

# Small clear-cuts in managed forests support trap-nesting bees, wasps and their parasitoids

Tristan Eckerter<sup>a,\*</sup>, Veronika Braunisch<sup>b,c</sup>, Gesine Pufal<sup>a</sup>, Alexandra M. Klein<sup>a</sup>

<sup>a</sup> Chair of Nature Conservation and Landscape Ecology, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany

<sup>b</sup> Forest Nature Conservation, Forest Research Institute of Baden-Wuerttemberg FVA, Wonnhaldestr. 4, Freiburg 79100, Germany

<sup>c</sup> Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstr. 6, Bern 3012, Switzerland

## ARTICLE INFO

### Keywords:

Parasitism  
Light  
Network structure  
Forest management  
Conservation

## ABSTRACT

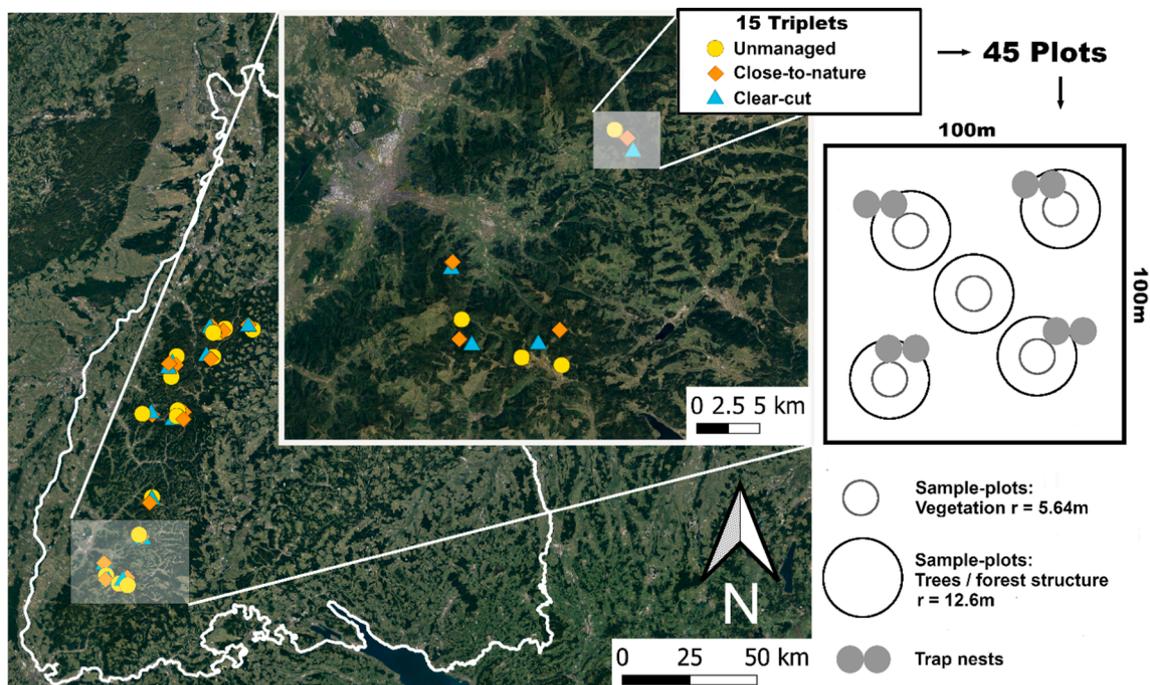
Most forests in Europe are managed but differ in their management intensity. This has different implications for structural- and environmental conditions and subsequently for the conservation of ecological communities, their interactions and functional consequences. Differences in silvicultural treatments, especially those promoting rare habitat structures, could foster trap-nesting bees, wasps and their parasitoids. We therefore tested how forest management and associated vegetation characteristics influence their abundance, richness, parasitism rates and the structure of the bee/wasp-parasitoid networks. Using 180 standardised trap nests on 45 forest plots (1 ha) in the Black Forest, Germany, we compared three management types representing a management intensity gradient: 'unmanaged', 'close-to-nature', and small 'clear-cuts'. Host and parasitoid abundance were highest on clear-cut plots and parasitoids were positively influenced by vegetation diversity, whereas bee and wasp richness were highest on clear-cut and close-to-nature plots. The wasp genus *Trypoxylon* had the highest abundance on clear-cut plots whereas abundance of *Deuteroagenia* was highest on the other management types. Unmanaged plots supported the lowest abundance and richness of the community. Whilst parasitism rate was not directly influenced by management, networks on clear-cut plots were less specialised and more linked. Our results highlight the importance of early successional habitats for trap-nesting bees, wasps and their parasitoids and the subsequent effect on the size and speciality of their networks. We demonstrate that different forest management types lead to changes in habitat suitability for some species, which translates to changes in host-parasitoid networks. Small-scale forest openings such as those created naturally by windthrows, and those created anthropogenically such as small-scale clear-cuts promote forest biodiversity and functions associated to Hymenoptera such as bees and wasps.

## 1. Introduction

In Europe, forests cover around 35% of land area and are mostly managed (Forest Europe, 2020). Different forest management interventions (e.g., clear-cuts vs. single tree removal) can have different implications for the change in forest structural and tree compositional conditions and hence influence ecological communities and forest biodiversity (Chaudhary et al., 2016). Generally, managed forests lack structural elements found in unmanaged and old-growth forests (Bauhus et al., 2009), as natural disturbances like windthrow and natural succession to the forest climax stages are suppressed (Jactel et al., 2009), which often reflects in lower biodiversity (Horák et al., 2019; Paillet et al., 2010).

That is why forest reserves are established, which are not managed for timber production to conserve and foster natural forest succession and the dieback of trees (Bollmann and Braunisch, 2013). However, their share amounts to only 0.7% of the European forest surface (Sabatini et al., 2018). In the remaining area, the magnitude and direction of how forest management influences forest structures, tree composition and associated biodiversity largely varies with the management regime (Schall et al., 2018). In most European countries, "close-to-nature silviculture", with permanent forest cover, selective cutting and natural regeneration (Brang et al., 2014), has replaced even-aged forestry with clearcutting and is now the predominant silvicultural system (Bauhus et al., 2013). This management, introduced to ensure multiple forest functions like wood production, soil conservation and

\* Corresponding author at: Department of Nature Conservation and Landscape Ecology, University of Freiburg, Tennenbacherstr. 4, 79106 Freiburg, Germany.  
E-mail address: [Tristan.Eckerter@gmx.de](mailto:Tristan.Eckerter@gmx.de) (T. Eckerter).



**Fig. 1.** On the left-hand side the study area in the Black Forest, Southwestern Germany, with 45 1-ha plots underlying three different management types: Unmanaged forests, close-to-nature silviculture and small (0.5–1 ha) clear-cuts. Three plots, one of each management type are arranged in “triplets” with similar forest and site conditions and with a distance to each other of 500–5000 m. On the right-hand side, the sampling design for collecting vegetation data (open circles, small radius) and forest structure (open circles, large radius), as well as the location of the trap nests in each plot is depicted. Map Data: Google.

conservation of biodiversity (Bauhus et al., 2013), has led to an increase in vertical structural heterogeneity at the stand scale, but also to a structural homogenisation at the landscape scale. As a consequence, close-to-nature-forests often lack open areas and early successional stages as created by natural or anthropogenic disturbances, as well as the associated biodiversity. However, these early successional stages, can be beneficial for bees and wasps as they increase flowering resources (Rubene et al., 2015; Sebek et al., 2016). Furthermore, by enhancing floral resources, the longevity of parasitoid wasps that use nectar resources is extended (Russell, 2015), altering the regulatory capacity of these parasitoids (Führer, 2000). The way and intensity forests are managed are thus expected to have a major influence on ecological communities, with a diversity of different intervention types, and an associated diversity of structural conditions, increasing functional diversity.

Beside diversity, forest management also changes key ecosystem functions such as herbivory (Gossner et al., 2014) and predation (Grushecky et al., 1998) but the role of forest management in other ecosystem functions such as insect pest control mediated through parasitism is only poorly understood (Pohjanmies et al., 2017). A study investigated the role of forest management on the functional diversity of parasite flies, but did not address the change of the associated function (Rodríguez et al., 2019). Thus, questions regarding the influence of forest management on ecological communities and the ecosystem function parasitism remain unanswered.

Trap-nesting bees, wasps and their natural enemies represent a model system to observe and quantify host-parasitoid networks and are useful bioindicators for environmental change (Staab et al., 2018). Trap-nesting Hymenoptera often have short foraging distances (Hofmann et al., 2020) and hence are responsive to changes in their nearby environment. While solitary bees are key pollinators (Klein et al., 2007), solitary wasps and parasitoids are important agents of biological control (Hawkins, 1994). Host-parasitoid network structure can differ along environmental gradients (Tylanakis and Morris, 2017) and is sensitive to species richness loss (Landi et al., 2018). Failing to understand how forest management influences these networks through changes in

habitats structure, quality and species richness (Paillet et al., 2010) could have counterproductive side effects on conservation, since networks hold key information on the stability and functionality of the ecosystem (Librán-Embúid et al., 2021).

To study the effect of forest management on host-parasitoid interactions, abundance and richness, we used standardized trap nests to sample trap-nesting species and their parasitoids (Staab et al., 2018) in the Black Forest (Germany). We sampled on 45 forest plots with three different management types, representing a gradient of forest management intensity: Unmanaged forests, Close-to-nature silviculture, and small clear-cuts, and tested the following hypotheses:

- Changes in biotic and abiotic conditions after implementation of small clear-cuts promote the abundance and richness of trap-nesting bees, wasps and their parasitoids.
- Forest management influences parasitism rate.
- Forest management alters network structure and indices such as H2 and linkage density.
- Providing early successional stages within a homogeneous forest matrix promotes not only bee, wasp and natural enemy diversity but also network size.

## 2. Methods

### 2.1. Study area

This study was conducted in the Black Forest (Baden-Württemberg, Germany) (Fig. 1), a low mountain range with a mixed coniferous forest (area ca. 7000 km<sup>2</sup>), dominated by Norway spruce (*Picea abies*). Beech (*Fagus sylvatica*) is the most common broad-leaved tree (BWI3: Thünen-Institut). Mean annual temperatures range from 3.9 °C to 8.1 °C (DWDa, 2020) and precipitation from 1000 mm to around 2100 mm (DWD, 2020).

To study the effect of management intensity, 45 1-hectare plots with three different management types were established in 2018. Plots were selected in triplets, similar in site conditions, main forest type and

exposition, each comprising 1) 1 ha unmanaged forest, 2) 1 ha close-to-nature silviculture, and 3) 1 ha with a small clear-cut.

Unmanaged forest plots were located in strictly protected areas with no forestry interventions for the last 15–107 years, close-to-nature plots have been and are continued to be managed according to the principles of “close-to-nature silviculture” (Bauhus et al., 2009), while on clear-cut plots, small experimental clear-cuts of 0.5–1.0 ha in size were logged and cleared in autumn 2018.

The plots of a triplet were selected within a distance of 500 to 5000 m distance to avoid spill-over effects, while at the same time referring to similar landscape conditions and the associated species pool. Triplets were replicated across the entire black forest within an elevational range between 668 m and 1328 m (a.s.l.).

## 2.2. Environmental variables

To characterise environmental conditions, five permanent sample-plots per 1-ha plot were established, at which several biotic and abiotic variables were measured within different radii (Fig. 1). Vegetation was recorded within  $r = 5.64$  m, corresponding to an area of  $a = 100$  m<sup>2</sup>. Vascular plants were identified to species level, the percent cover of each species per sample-plot was estimated and later extrapolated to hectare level, distinguishing between tree (>5 m), shrub (1.5 – 5 m) and herb layer (<1.5 m). In addition, we calculated the Shannon Diversity Index for the vegetation for every plot (from now vegetation diversity). Trees and associated forest structure were mapped within  $r = 12.6$  m ( $a = 500$  m<sup>2</sup>), following the forest inventory method of the forest reserve monitoring of Baden-Württemberg (Wevell von Krüger et al., 2015). As some Hymenoptera rely on tree resin as nesting material (i.e., *Passaloecus* spp.), we used the cover of resin producing coniferous trees (from now on “cover of coniferous trees”), to see whether nesting materials in forests play a role in the abundance (number of brood cells) of trap-nesting Hymenoptera.

We used light and elevation as abiotic variables since they structure host-parasitoid interactions (Kehoe et al., 2020; Staab et al., 2016). The mean light coefficient per 1-ha plot (defined as the percentage of canopy without cover) was calculated based on fish-eye photographs (CI-110 Plant Canopy Imager) taken at the centre of every sample-plot during overcast conditions and analysed following Frazer et al. (1997). Mean elevation per plot was taken from a digital elevation model (DHM 25), at the centre of the five sample-plots. All environmental variables were averaged from the five sample plots creating one value per plot.

## 2.3. Study organism and sampling

Study organisms in this study were herbivore bees that live of pollen and nectar, predatory wasps that hunt spiders, lepidoptera larvae and aphids and their parasitoids that are parasitoids (85%), consuming the hosts and cleptoparasitoids (15%), consuming the food of the hosts. Both feeding strategies lead to the death of the host (Staab et al., 2016). For simplicity we refer to them as parasitoids in this study. Trap nests were exposed from mid-April to mid-October in 2019. On each plot, we deployed four trap nests (a total of 180), each consisting of two 24 cm long PVC tubes with a diameter of 10 cm, filled with a random mix of reed internodes (*Phragmites australis*) (21 cm long; diameter 0.2–1 cm). Two trap nests were fixated on a pole at 1,5 m above ground, the other two were tied to trees at the same height. Poles were situated at the two outmost sample plots, while the other trap nests were placed near the two inner sample plots (Fig. 1). Traps were oriented to the east–west-axis to minimize irregular colonization (Martins et al., 2012). After retrieving the trap nests, reed internodes were inspected and all nests were cut open. For every nest, number of host brood cells and number of parasitised cells were counted per species. Afterwards they were placed into individual glass vials and stored in a 4 °C fridge for three months to initiate diapause. Offspring was reared at room temperature. Emerged host species were identified to species level (Amiet et al., 2004, 1996;

**Table 1**

Final generalised linear mixed models after model selection showing the relationship between biotic, abiotic and management-related predictor variables and the host and parasite community. Response variables and significant terms are in bold. We defined clear-cut plots as the intercept. Host and parasite abundance are defined as number of host cells and number of parasitised cells, respectively. P – values of abundance models are still significant after Benjamini-Hochberg correction.

| Model and tested variable     | Estimate ± SE    | z-value | P-value       |
|-------------------------------|------------------|---------|---------------|
| <b>Host abundance</b>         |                  |         |               |
| Management: Close-to-nature   | −0.6484 ± 0.1774 | −3.654  | < 0.001       |
| Management: Unmanaged         | −0.9491 ± 0.1819 | −5.218  | < 0.001       |
| <b>Passaloecus abundance</b>  |                  |         |               |
| Vegetation diversity          | 1.4842 ± 0.64276 | 2.309   | <b>0.0209</b> |
| Conifer cover                 | 0.02166 ± 0.0105 | 2.055   | <b>0.0399</b> |
| <b>Deuteragenia abundance</b> |                  |         |               |
| Management: Close-to-nature   | 0.8104 ± 0.2422  | 3.346   | <b>0.0008</b> |
| Management: Unmanaged         | 0.7230 ± 0.2426  | 2.980   | <b>0.0028</b> |
| <b>Trypoxylon abundance</b>   |                  |         |               |
| Management: Close-to-nature   | −1.9361 ± 0.3937 | −4.918  | < 0.001       |
| Management: Unmanaged         | −3.0981 ± 0.4262 | −7.270  | < 0.001       |
| Vegetation diversity          | 1.6998 ± 0.5725  | 2.969   | <b>0.0029</b> |
| Exposition: East              | 1.1202 ± 0.6693  | 1.674   | 0.0942        |
| Exposition: South             | 1.6909 ± 0.5527  | 3.059   | <b>0.0022</b> |
| Exposition west               | 0.8070 ± 0.6174  | 1.307   | 0.1911        |
| <b>Host richness</b>          |                  |         |               |
| Host abundance                | 0.0011 ± 0.00004 | 2.413   | <b>0.0158</b> |
| Management: Close-to-nature   | −0.1511 ± 0.1494 | −1.011  | 0.3119        |
| Management: Unmanaged         | −0.5929 ± 0.1828 | −3.243  | <b>0.0011</b> |
| <b>Parasite richness</b>      |                  |         |               |
| Host richness                 | 0.1037 ± 0.0226  | 4.573   | < 0.001       |
| <b>Parasitism rate</b>        |                  |         |               |
| Parasite abundance            | 0.0021 ± 0.0003  | 6.997   | < 0.001       |
| Exposition: East              | 0.04563 ± 0.0185 | 2.458   | <b>0.014</b>  |
| Exposition: South             | −0.0122 ± 0.0146 | −0.838  | 0.402         |
| Exposition: West              | 0.0088 ± 0.0172  | 0.515   | 0.0606        |

Jacobs, 2007; Neumeyer, 2019; Wolf, 1972), while the parasitoids were identified to species level if possible (66% of all parasitoid species) and otherwise assigned to morphospecies (33% of all parasitoid species) (Bogusch, 2021; Broad et al., 2018; Fitton et al., 1988; Goulet and Huber, 1993; Johansson and van Achterberg, 2016; Kunz, 1994; Paukunen et al., 2015; Unwin, 1981; Wiesbauer et al., 2020) (see Table A5). Hosts and parasitoids were assigned to each other when the host and enemy hatched from the same nest. In the rare case when all host cells were parasitised, we were able to assign the host species by inspecting the nest diameter, food resources, nesting material as well as other nests from the same trap. Voucher specimens are deposited at the University of Freiburg.

## 2.4. Statistical analyses

### 2.4.1. Management characteristics

Statistical analyses were conducted with R (R Core Team, 2021). Preceding analyses, data from the four trap nests from each plot were pooled resulting in one value per plot. To assess differences in environmental attributes and management types, mixed effect models (glmmTMB-Package) (Brooks et al., 2020) were performed with management as fixed effect and triplet as random intercept. Response variables (Table A1) were: vegetation diversity, deadwood (m<sup>3</sup>) with a Gaussian distribution and cover of tree, shrub and herb layer (%) and light coefficient (%), all with beta family error distribution and ziformula= $\sim 1$  to account for zero-inflation.

**Table A1**

Used environmental variable, description and usage in models. Sample plot size refers to the radius the variable was mapped (Fig. 1). All environmental variables were averaged from the five sample plots creating one value per plot.

| Variable             | Description   | Unit               | Usage                          | Sample plot size |
|----------------------|---|--------------------|--------------------------------|------------------|
| Light coefficient    | Mean canopy without cover   | %                  | Characterise management        | 5.64 m           |
| Vegetation diversity | Shannon index of all vascular plants per plot                         | Index              | Glmm, PERMANOVA                | 5.64 m           |
| Elevation            | Mean elevation per plot from a digital elevation model                | m                  | Glmm, PERMANOVA                | 5.64 m           |
| Tree layer cover     | Mean percent cover of vascular plants > 5 m height                    | %                  | Characterise management        | 5.64 m           |
| Shrub layer cover    | Mean percent cover of vascular plants 1.5 m-5 m height                | %                  | Characterise management        | 5.64 m           |
| Herb layer cover     | Mean percent cover of vascular plants < 1.5 m height                  | %                  | Glmm, PERMANOVA                | 5.64 m           |
| Conifer cover        | Mean percent cover of coniferous trees which produce resin            | %                  | Glmm, PERMANOVA                | 5.64 m           |
| Deadwood             | Deadwood volume of standing and lying deadwood of all decaying stages | m <sup>3</sup> /ha | Characterise 12.6 m management |                  |
| Exposition           | Majority of exposition on the plot: North; East; South; West          | Categorical        | Glmm, PERMANOVA                |                  |
| Management           | Management type Unmanaged; Close-to-nature; Clear-cut                 | Categorical        | Glmm, PERMANOVA                |                  |

#### 2.4.2. Host-parasitoid community

To compare sampling efficiency for management types, we calculated rarefaction curves and Chao1 estimators with the iNEXT-package (Hsieh et al., 2020). To assess the influence of management and environmental variables on the response variables host abundance (number of brood cells), host richness, parasite richness, parasitism rate and the abundance of the three most common wasp genera of our study (*Trypoxylon*, *Passaloecus* and *Deuteroagenia*), we used generalised linear mixed effect models (GLMM's) with Benjamini-Hochberg correction (Verhoeven et al., 2005). Environmental variables were pooled to plot level and tested for multicollinearity with the cor-function. Only variables with  $r < 0.7$  (Pearson) were used in models (Fig. A1). After considering multicollinearity, the relationship between management and the environment and known relationships between host, parasitoids and their environment (from literature), we used management, vegetation diversity, elevation, herb layer cover, cover of coniferous trees and exposition as fixed effects in the models (Table A1). (1|Triplet/Plot\_ID) was used as a random effect to incorporate the hierarchical structure of the experiment and account for overdispersion with plot\_ID as an observation level random effect. For abundance and richness responses, we used a Poisson error distribution and a gaussian error distribution for parasitism rate. Models were built using stepwise-backwards selection where we started with a full model and step by step excluded non-significant terms. Models were validated using the DHARMA-Package (Hartig, 2021). Post-hoc tests were performed to test the effect of management on host abundance and parasitism rate (emmeans-Package) (Lenth, 2020). A Moran's I Test was performed on the model residuals to test for spatial autocorrelation, using the DHARMA-Package. For all models we could not reject the null hypothesis ( $p > 0.05$ ).

Differences in community structure per management type and the influence of environmental variables were analysed with non-metric

**Table A2**

Post Hoc Tukey Test of the emmeans-Package of environmental variables (Table A1) influenced by management type.

| Contrast                     | Estimate ± SE   | df | t. ratio | P- value |
|------------------------------|-----------------|----|----------|----------|
| <b>Light coefficient (%)</b> |                 |    |          |          |
| Clear-cut – Close-to-nature  | 2.756 ± 0.224   | 40 | 12.288   | <0.0001  |
| Clear-cut – Unmanaged        | 2.485 ± 0.204   | 40 | 12.207   | <0.0001  |
| Close-to-nature – Unmanaged  | -0.272 ± 0.217  | 40 | -1.248   | 0.4323   |
| <b>Deadwood (Vol)</b>        |                 |    |          |          |
| Clear-cut – Close-to-nature  | -0.0756 ± 0.269 | 40 | -0.282   | 0.9573   |
| Clear-cut – Unmanaged        | -1.4380 ± 0.269 | 40 | -5353    | <0.0001  |
| Close-to-nature – Unmanaged  | -1.3623 ± 0.269 | 40 | -5072    | <0.0001  |
| <b>Shrub cover (%)</b>       |                 |    |          |          |
| Clear-cut – Close-to-nature  | -0.333 ± 0.271  | 40 | -1.230   | 0.4427   |
| Clear-cut – Unmanaged        | -0.947 ± 0.258  | 40 | -3.677   | 0.0005   |
| Close-to-nature – Unmanaged  | -0.614 ± 0.244  | 40 | -2.512   | 0.0418   |
| <b>Tree cover (%)</b>        |                 |    |          |          |
| Clear-cut – Close-to-nature  | -2.390 ± 0.397  | 40 | -6.019   | <0.0001  |
| Clear-cut – Unmanaged        | -2.269 ± 0.379  | 40 | -5.988   | <0.0001  |
| Close-to-nature – Unmanaged  | 0.122 ± 0.307   | 40 | 0.396    | 0.9173   |

multidimensional scaling (NMDS) (vegan-Package) (Oksanen et al., 2021). Ordinations were based on Bray-Curtis distances. Effects of the environment on hosts and parasitoids were further analysed with a PERMANOVA using the adonis2-function (vegan-Package) with the same variables as in the mixed-effect models (Table A1).

Host-parasitoid networks were illustrated and analysed with the bipartite-Package (Dormann et al., 2008). As network descriptors, we used complementary specialisation (H2) (Blüthgen et al., 2006) and weighted linkage density (LD) (Bersier et al., 2002). H2 describes the exclusiveness of interactions at the network level independent of the number of observations. LD was used as a quantitative descriptor to inspect network stability (Bersier et al., 2002). Networks were pooled per management into three meta-networks for visual interpretation (Fig. A2). Differences in network structure within each management type were tested with plot-level networks. We constructed 15 networks from clear-cut plots, followed by close-to-nature plots with 12 and unmanaged plots with 8 networks. In the remaining plots, interactions were too scarce to build meaningful networks. To assess mean differences of the networks descriptors H2 and LD between management types, networks were tested against null models, correcting for differences in species numbers and abundance, to test whether differences significantly differed from network properties expected by chance (Dormann et al., 2009).

### 3. Results

#### 3.1. Management characteristics

Clear-cut plots were characterised by a high light coefficient (Table A2), while close-to-nature and unmanaged plots had lower light conditions. Unmanaged plots had a higher shrub cover (Table A2) and more deadwood (Table A2) compared to close-to-nature and clear-cut plots. The percent cover of trees was lowest on clear-cut plots (Table A2). There was no relationship between management type and vegetation diversity ( $p > 0.05$ ).

#### 3.2. Host-parasitoid community

We collected 7746 brood cells belonging to 37 host species (Table A3). 878 cells (11%) were parasitised by 27 parasitoid species (66%) and morphospecies (33%). On unmanaged plots 12% of host species were red listed. Close-to-nature plots harboured 13% and clear-cut plots 16% red listed host species (Table A3). The most common host

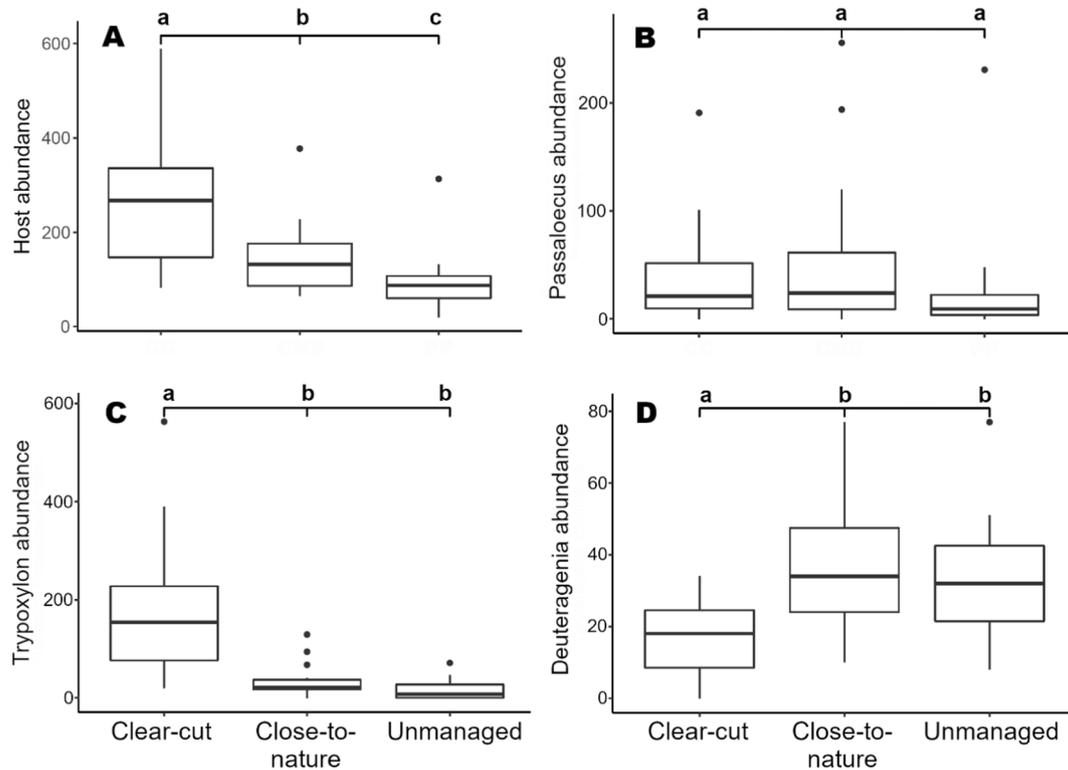
**Table A3**

Host and parasite abundance for the different management types and the corresponding network number for Fig. A2. Abundance of hosts and parasites is our definition of number of host brood cells and number of parasitised cells respectively. Endangerment Status of Red list: “n.e” not endangered, “1” threatened with extinction, “2” severely endangered, “3” endangered, “e.p” endangerment probable, “r” rare, “w.l” warning list (for wasps Schmid-Egger, 2010; for bees Westrich et al. 2011).

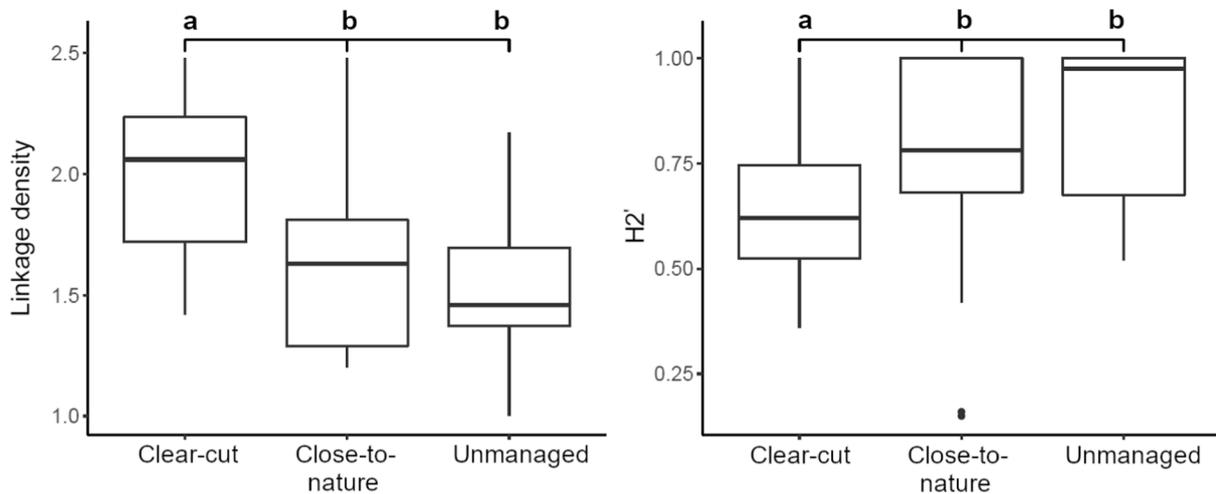
| Host species                               | Corresponding network number | Abundance on unmanaged plots | Abundance on close-to-nature plots | Abundance on clear-cut plots | Red list status |
|--|------------------------------|------------------------------|------------------------------------|------------------------------|-----------------|
| <i>Ampulex fasciata</i>                    |                              | 2                            | 8                                  | 12                           | 3               |
| <i>Ancistrocerus claripennis</i>           | 1                            | 0                            | 7                                  | 6                            | n.e.            |
| <i>Ancistrocerus gazella</i>               | 2                            | 2                            | 3                                  | 6                            | n.e.            |
| <i>Ancistrocerus nigricornis</i>           |                              | 1                            | 7                                  | 10                           | n.e.            |
| <i>Ancistrocerus renimacula</i>            | 3                            | 0                            | 1                                  | 8                            | 2               |
| <i>Ancistrocerus trifasciatus</i>          | 4                            | 135                          | 74                                 | 38                           | n.e.            |
| <i>Auplopus carbonarius</i>                |                              | 0                            | 4                                  | 0                            | n.e.            |
| <i>Deuteraenia bifasciata</i>              | 5                            | 10                           | 0                                  | 32                           | n.e.            |
| <i>Deuteraenia subintermedia</i>           | 6                            | 442                          | 479                                | 139                          | n.e.            |
| <i>Deuteraenia variegata</i>               |                              | 0                            | 0                                  | 10                           | n.e.            |
| <i>Hylaeus communis</i>                    |                              | 0                            | 8                                  | 11                           | n.e.            |
| <i>Hylaeus confusus</i>                    | 7                            | 11                           | 15                                 | 0                            | n.e.            |
| <i>Hylaeus difformis</i>                   | 8                            | 0                            | 42                                 | 127                          | n.e.            |
| <i>Nitela fallax</i>                       | 9                            | 0                            | 6                                  | 0                            | 2               |
| <i>Osmia caerulescens</i>                  | 11                           | 0                            | 0                                  | 2                            | n.e.            |
| <i>Passaloecus brevilabris</i>             | 12                           | 0                            | 1                                  | 31                           | n.e.            |
| <i>Passaloecus clypealis</i>               |                              | 6                            | 0                                  | 2                            | w.l.            |
| <i>Passaloecus corniger</i>                | 13                           | 16                           | 173                                | 50                           | n.e.            |
| <i>Passaloecus eremita</i>                 | 14                           | 0                            | 20                                 | 11                           | n.e.            |
| <i>Passaloecus gracilis</i>                |                              | 0                            | 0                                  | 2                            | n.e.            |
| <i>Passaloecus insignis</i>                | 15                           | 332                          | 435                                | 284                          | n.e.            |
| <i>Pemphredon baltica</i>                  |                              | 0                            | 0                                  | 3                            | e.p.            |
| <i>Pemphredon lugens</i>                   | 16                           | 7                            | 4                                  | 11                           | n.e.            |
| <i>Pemphredon lugubris</i>                 | 17                           | 0                            | 5                                  | 0                            | n.e.            |
| <i>Pemphredon morio</i>                    |                              | 0                            | 4                                  | 0                            | n.e.            |
| <i>Rhopalum clavipes</i>                   |                              | 3                            | 4                                  | 0                            | n.e.            |
| <i>Spilomena troglodytes</i>               | 10                           | 15                           | 1                                  | 4                            | n.e.            |
| <i>Symmorphus allobrogus</i>               |                              | 0                            | 0                                  | 24                           | n.e.            |
| <i>Symmorphus crassicornis</i>             | 18                           | 0                            | 11                                 | 28                           | n.e.            |
| <i>Symmorphus gracilis</i>                 | 19                           | 0                            | 17                                 | 11                           | n.e.            |
| <i>Trypoxylon beaumonti</i>                | 20                           | 0                            | 32                                 | 61                           | n.e.            |
| <i>Trypoxylon clavicerum</i>               | 21                           | 102                          | 182                                | 149                          | n.e.            |
| <i>Trypoxylon deceptorium / attenuatum</i> | 22                           | 13                           | 7                                  | 313                          | n.e.            |
| <i>Trypoxylon figulus / medium</i>         | 23                           | 43                           | 125                                | 1067                         | n.e.            |
| <i>Trypoxylon kolazyi</i>                  | 24                           | 0                            | 9                                  | 8                            | w.l.            |
| <i>Trypoxylon kostylevi</i>                |                              | 0                            | 2                                  | 4                            | n.e.            |
| <i>Trypoxylon minus</i>                    | 25                           | 18                           | 3                                  | 79                           | n.e.            |
| <i>Dermestidae larva_sp1</i>               | 26                           | 0                            | 0                                  | 2                            |                 |
| <i>Dermestidae_sp1</i>                     | 27                           | 0                            | 0                                  | 1                            |                 |
| <i>Chalcidoidea_sp1</i>                    | 28                           | 0                            | 0                                  | 1                            |                 |
| <i>Trichrysis cyanea</i>                   | 29                           | 6                            | 0                                  | 135                          |                 |
| <i>Omalus aeneus</i>                       | 30                           | 3                            | 10                                 | 9                            |                 |
| <i>Omalus puncticollis</i>                 | 31                           | 19                           | 22                                 | 48                           |                 |
| <i>Pseudomalus violaceus</i>               | 32                           | 2                            | 0                                  | 2                            |                 |
| <i>Pseudomalus pusillus</i>                | 33                           | 0                            | 1                                  | 0                            |                 |
| <i>Pseudomalus auratus</i>                 | 34                           | 1                            | 0                                  | 3                            |                 |
| <i>Chrysis ignita cf</i>                   | 35                           | 11                           | 17                                 | 7                            |                 |
| <i>Chrysis fulgida</i>                     | 36                           | 0                            | 1                                  | 0                            |                 |
| <i>Chrysis clarinicollis cf</i>            | 37                           | 0                            | 0                                  | 2                            |                 |
| <i>Pseudomalus triangulifer</i>            | 38                           | 0                            | 1                                  | 1                            |                 |
| <i>Philocetes bidentulus cf</i>            | 39                           | 0                            | 0                                  | 1                            |                 |
| <i>Sarcophagidae_sp1</i>                   | 40                           | 6                            | 3                                  | 2                            |                 |
| <i>Tachinidae_sp1</i>                      | 41                           | 0                            | 1                                  | 0                            |                 |
| <i>Tachinidae_sp2</i>                      | 42                           | 3                            | 2                                  | 0                            |                 |
| <i>Sarcophagidae_sp2</i>                   | 43                           | 18                           | 18                                 | 72                           |                 |
| <i>Gasteruption assectator</i>             | 44                           | 1                            | 4                                  | 15                           |                 |
| <i>Nematopodius debilis</i>                | 45                           | 10                           | 28                                 | 7                            |                 |
| <i>Poemenia collaris</i>                   | 46                           | 21                           | 50                                 | 2                            |                 |
| <i>Poemenia brachyura cf</i>               | 47                           | 2                            | 3                                  | 0                            |                 |
| <i>Paraperithous sp.</i>                   | 48                           | 0                            | 0                                  | 2                            |                 |
| <i>Ephialtes manifestator</i>              | 49                           | 2                            | 4                                  | 2                            |                 |
| <i>Ichneumonidae_sp6</i>                   | 50                           | 0                            | 2                                  | 6                            |                 |
| <i>Ichneumonidae_sp7</i>                   | 51                           | 0                            | 2                                  | 0                            |                 |
| <i>Melittobia acasta</i>                   | 52                           | 18                           | 29                                 | 235                          |                 |

genera were *Trypoxylon* (3499 cells / 7 host species), *Passaloecus* (1886 / 6) and *Deuteraenia* (1286 / 3) for wasps and *Hylaeus* (258 / 3) for bees. Parasitoid species belonged to Hymenoptera (743 / 21), Diptera (132 / 4) and Coleoptera (3 cells / 2 morphotypes) (Table A3).

The species richness estimator and species accumulation curves indicated high overall sampling efficiency across management types (unmanaged = 96%, close-to-nature = 80% and clear-cut = 96%).



**Fig. 2.** A: Boxplots for host abundance for the different management types. Boxes represent the interquartile range, the bold line represents the median, lower and upper whiskers correspond to the 25th and 75th percentile, respectively. Boxes with different letters indicate a significant difference, while the same letter indicates a non-significant difference. Pairwise differences were tested with a Post Hoc Tukey Test with the emmeans - Package. B-D: Boxplots for the abundance of the three most common genera for the different management types. Different responses for the genera for the management types become visible.



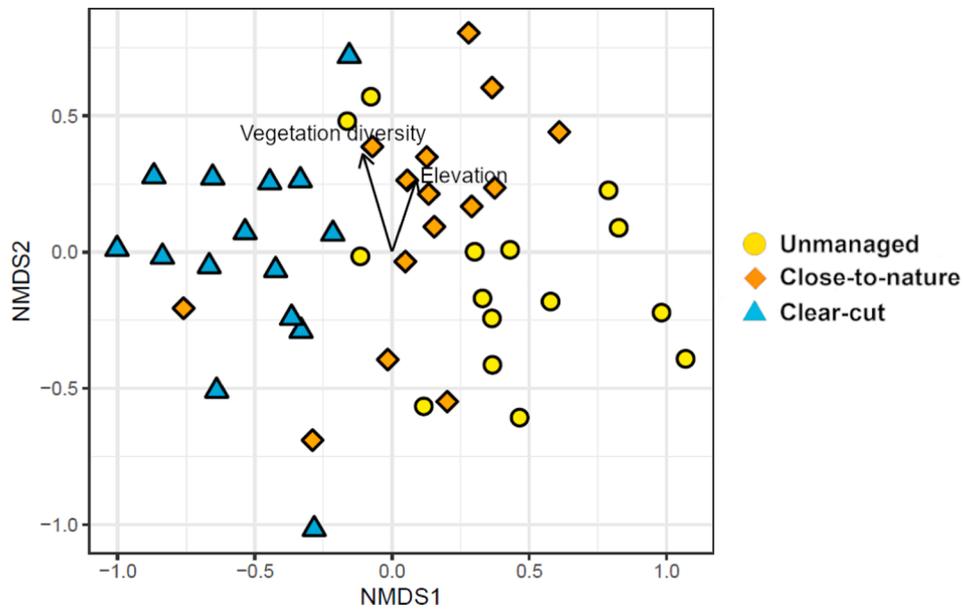
**Fig. 3.** Results from null model test of the bipartite package for the two network indices linkage density and H2 for the different management types. Boxes represent the interquartile range, the bold line represents the median, lower and upper whiskers correspond to the 25th and 75th percentile, respectively. Boxes with different letters indicate a significant difference, while the same letter indicates a non-significant difference. Significance testing was done with the help of null-model simulations based on Dormann et al. (2009).

### 3.3. Effects of management and environment

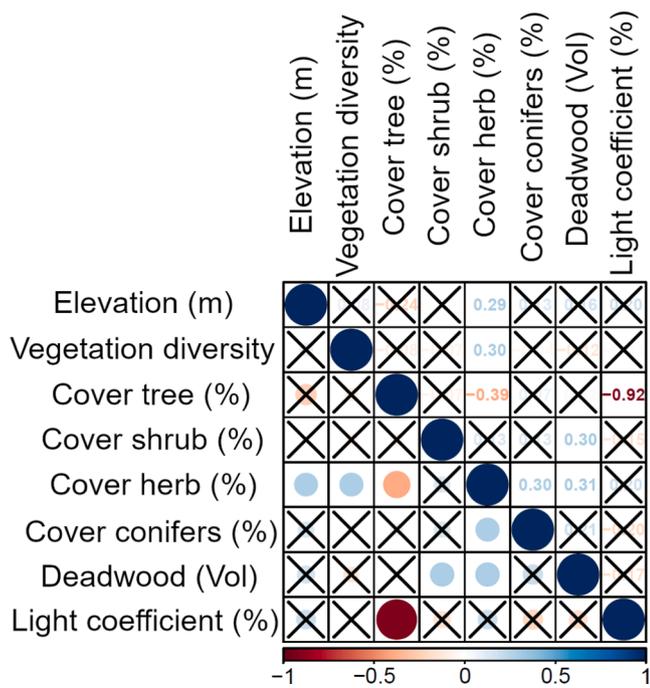
Host abundance was higher on clear-cut plots (Post Hoc both;  $p < 0.001$ ) ( $n = 4108$ ; mean =  $274 \pm 142$ ) compared to close-to-nature (2206;  $147 \pm 82$ ) and unmanaged (1432;  $95 \pm 68$ ) plots. *Passaloeocus* abundance increased with vegetation diversity and increased with high cover of resin producing conifers, but did not differ between management (Fig. 2). *Deuteragenia* abundance was highest on close-to-nature and unmanaged plots (Post Hoc; clear-cut – close-to-nature,  $p = 0.05$ ;

clear-cut – unmanaged,  $p = 0.01$ ; close-to-nature – unmanaged,  $p > 0.05$ ) and could not be explained by environmental variables. *Trypoxylon* abundance was positively related to vegetation diversity (Table 1), highest on clear-cut plots and lowest on unmanaged plots (Post Hoc; clear-cut – close-to-nature,  $p < 0.001$ ; clear-cut – unmanaged,  $p < 0.001$ ; close-to-nature – unmanaged,  $p = 0.02$ ) and higher on south exposed plots (Post Hoc; north – south,  $p = 0.02$ ) (Table 1).

Host species richness was highest on clear-cut and close-to-nature plots (Post Hoc; close-to-nature – clear-cut,  $p > 0.05$ ; unmanaged –



**Fig. 4.** Non-metric dimensional scaling (NMDS) of host and parasitoid communities in the different management types. Using the Bray-Curtis-Distance. Stress factor is 0.22. Arrows show significant variables of the continuous variables from the PERMANOVA analysis.



**Fig. A1.** Pearson correlation of continuous variables used as fixed effects in the models in this study. Terms with  $r > |0.7|$  were not used in the same model to avoid problems with collinearity. Crossed out boxes indicate low correlation ( $\leq 0.20$ ) between the variables.

close-to-nature,  $p = 0.009$ ; clear-cut – unmanaged,  $p = 0.003$ ) (Fig. 2 E) and positively correlated with host abundance (Table 1).

Parasitoid abundance was higher on clear-cut plots (555;  $37 \pm 24.8$ ) compared to unmanaged plots (123;  $8.2 \pm 8.6$ ) and close-to-nature plots (200;  $13.3 \pm 7.7$ ). Parasitoid richness increased with host richness (Table 1).

### 3.4. Changes in community composition and network structure

Community structure of host-parasitoid communities differed

between management types (Fig. 4). The PERMANOVA revealed a significant influence of management ( $p = 0.001$ ), vegetation diversity ( $p = 0.030$ ), and elevation ( $p = 0.001$ ) on the structure of the host community, while the parasitoid community was mainly structured by management ( $p = 0.001$ ) and elevation ( $p = 0.001$ ) (Table A4).

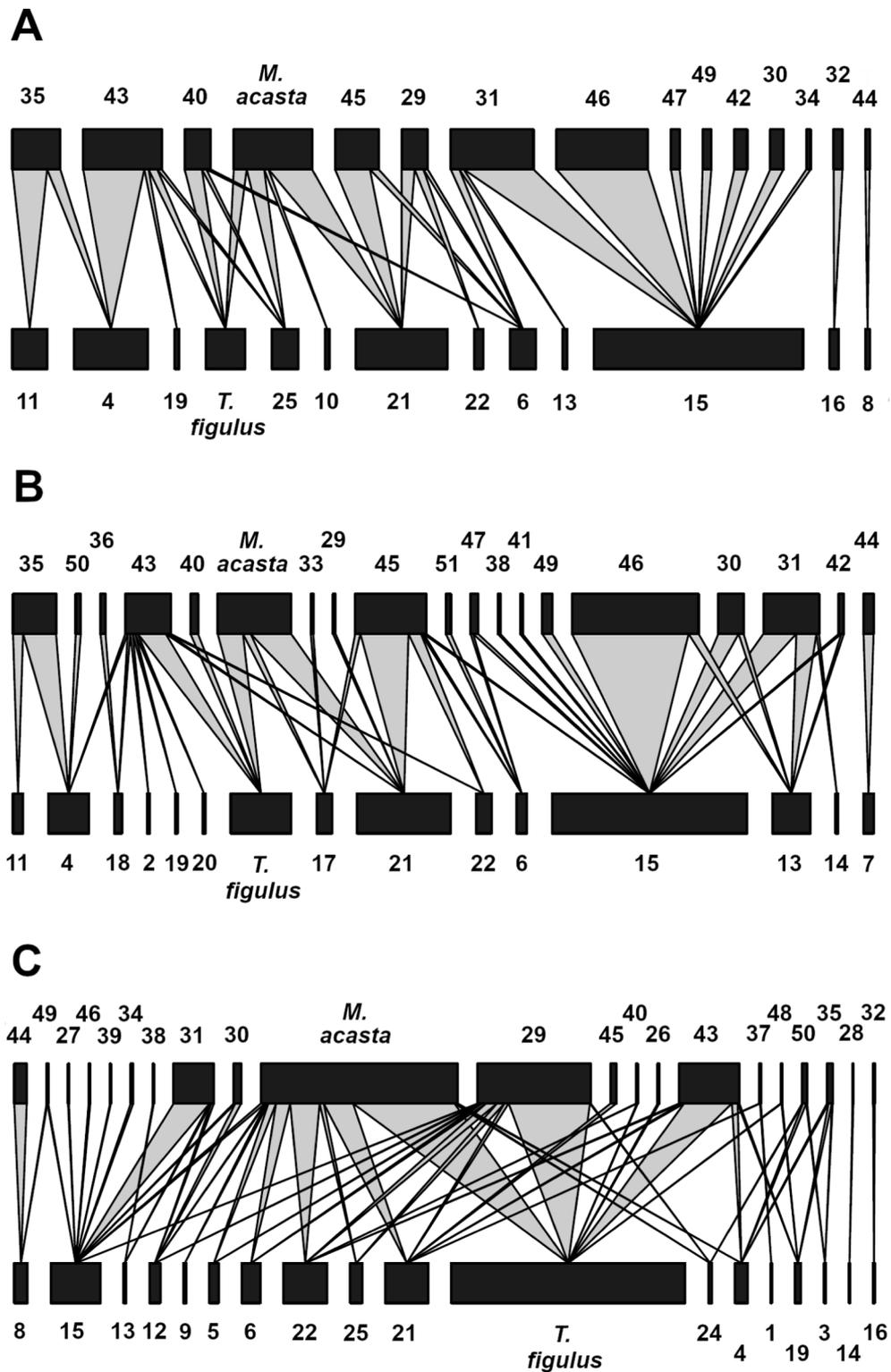
Networks on clear-cut plots had more interactions (555) than close-to-nature (200) and unmanaged (123) plots (Fig. A2). Close-to-nature plots (mean  $H2 = 0.81$ ) and unmanaged plots (mean  $H2 = 0.76$ ) were more specialised than clear-cut plots (mean  $H2 = 0.67$ ) ( $H2$ ; close-to-nature – clear-cut;  $p = 0.001$ ) ( $H2$ ; unmanaged – clear-cut;  $p = 0.001$ ), while close-to-nature and unmanaged plots were not significantly different in  $H2$  as expected from chance. Linkage density (LD) was higher on clear-cut plots (mean  $LD = 1.85$ ) compared to unmanaged plots (mean  $LD = 1.38$ ) and close-to-nature plots (mean  $LD = 1.59$ ) ( $LD$ ; close-to-nature – clear-cut;  $p = 0.004$ ) ( $LD$ ; unmanaged – clear-cut;  $p = 0.001$ ). Unmanaged and close-to-nature plots were not significantly different in  $LD$  as expected from chance (Fig. 3) (Fig. A3).

## 4. Discussion

Different forest management types resulted in dissimilar environmental conditions, which subsequently altered host abundance, host- and parasitoid richness and their associated networks. Not surprisingly, clear-cut plots had the highest amount of light and the lowest cover of trees, whereas unmanaged plots were characterised by high shrub cover. Since unmanaged plots were not managed for several decades, they also had the highest volume of deadwood – a direct result of the natural dieback of trees.

### 4.1. The influence of management on hosts and parasitoids

Host abundance was highest on clear-cut plots which are characterised by a high light coefficient. Most hosts in our study were solitary wasps that rely on good light conditions for foraging (Fornoff et al., 2021; Klein et al., 2004). However, the three most common wasp genera in our study responded differently to the management. While the abundance of *Passaloecus* was unaffected, *Deuteragenia* preferred close-to-nature and unmanaged plots. *Passaloecus* hunts aphids, which respond positively to plant diversity (Haddad et al., 2011). Since vegetation diversity did not differ between management types, the available



**Fig. A2.** Metanetworks for the different management types. A: Metanetwork for unmanaged forest plots. B: Metanetwork for close-to-nature silviculture plots and C: Metanetwork for clear-cut plots. *Melittobia acasta* and *Trypoxylon figulus* are written out to emphasize how the proportion of interactions differ for the different management types in these species, the remaining species are number coded with the code depicted in Appendix Table A3.

prey population for *Passaloecus* was probably similar on the plots of all management types. *Deuteragenia subintermedia*, the most common *Deuteragenia* species in our study hunts spiders mainly on tree trunks that are not present or very low in abundance on clear-cut plots (Schljachtenok, 1996), which may explain the species' preference for other management types. *Trypoxylon* shows strong preferences for light and warmth

(Blösch, 2000) and abundance was hence highest on clear-cut plots and south exposed sites. This indicates that the abundance of trap-nesting bees and wasps in our study was mainly driven by their respective life history traits and habitat requirements (Fornoff et al., 2021; Klein et al. 2002; Mayr et al., 2020), which were altered by forest management for some species.

**Table A4**

Results of PERMANOVA with the environmental variables of the glmm-models (Table 1). Significant p - values are in bold.

| PERMANOVA Host       |    |           |         |          |         |              |
|----------------------|----|-----------|---------|----------|---------|--------------|
|                      | Df | SumsOfSqs | MeanSqs | F. Model | R2      | Pr (>F)      |
| Management           | 2  | 2.5318    | 1.26590 | 6.7756   | 0.22698 | <b>0.001</b> |
| Vegetation diversity | 1  | 0.4625    | 0.46249 | 2.4754   | 0.04146 | 0.024        |
| Elevation            | 1  | 0.7899    | 0.78993 | 4.2280   | 0.07082 | <b>0.001</b> |
| Exposition           | 3  | 0.4617    | 0.15390 | 0.8237   | 0.04139 | 0.695        |
| Conifer cover        | 1  | 0.1825    | 0.18248 | 0.9767   | 0.01636 | 0.429        |
| PERMANOVA Parasite   |    |           |         |          |         |              |
|                      | Df | SumsOfSqs | MeanSqs | F. Model | R2      | Pr (>F)      |
| Management           | 2  | 2.6646    | 1.33228 | 4.4113   | 0.17150 | <b>0.001</b> |
| Vegetation diversity | 1  | 0.3481    | 0.34806 | 1.1525   | 0.02240 | 0.305        |
| Elevation            | 1  | 0.8614    | 0.86143 | 2.8523   | 0.05544 | <b>0.005</b> |
| Exposition           | 3  | 0.6405    | 0.21348 | 0.7069   | 0.04122 | 0.896        |
| Conifer cover        | 1  | 0.4521    | 0.45206 | 1.4968   | 0.02910 | 0.117        |

With higher cover of resin producing conifers, abundance of *Passaloecus* wasps increased significantly. A low availability of resin in combination with a low dispersal ability of these small wasps might decrease nesting suitability on plots with few conifer trees. Management of tree species composition might therefore influence Hymenoptera communities through the availability of nesting material.

Host abundance of *Trypoxylon* and *Passaloecus* responded positively to vegetation diversity. The enemies-hypothesis postulates that vegetation-rich habitats offer a variety of prey and shelter for predators and their parasitoids (Staab and Schuldt, 2020). This in turn results in a higher host abundance and richness which translates to a higher parasitoid abundance and richness (Gómez-Virués et al., 2009). While Sobek et al. (2009) observed direct effects of tree richness on host and parasitoid richness in forest, we could not detect a direct link between vegetation diversity and host- nor parasite richness. Rather, host richness was linked to host abundance and parasitoid richness (Staab et al., 2016), indicating a positive ripple effect of vegetation diversity to the highest trophic levels in our study system. Although we did not find a difference in vegetation diversity for the management types, a recent study indicates that plant richness in temperate forest ecosystems is related to light availability (Dormann et al., 2020). As we sampled only one year after the clear-cut measure, the response of the vegetation might take more time. Therefore, the suitability of clear-cut sites for trap-nesting Hymenoptera might increase the first years after the measure, before the natural plant succession again slowly changes the light conditions of the habitats (Fornoff et al., 2021). This was also already shown after controlled burning, where the species richness of bees and wasps was highest three years after the measure and declined afterwards, because of the grow back of vegetation (Bogusch et al., 2015). However, to see whether this is also true on clear-cuts, studies over longer time periods are needed.

Though host- and parasitoid abundance was highest on clear-cut plots and parasitism rates increased with parasitoid abundance, this did not translate into direct effects of management on parasitism rates. The positive relationship between parasitoid abundance and parasitism rate is in accordance with findings from subtropical forests (Staab et al., 2016). Interestingly, parasitism rate increased on east exposed plots. These receive sunlight earlier in the morning and warm more quickly. Warm conditions increase parasitoid activity (Virtanen and Neuvonen, 1999), which might translate into higher parasitism rates on these plots.

The abundance, diversity and number of interactions were lowest on unmanaged plots. Old growth forest attributes like open canopy or high structural heterogeneity through deadwood support trap nesters (Eckert et al., 2021) and one would expect these attributes in forest plots where natural dieback of trees and disturbance events are allowed

to occur. Braunisch et al., (2019) showed that canopy cover in mixed mountain forest reserves generally increased during the first decades after management cessation, until natural disturbances and decay of trees promoted more open, heterogeneous stands. The majority of our unmanaged plots therefore represent forest successional stages, which are characterised by strong understory growth (shrub cover) and darker conditions that are less suitable for Hymenoptera since nesting sites are not exposed to light and not as warm and therefore unfavourable for larval development (Radmacher and Strohm, 2011). This could explain overall smaller host and parasitoid populations in unmanaged forests in our study. Considering the structural homogenisation of close-to-nature silviculture at the landscape scale, the implementation of small-scale clear-cuts into forest management plans could help foster diverse Hymenoptera communities and red listed species. Additionally, these early successional habitats could also help to promote other forest insects like beetles, hoverflies, spiders (Hilmers et al., 2018) and some bird species (Hanberry and Thompson, 2019).

#### 4.2. Community composition and network structure

Communities on clear-cut and unmanaged plots were most different from each other whereas close-to-nature communities were situated between the management types (Fig. 4). Community composition was probably driven by preferences of dominant host species like *Deuteragenia* and *Trypoxylon* that preferred different management types tied to their hunting and nesting preferences, respectively.

Networks on close-to-nature and unmanaged plots were smaller and more specialised than networks on clear-cut plots. Generalisation on clear-cut plots seems to be mainly driven by *Melittobia acasta* (Walker), which parasitised many different hosts on clear-cut- compared to close-to-nature- and unmanaged plot networks (Fig. A2). Although *Melittobia* species (or spp.) have wings, walking and hopping are the main way of dispersal of this generalist parasite (Matthews et al., 2009). The high density of host nests on clear-cut plots might have acted in favour of the low dispersal ability of *M. acasta* and enabled parasitisation of a variety of hosts, lowering specialisation in these networks. Specialisation is driven by complex interactions between the environment and the abundance of hosts (Raffel et al., 2008). For example, less suitable environments, where resources are not immediately available for hosts increase specialisation of parasites (Hochberg and Baalen, 1998). Close-to-nature and unmanaged plots in our study were generally darker and therefore offered fewer resources for the host species, resulting in higher network specialisation level. A higher specialisation might lead to a higher fragility of networks in the case of species loss (Memmott et al., 2004).

In general, linkage density is sensitive to species richness (Goldwasser and Roughgarden, 1997), which was similar in clear-cut and close-to-nature plots. However, we observed that linkage density was highest on clear-cut plots and rather seemed to be driven by host abundance with higher host numbers supporting a greater parasitoid population and therefore increasing the number of interactions. As a measure of interaction diversity (Tylianakis et al., 2010), a greater linkage density may support a higher rate of important ecosystem functions (Snyder et al., 2006). In clear-cut plots, it is likely that early succession will strongly change habitat conditions within short timeframes and a higher interaction diversity could help stabilise parasitism throughout these fluctuating conditions as a diverse community will ensure that another species will carry out the function in the case of species loss (Yachi and Loreau, 1999).

## 5. Conclusions

Our study demonstrates that different forest management types favour distinct forest structures and abiotic conditions, which influence the suitability of these forest habitats for some host species. These differences in host community composition, abundance and diversity translate to the highest trophic levels and alter the network structure of

Table A5

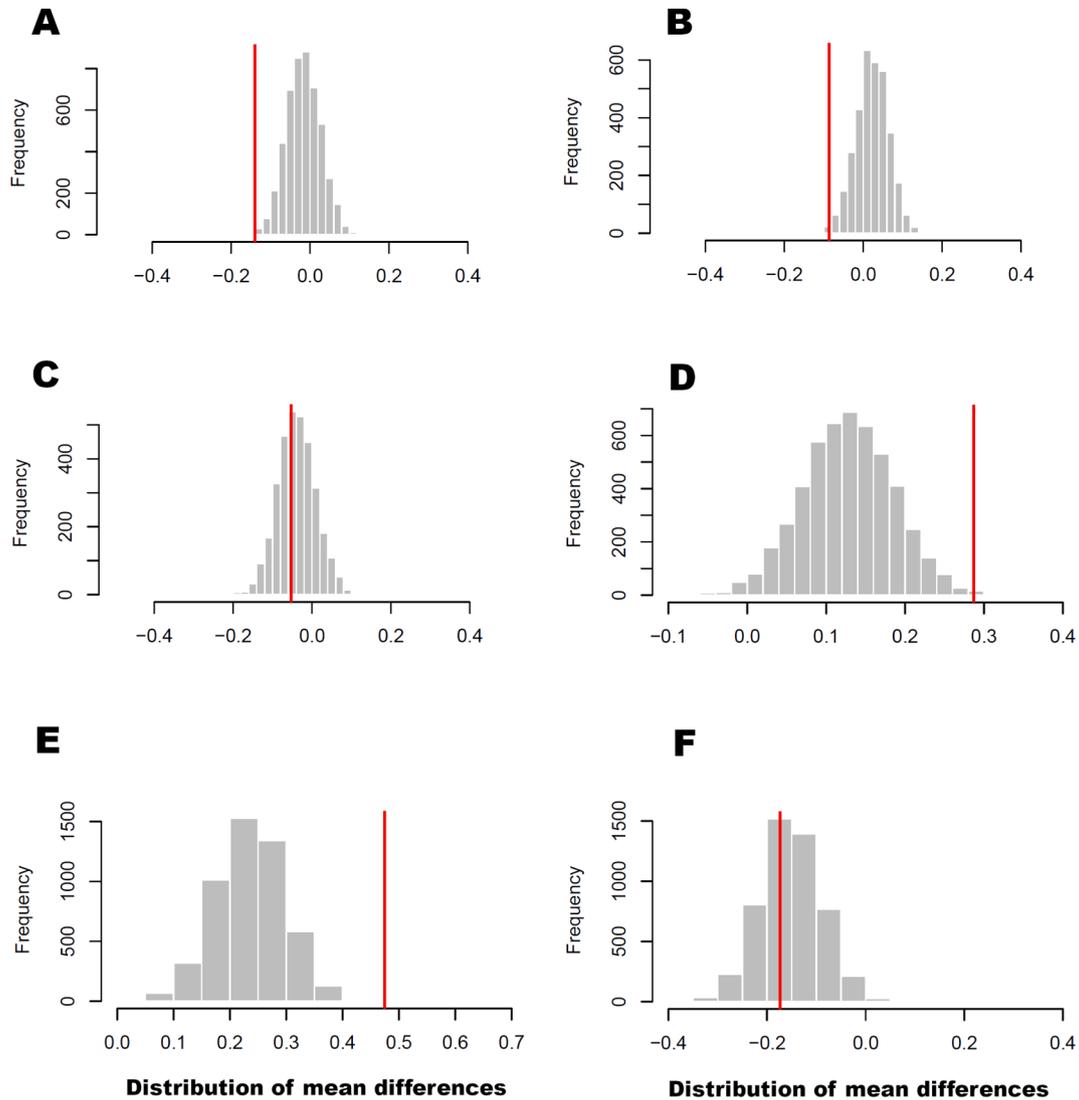
Morphological traits and keys used to classify the morphotypes and species of the parasites in this study.

|  | Head   | Thorax  | Abdomen   | Legs  |
|--|--|---|---|---|
| <b>Morphotype Ichneumonidae</b>              |  |   |   |   |
| 1 <i>Nematopodius debilis</i>                | white marks beside compound eyes, clypeus white  | dorsal view of mesoscutum near pronotum black, middle part brown, near scutellum white. Scutellum and propodeum edges are brown       | black to brown with a light blue shimmer, tergum bases with brown bands   | coxa of the third leg black and white, first and second leg nut-brown, tibia of third leg orange  |
| 2 <i>Poemenia collaris</i>                   | head black, scape white, clypeus brown-yellow and crescent-shaped  | tergum black, no blue shimmer, lateral view of pronotum: white to yellow  | black with deep crater like dots, dots are closely together   | first leg completely white-yellow, coxa of the second leg orange, third leg tibia and coxa orange |
| 3 <i>Poemenia brachyura</i>                  | head black, scape brown, flagellum of antenna brown from the dorsal view   | completely black  | superficial dots, dots are closely together, tergum ends orange   | all legs are orange   |
| 4 <i>Paraperithous</i> sp.                   | head completely black as well as the antenna, clypeus broad and brown  | completely black  | completely black, tergum two upper corners have a large dent  | completely orange   |
| 5 <i>Ephialtes manifestator</i>              | head black, clypeus only with a small brown line, scapus light brown   | completely black  | completely black, no large dent   | first leg completely white, coxa of the second leg orange, third leg tibia and coxa orange        |
| 6  | head black, clypeus bright yellow  | completely black  | completely black  | all legs dark orange  |
| 7  | clypeus brown and straight, mandible brown, beside the compound eyes white stripes   | completely black  | black with a light shimmer  | legs black beside coxa 3, which is orange   |
| <b>Morphotype Diperta</b>                    |  |   |   |   |
| 1 <i>Sarcophagidae</i>                       | frons dorsal view thin and red, red compound eyes  | black and grey, posterior callus grey and blown up  | black and grey, abdomen rounder than 4  | legs shorter  |
| 2 Tachinidae                                 | frons thick and brown  | arched scutellum, posterior callus almost not visible   | black and only small portions of grey   | long legs   |
| 3 Tachinidae                                 | frons thick, silver and black, eyes red  | arched scutellum, posterior callus almost not visible   | black and grey  | long legs   |
| 4 <i>Sarcophagidae</i>                       | frons thin and black   | black and grey, posterior callus grey and blown up, similar to 1  | conical abdomen   | legs short  |
| <b>Morphotype Chrysididae</b>                |  |   |   |   |
| 1 <i>Trichrysis cyanea</i>                   | head is shimmering blue-green, first to third flagellum green shimmering   | pronotum acute-angled, notauli are not reaching the pronotum  | tergum blue-green shimmering, rear edge has three teeth, tergum two has two black stains  | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 2 <i>Omalus aeneus</i>                       | head green-yellow shimmering between the antenna almost no dots, flagellomere parts are longer than wide   | green yellow mesoscutum, almost no dots, if yes then only superficial, almost no hair   | last tergum semi-circular with a small incision, ovate  | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 3 <i>Omalus puncticollis</i>                 | head green-yellow shimmering between the antenna almost no dots  | black shimmering mesoscutum, deep dots around the notauli, some bristle-like hair   | last tergum semi-circular with a deeper incision, ovate   | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 4 <i>Pseudomalus violaceus</i> (sturdy body) | head green-yellow shimmering between the antenna no dots, flagellum with no sculpture until the fourth flagellomere                                | blue shimmering, only a few dots  | ovate, shimmering red-yellow, broad shallow incision in comparison to the other pseudomalus   | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 5 <i>Pseudomalus pusillus</i>                | head green shimmering between the antenna no dots, flagellum with no sculpture until the third flagellomere  | green-golden shimmering, only a few dots, mesopleuron is strongly projecting ventrally, with short bristle hair                       | ovate, green-golden shimmering, deep incision   | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 6 <i>Pseudomalus auratus</i>                 | head green shimmering between the antenna no dots, middle flagellomeres are as long as broad (different trait to <i>Pseudomalus triangulifer</i> ) | blue-green shimmering, mesopleuron is strongly projecting ventrally, longer thinner hair  | ovate, red shimmering, deep incision  | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 7 <i>Chrysis ignita</i> cf                   | head is shimmering blue-green  | mesoscutum blue shimmering with crater like dots  | tergum 2 has a ridge without dots, third tergum has four "sharp" teeth, the middle teeth are prominent  | legs are shimmering in the same colour as head and thorax   |
| 8 <i>Chrysis fulgida</i>                     | head is shimmering blue-green  | mesoscutum blue shimmering with crater like dots  | Tergum 2 with a blue semicircle spot (see Fig. 93. page 51 Paukkunen et al., 2015)  | legs are shimmering in the same colour as head and thorax   |
| 9 <i>Chrysis clarinicollis</i> cf            | head is shimmering blue-green  | mesoscutum dark blue shimmering, darker than pronotum and scutellum, with crater like dots  | lateral view of first tergum is green-yellow in comparison to <i>Chrysis ignita</i> which has a completely red abdomen, third tergum has four teeth | legs are shimmering in the same colour as head and thorax   |
| 10 <i>Pseudomalus triangulifer</i>           | head is shimmering blue-green, flagellomeres are longer than <i>P. auratus</i>   | blue-green shimmering, mesopleuron is strongly projecting ventrally, longer thinner hair  | ovate, shimmering red-yellow, deep incision   | legs are shimmering in the same colour as head, thorax and abdomen                                |
| 11 <i>Philocetes bidentulus</i> cf           | head green shimmering between the antenna no dots, middle flagellomeres are as long as broad, no "check keel"                                      | blue-green shimmering, deep dots only around the notauli, mesopleuron is projecting ventrally, but is rounder than <i>Pseudomalus</i> | more conical than ovate, shimmering red- to red-gold  | legs are shimmering in the same colour as head, thorax and abdomen                                |
| <b>Morphotype Chalcidoidea</b>               |  |   |   |   |

(continued on next page)

Table A5 (continued)

|                                  | Head                  | Thorax   | Abdomen                                    | Legs   |
|----------------------------------|-----------------------|--|--|--|
| 1 <i>Chalcidoidea</i> sp.        |                       | reduced wing cells   | green and flat, shape round                |  |
| <b>Morphotype</b>                |                       |  |  |  |
| <b>Gasteruptionidae</b>          |                       |  |  |  |
| 1 <i>Gasteruption assectator</i> | head completely black | completely black, abdomen fixated directly under the scutellum | black-brown with orange bands              | basitarsus of third leg oval shaped and expanded |
| <b>Morphotype</b>                |                       |  |  |  |
| <b>Coleptera</b>                 |                       |  |  |  |
| 1 Beetle Dermestidae             | small antennae        | body covered with small hair/scales, oval shaped body          | dorsal hair/scales form two round patterns |  |
| 2 Larva Dermestidae              |                       |  |  |  |



**Fig. A3.** Distribution of mean differences in H2 (A-C) and linkage density (D-F) of host-parasite networks in different forest management types with clear-cuts, close-to-nature and unmanaged plots. A: mean difference of H2 between clear-cut and close-to-nature plot-level networks, correcting for species numbers and observation intensity with use of null models (n = 5000). Grey bars indicate the distribution of mean differences after 5000 iterations. The red line indicates observed differences. Observed difference is significantly different from null-model expectations. B: mean difference of H2 between clear-cut and unmanaged plots. Observed difference is significantly different from null-model expectations. C: mean difference in H2 between close-to-nature and UF plots. Observed difference is not significantly different from null model expectations. D: mean difference of LD between clear-cut and close-to-nature plots. Observed difference is significant. E: mean difference of LD between clear-cut and unmanaged plots. Observed difference is significant. F: mean difference between close-to-nature and unmanaged plots. Observed difference is not different from what would be expected by chance. *Conservation targets linked to Forest management.*

host-parasitoid communities. Some management consequences, for example in clear-cuts, are immediately visible, such as the loss of tree cover and subsequent increase in light availability, but this is not necessarily directly reflected in the vegetation, due to the time-lag in

vegetation response. However, network responses are strong even in the year after the clear-cut measure, which emphasizes the bottom-up effect of forest structure on these ecological communities. In particular, the interaction networks in these early successional habitats are more linked

and could provide a higher rate of the associated ecosystem functions in comparison to unmanaged and close-to-nature managed plots. Thus, our results highlight the importance of early successional forest stages for the conservation of trap-nesting bees, wasps and their associated parasitoids. These early successional stages are usually underrepresented in close-to-nature forests compared to natural forests, especially in the absence of natural disturbances. Including small clear-cuts into a close-to-nature regime may thus not only enhance the ecological and functional complexity of this community, but also benefit other photophilic insect groups with similar requirements. We advocate to include the distinct response of insect species and networks to changing structural and abiotic conditions into forest management considerations, instead of merely relying on species richness indicators, to better promote complex species communities of Hymenoptera such as bees and wasps and foster their important ecosystem functions.

### CRedit authorship contribution statement

**Tristan Eckerter:** Writing – original draft, Visualization, Formal analysis. **Veronika Braunisch:** Methodology, Writing – review & editing, Resources. **Gesine Pufal:** Writing – review & editing, Formal analysis, Visualization. **Alexandra M. Klein:** Methodology, Supervision, Resources, Writing – review & editing.

### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

### Acknowledgements

We thank the Deutsche Bundesstiftung Umwelt for making the research possible via a PhD scholarship. We thank the whole team of the “Forest Reserves” group (Forest Research Institute of Baden-Württemberg, FVA) for the selection and maintenance of the plots, Gabriel Holz and Sabine Mayer and for recording the vegetation data and Katharina Friedmann and Klaus Winkler for forest structure mapping. Working on the remote plots would not have been possible without the help of Wanja Wolf, Sarah Niekrenz, Michael Kraft and Sanja Dietrich – thank you for your help! We thank Dr. Mike Herrmann and Nolan Rappa for help with the identification of some wasp individuals. We also thank two anonymous reviewers for their valuable comments that greatly improved the manuscript.

### References

- Amiet, F., Müller, A., Neumeyer, R., 1996. Apidae 2, *Colletes*, *Dufourea*, *Hylaeus*, *Nomia*, *Nomioides*, *Rhopitoides*, *Rophites*, *Sphecodes*, *Systropha*. Fauna Helvetica, 4. CSCF und SEG, Neuchâtel, Switzerland.
- Amiet, F., Herrmann, M., Müller, A., Neumeyer, R., 2004. Apidae 4: *Anthidium*, *Chelostoma*, *Coelioxys*, *Dioxys*, *Heriades*, *Lithurgus*, *Megachile*, *Osmia*, *Stelis*. Fauna Helvetica 9. CSCF und SEG, Neuchâtel, Switzerland.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. For. Ecol. Manag. 258 (4), 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>.
- Bauhus, J., Puettmann, K.J., Kühne, C., 2013. Close-to-nature forest management in Europe: does it support complexity and adaptability of forest ecosystems? In: Messier, C., Puettmann, K.J., Coates, K.D. (Eds.), *Managing Forests as Complex Adaptive Systems: building resilience to the challenge of global change*. Routledge, The Earthscan forest library, pp. 187–213.
- Bersier, L.F.L., Richter, C.B., Cattin, M.F., 2002. Quantitative descriptors of food-web matrices. Ecology 83, 2394–2407. [https://doi.org/10.1890/0012-9658\(2002\)083\[2394:QDOFWM\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2394:QDOFWM]2.0.CO;2).
- Blösch, M., 2000. Die Grabwespen Deutschlands: Lebensweise, Verhalten, Verbreitung (Die Tierwelt Deutschlands). Goecke & Evers, Keltern, Germany.
- Blüthgen, N., Menzel, F., Blüthgen, N., 2006. Measuring specialization in species interaction networks. BMC Ecol. 6, 9. <https://doi.org/10.1186/1472-6785-6-9>.
- Bogusch, P., Blažej, L., Trýzna, M., Heneberg, P., 2015. Forgotten role of fires in Central European forests: critical importance of early post-fire successional stages for bees and wasps (Hymenoptera: Aculeata). Eur. J. For. Res. 134 (1), 153–166. <https://doi.org/10.1007/s10342-014-0840-4>.

- Bogusch, P., 2021. The genus *Gasteruption* Latreille, 1796 (Hymenoptera: Gasteruptionidae) in the Czech Republic and Slovakia: distribution, checklist, ecology, and conservation status. Zootaxa 4935, 1–63. <https://doi.org/10.11646/zootaxa.4935.1.1>.
- Bollmann, K., Braunisch, V., 2013. 1.1 To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests. European Forest Institute, Freiburg. In Focus: Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Bonn, Germany.
- Brang, P., Spathelf, P., Larsen, J.B., Bauhus, J., Boncina, A., Chauvin, C., Drossler, L., Garcia-Guemes, C., Heiri, C., Kerr, G., Lexer, M.J., Mason, B., Mohren, F., Muhlethaler, U., Nocentini, S., Svoboda, M., 2014. Suitability of close-to-nature silviculture for adapting temperate European forests to climate change. Forestry 87 (4), 492–503. <https://doi.org/10.1093/forestry/cpu018>.
- Braunisch, V., Roder, S., Coppes, J., Froidevaux, J.S.P., Arlettaz, R., Bollmann, K., 2019. Structural complexity in managed and strictly protected mountain forests: Effects on the habitat suitability for indicator bird species. For. Ecol. Manag. 448, 139–149. <https://doi.org/10.1016/j.foreco.2019.06.007>.
- Broad, G., Shaw, M., Fitton, M., 2018. Ichneumonid wasps (Hymenoptera: Ichneumonidae): their classification and biology, Handbooks for the Identification of British Insects. Royal Entomological Society and Field Studies Council, London, UK.
- Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2020. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R J. 9, 378–400. <https://journal.r-project.org/archive/2017/RJ-2017-066/index.html>.
- BWI3: Thünen-Institut, Dritte Bundeswaldinventur - Ergebnisdatabank, <https://bwi.info>, Aufruf am: 07.09.2021, Auftragskürzel: 77Z1J1\_L235of\_2012\_bi, Archivierungsdatum: 2014-6-10 16:7:59.927, Überschrift: Waldfläche [ha] nach Land und Baumartengruppe.
- Chaudhary, A., Burivalova, Z., Koh, L.P., Hellweg, S., 2016. Impact of forest management on species richness: global meta-analysis and economic trade-offs. Sci. Rep. 6 (1) <https://doi.org/10.1038/srep23954>.
- DHM 25. Digitales Höhenmodell mit 25m Raster. Landesamt für Geoinformation und Landentwicklung Baden-Württemberg, Germany.
- Dormann, C.F., Frund, J., Blüthgen, N., Gruber, B., 2009. Indices, graphs and null models: analyzing bipartite ecological networks. Open Ecol. J. 2 (1), 7–24. <https://doi.org/10.2174/1874213000902010007>.
- Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite package: analysing ecological networks. R News 8, 8–11.
- Dormann, C.F., Bagnara, M., Boch, S., Hinderling, J., Janeiro-Otero, A., Schäfer, D., Schall, P., Hartig, F., 2020. Plant species richness increases with light availability, but not variability, in temperate forests understorey. BMC Ecol. 20, 43. <https://doi.org/10.1186/s12898-020-00311-9>.
- DWDa Temperature Feldberg (Station ID: 1346) and Baiersbronn (Station ID: 368) for the period 1981–2010: [https://opendata.dwd.de/climate\\_environment/CDC/observations\\_germany/climate/multi\\_annual/mean\\_81-10/Temperatur\\_1981-2010\\_festerStandort.txt](https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/multi_annual/mean_81-10/Temperatur_1981-2010_festerStandort.txt); visited 08.04.2021.
- DWDb Precipitation Bad-Wildbad (Station ID: 5559) and Baiersbronn-Ruhestein (Station ID 4315) for the period 1981–2010: [https://opendata.dwd.de/climate\\_environment/CDC/observations\\_germany/climate/multi\\_annual/mean\\_81-10/Niederschlag\\_1981-2010\\_aktStandort.txt](https://opendata.dwd.de/climate_environment/CDC/observations_germany/climate/multi_annual/mean_81-10/Niederschlag_1981-2010_aktStandort.txt); visited 08.04.2021.
- Eckerter, T., Buse, J., Bauhus, J., Förstner, M.L., Klein, A.M., 2021. Wild bees benefit from structural complexity enhancement in a forest restoration experiment. For. Ecol. Manag. 496, 119412. <https://doi.org/10.1016/j.foreco.2021.119412>.
- Fitton, M.G., Shaw, M.R., Gauld, I.D., 1988. Handbooks for the identification of British insects. Pimpline Ichneumon-flies: Hymenoptera, Ichneumonidae (Pimplinae) Vol. 7, Pt. 1.
- Forest Europe, 2020: State of Europe's Forests 2020. [https://foresteurope.org/wp-content/uploads/2016/08/SoEF\\_2020.pdf](https://foresteurope.org/wp-content/uploads/2016/08/SoEF_2020.pdf).
- Fornoff, F., Staab, M., Zhu, C.D., Klein, A.M., 2021. Multi-trophic communities re-establish with canopy cover and microclimate in a subtropical forest biodiversity experiment. Oecologia 196, 289–301.
- Frazer, G.W., Trofymow, J.A., Lertzman, K.P., 1997. A method for estimating canopy openness, effective leaf area index, and photosynthetically active photon flux density using hemispherical photography and computerized image analysis techniques, Information Report. Can. For. Serv., Pacific Forestry Centre, Victoria, USA.
- Führer, E., 2000. Forest functions, ecosystem stability and management. For. Ecol. Manag. 132 (1), 29–38. [https://doi.org/10.1016/S0378-1127\(00\)00377-7](https://doi.org/10.1016/S0378-1127(00)00377-7).
- Gámez-Virúés, S., Gurr, G., Raman, A., La Salle, J., Nicol, H., 2009. Effects of flowering groundcover vegetation on diversity and activity of wasps in a farm shelterbelt in temperate Australia. Biocontrol 54 (2), 211–218. <https://doi.org/10.1007/s10526-008-9182-9>.
- Goldwasser, L., Roughgarden, J., 1997. Sampling effects and the estimation of food-web properties. Ecology 78, 41–54. <https://doi.org/10.2307/2265977>.
- Gosner, M.M., Pašalić, E., Lange, M., Lange, P., Boch, S., Hennenmöller, D., Müller, J., Socher, S.A., Fischer, M., Schulze, E.-D., Weisser, W.W., Bruun, H.H., 2014. Differential responses of herbivores and herbivory to management in temperate European beech. PLoS ONE 9 (8), e104876. <https://doi.org/10.1371/journal.pone.0104876>.
- Goulet, H., Huber, J.T. 1993. Hymenoptera of the world: an identification guide to families. Can. Comm. Group. Agriculture Canada Publication, Ottawa, Canada.
- Grushecky, S.T., Liebhold, A.M., Greer, R., Smith, R.L., 1998. Does forest thinning affect predation on gypsy moth (Lepidoptera: Lymantridae) larvae and pupae? Environ. Entomol. 27, 268–276. <https://doi.org/10.1093/ee/27.2.268>.

- Haddad, N.M., Crutsinger, G.M., Gross, K., Haarstad, J., Tilman, D., 2011. Plant diversity and the stability of foodwebs: Plant diversity and foodweb stability. *Ecol. Lett.* 14, 42–46. <https://doi.org/10.1111/j.1461-0248.2010.01548.x>.
- Hartig, F., 2021. DHARMA: Residual diagnostics for hierarchical (multi-level / mixed) regression models. R package version (3), 4. <https://CRAN.R-project.org/package=DHARMA>.
- Hanberry, B.B., Thompson, F.R., 2019. Open forest management for early-successional Birds. *Wil. Soc. Bull.* 43 (1), 141–151.
- Hawkins, B.A., 1994. Pattern and process in host-parasite interactions. Cambridge University Press. <https://doi.org/10.1017/CBO9780511721885>.
- Hilmers, T., Friess, N., Bässler, C., Heurich, M., Brandl, R., Pretzsch, H., Seidl, R., Müller, J., Butt, N., 2018. Biodiversity along temperate forest succession. *J. Appl. Ecol.* 55 (6), 2756–2766. <https://doi.org/10.1111/1365-2664.13238>.
- Hochberg, M., Baalen, M., 1998. Antagonistic coevolution over productivity gradients. *Am. Nat.* 152 (4), 620–634. <https://doi.org/10.1086/286194>.
- Horák, J., Brestovanská, T., Mladenović, S., Kout, J., Bogusch, P., Haldá, J.P., Zasadil, P., 2019. Green desert?: Biodiversity patterns in forest plantations. *For. Ecol. Manag.* 433, 343–348. <https://doi.org/10.1016/j.foreco.2018.11.019>.
- Hofmann, M.M., Fleischmann, A., Renner, S.S., 2020. Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. *J. Hymenopt. Res.* 77, 105–117. <https://doi.org/10.3897/jhr.77.51182>.
- Hsieh, T.C., Ma, K.H., Chao, A., 2020. iNEXT: Interpolation and Extrapolation for Species Diversity. R package version 2, 20. [http://chao.stat.nthu.edu.tw/wordpress/software\\_download/](http://chao.stat.nthu.edu.tw/wordpress/software_download/).
- Jacobs, H.J., 2007. Die Grabwespen Deutschlands - Bestimmungsschlüssel. Goecke & Evers, Kelttern, Germany. Tierwelt Deutschlands 79.
- Jactel, H., Nicoll, B.C., Branco, M., Gonzalez-Olabarria, J.R., Grodzki, W., Långström, B., Moreira, F., Netherer, S., Orazio, C., Piou, D., Santos, H., Schelhaas, M.J., Tojic, K., Vodde, F., 2009. The influences of forest stand management on biotic and abiotic risks of damage. *Ann. For. Sci.* 66, 701–701. <https://doi.org/10.1051/forest/2009054>.
- Johansson, N., van Achterberg, C., 2016. Revision of the Palaearctic Gasteruption assectator aggregate, with special reference to Sweden (Hymenoptera, Gasteruptionidae). *ZooKeys* 615, 73–94. <https://doi.org/10.3897/zookeys.615.8857>.
- Kehoe, R., Sanders, D., Cruse, D., Silk, M., Gaston, K.J., Bridle, J.R., Veen, F., 2020. Longer photoperiods through range shifts and artificial light lead to a destabilizing increase in host–parasite interaction strength. *J. Anim. Ecol.* 89, 2508–2516. <https://doi.org/10.1111/1365-2656.13328>.
- Klein, A.-M., Steffan-Dewenter, I., Buchori, D., Tschamtké, T., 2002. Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv. Biol.* 16 (4), 1003–1014. <https://doi.org/10.1046/j.1523-1739.2002.00499.x>.
- Klein, A.-M., Steffan-Dewenter, I., Tschamtké, T., 2004. Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *J. Anim. Ecol.* 73 (3), 517–525. <https://doi.org/10.1111/j.0021-8790.2004.00826.x>.
- Klein, A.-M., Vaissière, B.E., Cane, J.H., Steffan-Dewenter, I., Cunningham, S.A., Kremen, C., Tschamtké, T., 2007. Importance of pollinators in changing landscapes for world crops. *Proc. R. Soc. B Biol. Sci.* 274 (1608), 303–313. <https://doi.org/10.1098/rspb.2006.3721>.
- Kunz, P., 1994. Die Goldwespen (Chrysididae) Baden-Württembergs: Taxonomie, Bestimmung, Verbreitung, Kartierung und Ökologie. Mit einem Bestimmungsschlüssel für die deutschen Arten. Landesanstalt für Umwelt, Messungen und Naturschutz Baden-Württemberg, Germany. Ausgabe von 1994-01-01. ISBN 3882511923.
- Landi, P., Minoarivelo, H.O., Brännström, Å., Hui, C., Dieckmann, U., 2018. Complexity and stability of ecological networks: a review of the theory. *Popul. Ecol.* 60 (4), 319–345. <https://doi.org/10.1007/s10144-018-0628-3>.
- Lenth, R., 2020. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.5.0. <https://CRAN.R-project.org/package=emmeans>.
- Librán-Embíd, F., Grass, I., Emer, C., Ganuza, C., Tschamtké, T., Jordan, F., 2021. A plant–pollinator metanetwork along a habitat fragmentation gradient. *Ecol.* 24 (12), 2700–2712. <https://doi.org/10.1111/ele.13892>.
- Martins, C.F., Ferreira, R.P., Carneiro, L.T., 2012. Influence of the orientation of nest entrance, shading, and substrate on sampling trap-nesting bees and wasps. *Neotrop. Entomol.* 41 (2), 105–111. <https://doi.org/10.1007/s13744-012-0020-5>.
- Matthews, R.W., González, J.M., Matthews, J.R., Deyrup, L.D., 2009. Biology of the parasite *Melittobia* (Hymenoptera: Eulophidae). *Ann. Rev. Entomol.* 54, 251–266. <https://doi.org/10.1146/annurev.ento.54.110807.090440>.
- Mayr, A.V., Peters, M.K., Eardley, C.D., Renner, M.E., Röder, J., Steffan-Dewenter, I., 2020. Climate and food resources shape species richness and trophic interactions of cavity-nesting Hymenoptera. *J. Biogeogr.* 47 (4), 854–865. <https://doi.org/10.1111/jbi.13753>.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. Lond. B Biol. Sci.* 271 (1557), 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>.
- Neumeyer, R., 2019. Vespidea. Fauna Helvetica 31, Info fauna CSCF, Neuchâtel, Switzerland.
- Oksanen, J., Blanchet F.G., Friendly M., Kindt R., Legendre P., McGlinn D., Minchin P.R., O'Hara R.B., Simpson G.L., Solymos P., Stevens M.H.H., Szoecs E., Wagner H., 2021. vegan: Community Ecology Package. R package version 2.5-2. <https://CRAN.R-project.org/package=vegan>.
- Paillet, Y., Berges, L., Hjalten, J., Dor, P.O., Avon, C., Mermann, M.B.-R., Bijlsma, R.-J., Bruyn, L.D., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, L., Standovar, T., Thmeres, B.T., Uotila, A., ...Virtanen, R., 2010. Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. *Conserv. Biol.* 24, 13. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>.
- Paukkunen, J., Berg, A., Soon, V., Odegaard, F., Rosa, P., 2015. An illustrated key to the cuckoo wasps (Hymenoptera, Chrysididae) of the Nordic and Baltic countries, with description of a new species. *ZooKeys* 548, 1–116. <https://doi.org/10.3897/zookeys.548.6164>.
- Pohjannies, T., Trivino, M., Le Tortorec, E., Mazziotta, A., Snäll, T., Mönkkönen, M., 2017. Impacts of forestry on boreal forests: An ecosystem services perspective. *Ambio* 46 (7), 743–755. <https://doi.org/10.1007/s13280-017-0919-5>.
- Radmacher, S., Strohm, E., 2011. Effects of constant and fluctuating temperatures on the development of the solitary bee *Osmia bicornis* (Hymenoptera: Megachilidae). *Apidologie* 42 (6), 711–720. <https://doi.org/10.1007/s13592-011-0078-9>.
- Raffel, T.R., Martin, L.B., Rohr, J.R., 2008. Parasites as predators: unifying natural enemy ecology. *Trends Ecol. Evol.* 23 (11), 610–618. <https://doi.org/10.1016/j.tree.2008.06.015>.
- R Development Core Team, 2021. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>.
- Rodríguez, A., Pohjoismäki, J.L.O., Kouki, J., 2019. Diversity of forest management promotes parasite functional diversity in boreal forests. *Biol. Conserv.* 238, 108205. <https://doi.org/10.1016/j.biocon.2019.108205>.
- Rubene, D., Schroeder, M., Ranius, T., Didham, R., 2015. Estimating bee and wasp (Hymenoptera: Aculeata) diversity on clear-cuts in forest landscapes - an evaluation of sampling methods. *Insect Conserv. Divers.* 8 (3), 261–271. <https://doi.org/10.1111/icad.12105>.
- Russell, M., 2015. A meta-analysis of physiological and behavioral responses of parasite wasps to flowers of individual plant species. *Biol. Control* 82, 96–103. <https://doi.org/10.1016/j.biocontrol.2014.11.014>.
- Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Marques Duarte, I., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillingard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., Essl, F., 2018. Where are Europe's last primary forests? *Divers. Distrib.* 24 (10), 1426–1439. <https://doi.org/10.1111/ddi.12778>.
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.-D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., Mori, A., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55 (1), 267–278. <https://doi.org/10.1111/1365-2664.12950>.
- Schlächter, A.S., 1996. Über die Beutespinnen (Aranei) einiger Wegwespen (Hym., Pompilidae). *Entomol. Nachrichten Berichte* 40, 169–172.
- Schmid-Egger, C., 2010. Die Rote Liste der Wespen Deutschlands. *Ampulex* 1, 5–39.
- Snyder, W.E., Snyder, G.B., Finke, D.L., Straub, C.S., 2006. Predator biodiversity strengthens herbivore suppression. *Ecol. Lett.* 9 (7), 789–796. <https://doi.org/10.1111/j.1461-0248.2006.00922.x>.
- Sebek, P., Vodka, S., Bogusch, P., Pech, P., Tropek, R., Weiss, M., Zimova, K., Cizek, L., 2016. Open-grown trees as key habitats for arthropods in temperate woodlands: The diversity, composition, and conservation value of associated communities. *For. Ecol. Manag.* 380, 172–181. <https://doi.org/10.1016/j.foreco.2016.08.052>.
- Sobek, S., Tschamtké, T., Scherber, C., Schiele, S., Steffan-Dewenter, I., 2009. Canopy vs. understory: Does tree diversity affect bee and wasp communities and their parasites across forest strata? *For. Ecol. Manag.* 258, 609–615. <https://doi.org/10.1016/j.foreco.2009.04.026>.
- Saab, M., Bruelheide, H., Durka, W., Michalski, S., Purschke, O., Zhu, C.-D., Klein, A.-M., 2016. Tree phylogenetic diversity promotes host–parasite interactions. *Proc. R. Soc. B Biol. Sci.* 283, 20160275. <https://doi.org/10.1098/rspb.2016.0275>.
- Saab, M., Pufal, G., Tschamtké, T., Klein, A.-M., Iossa, G., 2018. Trap nests for bees and wasps to analyse trophic interactions in changing environments—A systematic overview and user guide. *Methods Ecol. Evol.* 9 (11), 2226–2239. <https://doi.org/10.1111/2041-210X.13070>.
- Saab, M., Schuldt, A., 2020. The Influence of Tree Diversity on Parasites—a Review of the “Enemies” Hypothesis in Forests. *Curr. For. Rep.* 6, 243–259. <https://doi.org/10.1007/s40725-020-00123-6>.
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Conserv.* 143 (10), 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>.
- Tylianakis, J.M., Morris, R.J., 2017. Ecological Networks Across Environmental Gradients. *Annu. Rev. Ecol. Syst.* 48 (1), 25–48. <https://doi.org/10.1146/annurev-ecolsys-110316-022821>.
- Unwin, D.M., 1981. A key to the families of british diptera. AIDGAP Guides Vol. 5, Field Studies Council, Shrewsbury, England.
- Verhoeven, K.J.F., Simonsen, K.L., McIntyre, L.M., 2005. Implementing false discovery rate control: increasing your power. *Oikos* 108, 643–647. <https://doi.org/10.1111/j.0030-1299.2005.13727.x>.
- Virtanen, T., Neuvonen, S., 1999. Performance of moth larvae on birch in relation to altitude, climate, host quality and parasites. *Oecologia* 120, 92–101. <https://doi.org/10.1007/s004420050837>.
- Westrich, P., Frommer, U., Mandery, K., Riemann, H., Ruhnke, H., Saure, C., Voith, J., 2011. Rote Liste und Gesamtartenliste der Bienen (Hymenoptera, Apidae) Deutschlands. – In: Rote Liste gefährdeter Tiere, Pflanzen und Pilze Deutschlands.

- Band 3: Wirbellose Tiere, Münster, Naturschutz und Biologische Vielfalt 70, 373-416.
- Wevell von Krüger, A., Moosmann, S., Winkler, K., Kärcher, R., 2015. Methodenhandbuch für die WSA-Aufnahme. Forstliche Versuchs- und Forschungsanstalt Baden-Württemberg, Naturverwaltung Luxemburg, Germany., p. 61
- Wiesbauer, H., Rosa, P., Zettel, H. 2020. Die Goldwespen Mitteleuropas: Biologie, Lebensräume, Artenportraits: Biologie, Lebensräume, Artensteckbriefe. Ulmer, Stuttgart, Germany. ISBN 13. 978-3818611491.
- Wolf, H. 1972. Pompilidae. Insecta Helvetica. Fauna 5, 1-176. Schweizerische Entomologische Gesellschaft, Zürich, Switzerland.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. Proc. Natl. Acad. Sci. U.S.A. 96 (4), 1463–1468. <https://doi.org/10.1073/pnas.96.4.1463>.