity research: the Biodiversity Exploratories. *Basic Appl Ecol* 11:473–485
- Fontana A, Reichelt M, Hempel S, Gershenson J, Unsicker SB (2009) The effects of arbuscular mycorrhizal fungi on direct and indirect defense metabolites of *Plantago lanceolata* L. *J Chem Ecol* 35:833–843
- Ghirardo A, Heller W, Fladung M, Schnitzler JP, Schroeder H (2012) Function of defensive volatiles in pedunculate oak (*Quercus robur*) is tricked by the moth *Tortrix viridana*. *Plant Cell Environ* 35:2192–2207
- Gladbach DJ, Holzschuh A, Scherber C, Thies C, Dormann CF, Tschamtké T (2011) Crop–noncrop spillover: arable fields affect trophic interactions on wild plants in surrounding habitats. *Oecologia* 166:433–441
- Goodwin BJ, Fahrig L (2002) Effect of landscape structure on the movement behaviour of a specialized goldenrod beetle, *Trirhabda borealis*. *Can J Zool* 80:24–35

- Gossner MM (2009) Light intensity affects spatial distribution of Heteroptera in deciduous forests. *Eur J Entomol* 106:241–252
- Haddad NM, Crutsinger GM, Gross K, Haarstad J, Tilman D (2011) Plant diversity and the stability of foodwebs. *Ecol Lett* 14:42–46
- Halitschke R, Stenberg JA, Kessler D, Kessler A, Baldwin IT (2008) Shared signals—‘alarm calls’ from plants increase apparency to herbivores and their enemies in nature. *Ecol Lett* 11:24–34
- Hannunen S (2002) Vegetation architecture and redistribution of insects moving on the plant surface. *Ecol Model* 155:149–157
- Hare JD (2011) Ecological role of volatiles produced by plants in response to damage by herbivorous insects. *Annu Rev Entomol* 56:161–180
- Heil M (2008) Indirect defence via tritrophic interactions. *New Phytol* 178:41–61
- Heil M, Silva Bueno JC (2007) Within-plant signaling by volatiles leads to induction and priming of an indirect plant defense in nature. *Proc Natl Acad Sci USA* 104:5467–5472
- Herbst C et al (2013) Land use intensification in grasslands: higher trophic levels are more negatively affected than lower trophic levels. *Entomol Exp Appl* 147:269–281
- Hilsczanski J et al (2005) Parasitoids (Hymenoptera, Ichneumonidae) of saproxylic beetles are affected by forest successional stage and dead wood characteristics in boreal spruce forest. *Biol Conserv* 126:456–464
- Holzke C, Dindorf T, Kesselmeier J, Kuhn U, Koppmann R (2006) Terpene emissions from European beech (*Fagus sylvatica* L.): pattern and emission behaviour over two vegetation periods. *J Atmos Chem* 55:81–102
- Jäkel A, Roth M (2004) Conversion of single-layered Scots pine monocultures into close-to-nature mixed hardwood forests: effects on parasitoid wasps as pest antagonists. *Eur J Forest Res* 123:203–212
- Jonsson M, Buckley HL, Case BS, Wratten SD, Hale RJ, Didham RK (2012) Agricultural intensification drives landscape-context effects on host–parasitoid interactions in agroecosystems. *J Appl Ecol* 49:706–714
- Joó É et al (2010) Variation in biogenic volatile organic compound emission pattern of *Fagus sylvatica* L. due to aphid infection. *Atmos Environ* 44:227–234
- Joulain D, König WA (1998) The atlas of spectral data of sesquiterpene hydrocarbons. EB-Verlag, Hamburg
- Kigathi RN, Weisser WW, Veit D, Gershenson J, Unsicker SB (2013) Plants suppress their emission of volatiles when growing with conspecifics. *J Chem Ecol* 39:537–545
- Klein AM, Steffan DI, Tschamtk T (2002) Predator–prey ratios on cocoa along a land-use gradient in Indonesia. *Biodivers Conserv* 11:683–693
- Klemola T, Ammunt T, Andersson T, Klemola N, Ruohomäki K (2012) Larval parasitism rate increases in herbivore-damaged trees: a field experiment with cyclic birch feeding moths. *Oikos* 121:1525–1531
- Lambin EF et al (2001) The causes of land-use and land-cover change: moving beyond the myths. *Glob Environ Change Hum Policy Dimens* 11:261–269
- Lange M et al (2011) The impact of forest management on litter-dwelling invertebrates: a subtropical–temperate contrast. *Biodivers Conserv* 20:2133–2147
- Letourneau DK, Bothwell SG, Stireman JO (2012) Perennial habitat fragments, parasitoid diversity and parasitism in ephemeral crops. *J Appl Ecol* 49:1405–1416
- Meiners T, Obermaier E (2004) Hide and seek on two spatial scales—vegetation structure effects herbivore oviposition and egg parasitism. *Basic Appl Ecol* 5:87–94
- Mulder C et al (2011) A belowground perspective on Dutch agroecosystems: how soil organisms interact to support ecosystem services. In: Woodward G (ed) *Advances in ecological research*, vol 44. Elsevier, San Diego, pp 277–357
- Mumm R, Dicke M (2010) Variation in natural plant products and the attraction of bodyguards involved in indirect plant defense. *Can J Zool* 88:628–667
- Obermaier E, Heisswolf A, Poethke HJ, Randlkofer B, Meiners T (2008) Plant architecture and vegetation structure: two ways for insect herbivores to escape parasitism. *Eur J Entomol* 105:233–240
- Paillet Y et al (2010) Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv Biol* 24:101–112
- R Development Team (2013) R: a language and environment for statistical computing, 3.0.2 edn. R Foundation for Statistical Computing, Vienna
- Rand TA, van Veen FJF, Tschamtk T (2012) Landscape complexity differentially benefits generalized fourth, over-specialized third, trophic-level natural enemies. *Ecography* 35:97–104
- Randlkofer B, Obermaier E, Casas J, Meiners T (2010) Connectivity counts: disentangling effects of vegetation structure elements on the searching movement of a parasitoid. *Ecol Entomol* 35:446–455
- Robert CA et al (2013) Genetically engineered maize plants reveal distinct costs and benefits of constitutive volatile emissions in the field. *Plant Biotechnol J* 11:628–639
- Sala OE et al (2000) Global biodiversity scenarios for the year 2100. *Science* 287:1770–1774
- Scanlon JT, Willis DE (1985) Calculation of flame ionization detector relative response factors using the effective carbon number concept. *J Chromatogr Sci* 23:333–340
- Schall P, Ammer C (2013) How to quantify forest management intensity in Central European forests. *Eur J Forest Res* 132:379–396
- Simpson M et al (2011) Insect attraction to synthetic herbivore-induced plant volatile-treated field crops. *Agric For Entomol* 13:45–57
- Sobek S, Scherber C, Steffan-Dewenter I, Tschamtk T (2009) Sapling herbivory, invertebrate herbivores and predators across a natural tree diversity gradient in Germany’s largest connected deciduous forest. *Oecologia* 160:279–288
- Springate ND, Basset Y (1996) Diel activity of arboreal arthropods associated with Papua New Guinean trees. *J Nat Hist* 30:101–112
- Tollsten L, Müller PM (1996) Volatile organic compounds emitted from beech leaves. *Phytochemistry* 43:759–762
- Tschamtk T, Klein AM, Krüess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity—ecosystem service management. *Ecol Lett* 8:857–874
- Turlings TCJ, Tumlinson JH (1992) Systemic release of chemical signals by herbivore-injured corn. *Proc Natl Acad Sci USA* 89:8399–8402
- Tylianakis JM, Romo CM (2010) Natural enemy diversity and biological control: making sense of the context-dependency. *Basic Appl Ecol* 11:657–668
- Tylianakis JM, Tschamtk T, Lewis OT (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* 445:202–205
- Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecol Lett* 11:1351–1363
- Unsicker SB, Kunert G, Gershenson J (2009) Protective perfumes: the role of vegetative volatiles in plant defense against herbivores. *Curr Opin Plant Biol* 12:479–485
- Wachmann E, Melber A, Deckert J (2004–2012) *Wanzen Band 1–5*. Goecke & Evers, Keltern