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ORIGINAL PAPER

Effects of species traits on the catchability of butterflies with different types of Malaise traps and implications for total catch biomass

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Abstract

Increasing evidence for insect biodiversity decline requires an identification of the causes but also an improved understanding of the limitations of the various underlying sampling methods. Trap comparisons foster comparability of larger-scale biodiversity studies by providing a deeper understanding of the variations in species abundances and trait compositions due to variations in trap characteristics. In our study, we compared five Malaise trap types on their catchability of butterfly species and noctuid moths and examined for the butterflies how this can be related to traits. We showed marked differences in species and trait occurrence in the samples of the different trap types which seemed to be influenced by roof colour (white, black) and trap shape (Townes trap: high, wide roof, Bartak trap: low, narrow roof). We found most butterfly species and most butterfly biomass in the white-roofed Townes trap. All butterfly traits were represented with most individuals in this trap. Compared with its black counterpart, it showed increased catches for pale butterflies and forest species. We found that dark-roofed traps captured fewer butterfly species and had a lower butterfly biomass. Townes traps captured more butterflies with larger wingspans, egg-laying locations higher above ground, and tree feeding behaviour compared to Bartak traps. Depending on the season and habitat, the differences in species capture may affect overall insect biomass.

Keywords Insect monitoring · Butterfly · Malaise trap · Trait · Bartak trap · Townes trap

Implications for insect conservation

Our findings support adjustments of species abundances, trait compositions and total biomass between studies using different Malaise trap types, thus facilitating comparisons across studies and data compilation for large-scale studies.

Introduction

Increasing evidence for insect biodiversity decline (Burner et al. 2021; Hallmann et al. 2021; Warren et al. 2021) emphasizes the need for the initialization of new, harmonized insect monitoring programmes and a comprehensive compilation of existing monitoring data (Welti et al. 2021; Uhler et al. 2022a; Kerner et al. 2024). Such large collections of data could help provide a more comprehensive picture of large-scale spatial and temporal patterns in insect communities worldwide (Kerner et al. 2024). However, the potential of joint analyses can only be realized if we succeed in merging insect data from different sampling techniques that scientists have used (Barkmann et al. 2023; Mora-Aguilar et al. 2023). This requires a better understanding of how differences in trap characteristics affect the species abundance in samples.

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Research on differences in insect catchment due to differences in trap characteristics, such as colour or shape, has been conducted for several trap types (Brown and Matthews 2016; Shrestha et al. 2019; Gonzalez et al. 2020). This includes Malaise traps (Malaise 1937), which are one of the sampling methods for which many variants are being used by scientists. The Malaise trap is widely used for the monitoring of insects (Meserve et al. 2016; Hallmann et al. 2017; Welti et al. 2022; Lenzi et al. 2023), because it captures a large range of insect orders (Karlsson et al. 2020). The trap was originally developed for Diptera research (Sjöberg 2004) and captures predominantly Hymenoptera, Hemiptera and Diptera species, but also a markable number of Lepidoptera species (Remmel et al. 2024).

Insect occurrence in Malaise trap samples was found to be influenced by trap size, mesh size, shape, the colour of the lower intercept panel (Darling and Packer 1988; Irvine and Woods 2007; Uhler et al. 2022a), and the colour of the roof (Duarte et al. 2010; Uhler et al. 2022a; van Achterberg 2009). Until now, the dependency of capture efficiency on trap characteristics has been confirmed and explained, but studies have remained largely limited to the level of insect order or indicator groups. Consequently, the support for data compilation provided by these findings is limited to studies at the level of order. A better understanding of the differences in species capture between Malaise trap types due to trap characteristics can help interpret species abundances according to the trap type used and to homogenise species abundances of different studies, thus facilitating their comparison and data compilation.

Functional species traits can help discover the relationship between trap characteristics and species abundances because they affect insect behaviour in relation to traps (Cadotte et al. 2011). For example, given a trap with a narrow roof, a small species would be held back by the roof and prevented from escaping, but a large species could overcome the barrier and escape (McCravy et al. 2019). Consequently, a trap with a narrow roof design could include fewer large species than a trap with a wide roof. In order to measure this catchability of species with different traits, a simultaneous operation of different Malaise trap types could help directly compare species, and hence trait abundances.

Concomitant differences in insect trait distribution among trap types are crucial to determine because they could also result in an over- and under-representation of traits in samples of different Malaise trap types. Such biases need to be taken into account when combining data from different trap designs in analyses. For example, trait data generated by Malaise traps is used as a basis for functional diversity studies for a large range of insect orders: Coleoptera (Grimbacher and Stork 2007; Choi et al. 2010; Canovai and Loni 2019), Hymenoptera (Ngo et al. 2013; Kendall and Ward 2016; de Souza et al. 2020; Turo et al. 2021; Warne et al. 2020), Diptera (Sjöberg 2004; Marcos-Garcia et al. 2012; Larrieu et al. 2015), and Trichoptera (Smith et al. 2002). The most studied functional species traits in these studies include behavioural traits such as feeding behaviour, habitat preferences, migratory behaviour, sociality, and nesting location, and morphological traits such as body size, colour, or type of insect mouthpart.

For a comparative study between Malaise trap types, including species and their traits, butterflies are particularly suitable. They are among the insect families whose functional species traits are well studied (Middleton-Welling et al. 2020; Shirey et al. 2022); thus, it is easier to identify traits involved in the interaction between trap type and species. Additionally, they are often used as a model group in animal ecology studies, such as mobility research (Öckinger et al. 2010; Betzholtz and Franzen 2011; Kuussaari et al. 2014) and as flagship species for invertebrate conservation (Barua et al. 2012). Many butterfly species show considerable decline (Warren et al. 2021; Burner et al. 2021; but see: Macgregor et al. 2019). Furthermore, a study revealing differences between Malaise trap types for butterfly capture can support the extraction of quantifiable and unbiased butterfly community data from Malaise trap samples of monitoring programmes for conservation purposes (Buchner et al. 2024). Therefore, these Malaise trap samples can be used as a further data source, in addition to traditional methods such as transect walks (Barkmann et al. 2023) and light traps (Jonason et al. 2014).

In our study, we investigated the catchability of butterfly species and noctuid moths in five different Malaise trap types differing in shape and roof colour. Therefore, we recorded the abundances of butterfly species and noctuid moths in the Malaise trap catches. The traps were placed as a defined set on a meadow and a forest clearing site in three regions of southwestern Germany and were operated simultaneously (Uhler et al. 2022a). In search of the causes for the different species abundances, we substituted butterfly species with their functional species traits and analysed how butterflies with certain traits are represented in the trap catches. We discussed differences in the number of individuals per trait in the catches as well as the resulting trap catch efficiency with regard to the possible trap components and design differences that could be responsible. From trait composition, we further obtained information about over- and under-representation of traits in the trap catches, which can serve as key information in the interpretation of trait data from various Malaise trap types. To check for possible impacts of trap-specific trait compositions on the butterfly biomass of the Malaise traps, we calculated butterfly biomasses from species abundances and species body masses and compared them between trap types. Also, the noctuid

moth biomasses were compared between the trap types. Finally, we explored the relationship between Malaise trap type, butterfly biomass and total insect biomass for each trap type using a generalized linear mixed-effects model to reveal the contribution of butterfly biomass to total biomass of Malaise trap samples. Another model was built including the noctuid moth biomass instead of the butterfly biomass.

Our results support the integration of species and trait data obtained with different trap designs. We used butterflies as a model group for our study, but by extending the analyses to the trait level, we have also paved the way for the transferability of our results to other insect orders.

Materials and methods

Sampling design

Insect samples were collected from the end of May to the end of August 2020 in three lower mountain range regions of southwestern Germany (Hunsrück, Spessart, and Steigerwald). The sites in Hunsrück (Hunsrück-Hochwald National Park) and Spessart (Rhine-Main-Observatory) belong to the Long-Term Ecological Research Network (LTER, Haase et al. (2016); Mirtl et al. (2018). In each region, a defined set of five different Malaise trap types was placed each on a meadow and a forest clearing site (see Uhler et al. 2022a and supplementary material Fig. S1). Insects were captured with five different Malaise trap types: three variants of the Townes Malaise trap and two variants of the Bartak Malaise trap. The tent-like traps were operated at catching intervals averaging 14 days. Ethanol 80% was used as a preservative. Traps varied in shape, roof colour and capture bottle (Fig. 1). There were two large Townes traps of equal size, one with a white roof (Townes large white: TowLW) and one with a black roof (Townes large black: TowLB). The large Townes traps had a roof width of 0.6 m at each side. The third Townes model was a smaller variant of the black Townes trap (Townes small black: TowSB) and is currently used in the LTER-D Malaise trap program (Welti et al. 2022). It was lower but as long as the other Townes models and had a roof width of 0.53 m at each side. The roof of the Townes traps reached down 44% of their total trap height at the front and 18% resp. 33% (TowLB/TowSB) at the back. Besides Townes models, there were two variants of a brown-green Bartak trap. There was one variant having an eclector bottle (Bartak Eclector: BarEcl), which was supposed to increase phototrophic attraction (Uhler et al. 2022a), and one having a conventional capture bottle (Bartak Conventional: BarConv). Bartak traps had a longer shape than Townes traps and a roof with a width of 0.5 m maximum at each side (front). The roof of the Bartak traps reached down 25% maximum of their total trap height at the front. Both trap shapes (Townes and Bartak) were highest at the front, but while the back of the Townes trap was ~0.8 cm lower than the front, the back of the Bartak traps went all the way to the ground.

Species determination and weighing

A total of 130 samples were screened for butterflies and noctuid moths. Noctuid moths were chosen because they belong to the heaviest insect families in a Malaise trap sample, similar to butterflies, and the aim of the study was to identify the impact of catching bias on total insect biomass. Half of the samples came from the Hunsrück region and one quarter each from Spessart and Steigerwald. By catching butterflies over a sampling period of three months, we took care of the weekly fluctuations in the occurrence of adult butterfly species and increased the diversity captured.

Butterflies were identified to species based on morphology using Settele et al. (2015). Because of damage, some individuals were assigned a higher taxonomic level and marked with 'sp.' (Hoffmann et al. 2024a). Noctuid moths were identified to family using the determination key for noctuidae in Schaefer (2017) and a field guide by Steiner et al. (2014). They were assigned to a size class depending on their forewing length (see supplementary material Table S1). Therefore, only the abundance for each size class was noted without identification to species. The classification facilitated the calculation of the noctuid moth mass per sample from classified individuals and a class-specific mean body mass.

The total insect biomass was extracted from Uhler et al. (2022b). Up to six well-preserved specimens of each species were weighed (Hoffmann et al. 2024b). The number of weighed individuals per species varied between one to six because specimens were damaged or occurred only in low numbers. Weighing was performed by removing the specimens from alcohol, shaking them briefly to remove residual alcohol, and placing them on a precision scale (0.001 g). Butterflies were weighed wet, in accordance with the wet weighing of the total catch biomass (Uhler et al. 2022a; Welti et al. 2022). Afterwards, the mean wet mass of each butterfly species and noctuid moth size class was calculated. For further data processing, the mass of *Phengaris teleius* was used as a mass for *Phengaris nausithous* because of the poor condition of the wings of the latter species. For groups of individuals that could not be determined to species level, the mass of each group was calculated as the mean of the masses of their subordinate species present in our samples. A similar procedure applies to the group of individuals for which no colour pattern was visible at all (group "*Lepidoptera*"). These individuals were monochromous and most

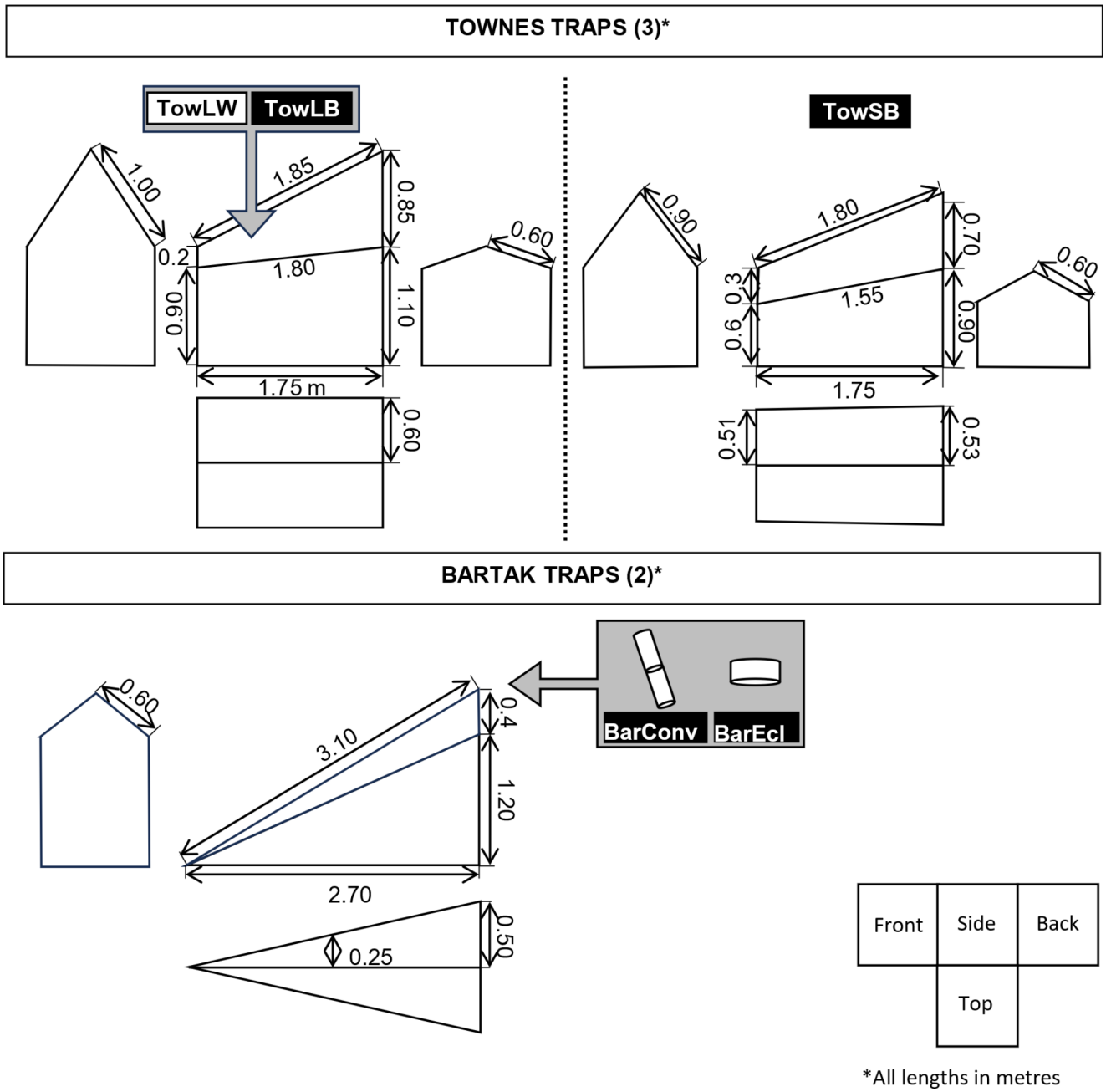

Fig. 1 Trap characteristics of the five different Malaise trap types included in the trap comparison: Three Townes Malaise traps and two Bartak traps. The Townes traps were two large variants differing in roof colour (TowLW in white and TowLB in black) and a smaller variant with a black roof (TowSB). Bartak traps were of dark colour and differed from each other in the capture bottle, with one having an eclector bottle (BarEcl) and one having a conventional capture bottle (BarConv). Traps are illustrated to scale

likely *Maniola jurtina*, *Aphantopus hyperanthus*, *Pieris rapae*, or *Pieris napi.* Therefore, the mass of this group was calculated from the average masses of these species.

Butterfly species traits

Each butterfly species was matched with physical and behavioural traits from seven categories (see supplementary material Table S2). (1) Body size was used as a continuous variable, while (2) egg laying location, (3) feeding behaviour, (4) mate locating location, (5) basking site, (6) wing colour, and (7) habitat preference were used as categorical variables. The selection of traits was based on their possible influence on butterfly response to trap characteristics. Typical butterfly actions like flying, feeding, resting, interaction and oviposition served as a guidance (Popović et al. 2022).

(1) For butterfly body size, the average wingspan (in mm) of female butterflies was retrieved (Komonen et al. 2004; Öckinger et al. 2010; Kuussaari et al. 2014). Average female wingspans were extracted from the trait database of European and Maghreb butterflies by Middleton-Welling et al. (2020). Wingspans were classified into five categories (see supplementary material Table S3), similar to Blitzer et al. (2016).

(2) Uhler et al. (2022a) showed that differences in the residence height of insects above the ground can lead to different species compositions in Malaise trap types. We therefore characterised insects according to their egg-laying location, assuming that a considerable amount of time is used for oviposition (Popović et al. 2022) and butterflies fly at the height of their hostplant in that time (Beccaloni 1997). We matched the traits to the species following the classification of Pöyry et al. (2009): 'grass', 'herb' and 'woody plant', expecting a different catchability of butterflies caused by higher (woody plants) and lower flight heights (grass and herb). Data was extracted from Settele et al. (2015). *Melanargia galathea*, which drops its eggs from the air while flying close to the vegetation, was matched with the egg-laying location 'grass'.

(3) In terms of feeding behaviour, all detected butterfly species feed as adults on flowering herbs (Middleton-Welling et al. 2020). Because of the assumed impact of habitat height above the ground, butterflies were categorised into adult tree-feeders which can additionally feed on shrubs or trees and adult non-tree-feeders which do not use woody plants as a food resource. Data was derived from Middleton-Welling et al. (2020).

(4) Each species was classified into its preferred mate locating location using the grass zone as a threshold to distinguish between species spending their time near ground level or above. Consequently, species were split into those for which grass is a potential mate-locating location and those which have never been observed searching for a partner in the grass zone. The data was derived from Middleton-Welling et al. (2020), supplemented by data for *P. teleius* by Popović et al. (2022).

(5) For the basking site, the grass zone was used as a threshold, too. Following mate locating location, species were split into those for which grass is a potential basking site and those which have never been observed basking in the grass. Data was extracted from the dataset of Middleton-Welling et al. (2020).

(6) Wing colour was categorized as an ordered categorical variable with brightness levels on a scale from 1 (white) to 6 (black) following Bladon et al. (2020). Brightness levels were additionally classified into three different wing colour categories (see supplementary material Table S4).

(7) The classification of the habitat preference in open habitat, habitat generalist and forest is based on Betzholtz and Franzen (2011), without an additional differentiation in deciduous and coniferous forests. Data on habitat preference was extracted from Settele et al. (2015).

Statistical analysis

Analyses were performed using R version 4.1.2. In the first step, we calculated the relative occurrences of individuals per species for each trap type. The species abundances of a trap type in different regions and sites (meadow/forest) were pooled. To see the catchability of the butterfly species with the different trap types, we used these relative species abundances for a principal components analysis (PCA). For the PCA, we only used species occurring with at least two individuals and butterflies that were determined to the species level.

For each species, we calculated and extracted the trap type(s) with the strongest deviation from an assumed even distribution of individuals across all five trap types (20% TowLW, 20% TowLB, 20% TowSB, 20% BarConv, 20% BarEcl), and classified species according to the resulting trap bias. Species with a positive deviation of 30–50% of their individuals from an even distribution in one or more trap type(s) were assumed to have a *pronounced bias* on that trap type(s) and those with a positive deviation of more than 50% of their individuals from an even distribution to have a *strong bias*. Species with a deviation of 15% maximum from an even distribution in any trap type were assumed to be *evenly distributed* over all trap types. For example, *Ochlodes sylvanus*, of which 52% of individuals flew into TowLW, 21% into TowLB, 17% into TowSB, 3% into BarConv and 7% into BarEcl, had a positive deviation of + 32% from an even distribution in trap type TowLW and thus a pronounced bias on that trap type. The remaining species were considered to have a comparably *weak bias* on one or more trap type(s) which was not further discussed.

In the second step, we computed the relative occurrences of individuals per trait for each trap type and further processed them in a PCA followed by a cluster analysis to group butterfly traits according to their similarities regarding the individuals with these traits being caught by the different trap types. For cluster analysis, the K-means cluster algorithm was applied, for which the optimal number of clusters was computed using the total within sum of square method. To ensure that no correlated metrics were used in the PCA and the cluster analysis, butterfly traits were checked for pairwise correlations. Cramer´s V test was used to evaluate correlations between categorical variables and the function 'polyserial' (package 'polycor' in Fox 2022) for relationships between categorical variables and the

continuous variable wingspan. No strong correlations (correlation coefficient > 0.8) were found, and no butterfly traits were excluded (see supplementary material Fig. S2).

Comparisons of species number, total insect biomass, butterfly and noctuid moth biomass between trap types were examined by performing Kruskal-Wallis rank sum tests, followed by Dunn's tests with "bonferroni" as a method to adjust p values for multiple comparisons. In a preliminary step, the butterfly biomass, the noctuid biomass and the total catch biomass were corrected for the number of days a trap was active because 10 of the 130 samples were collected for 13 instead of 14 days.

In the last step, to explore the contribution of butterfly and noctuid moth biomass to total biomass, we used a generalized linear mixed-effects model (GLMM). There were two models created, one for the butterflies and one for the noctuid moths. The butterfly, respectively noctuid moth biomass of a sample was modelled as a fixed predictor for the total catch biomass. To examine if the effects of butterfly and noctuid moth biomass on total biomass vary among trap types, an interaction with the trap type was set. Further, we included the region as a random factor because there was no focus on the differences in total biomass between regions. Since the residuals of the total insect biomass were not normally distributed, we used a gamma distribution in combination with its canonical link function 'inverse'.

Results

Across all 130 samples, we found a total of 1.621 butterflies covering 37 species (see supplementary material Table S5). Out of that total, 136 individuals were determined to a higher taxonomic level because individuals were damaged. Additionally, we found 1.575 noctuid moths (see supplementary material Table S6). TowLW having a white, high and wide roof caught most butterfly species on average per sample and significantly more species than BarEcl and BarConv which had a low and narrow roof (Fig. 2a, $p < 0.01$). Second most butterfly species on average were caught by TowLB and TowSB. They mostly differed from BarEcl and BarConv in terms of trap shape, not capture area. For each butterfly captured, we found the butterfly biomass of Townes traps to increase more than the one of Bartak traps indicating different catchabilities of species with different body sizes for these trap types (Fig. 2b). This led to differences in butterfly biomass per sample between traps of different shape and roof colour (TowLW and BarConv/BarEcl, Fig. 2c, $p < 0.01$), but not between traps of different shape and equal roof colour (TowLB, TowSB, BarEcl, BarConv). For noctuid moths, we did not find any significant differences in their biomass per sample between trap types (see supplementary material Fig. S3). We found the highest total insect biomass per sample in TowLW and a significantly lower total insect biomass in TowSB, BarConv and BarEcl (Fig. 2d, $p < 0.001$). Depending on the trap type and the season, the proportion of butterfly biomass on the total insect biomass per sample ranged between 0 and 18%.

We found butterfly species to be caught differently by the Malaise trap types (Fig. 3). In our PCA, there were 66.4% of the variance in butterfly species catchability with the different trap types explained by the first two PCA axes. Fourteen species had a pronounced bias on a trap type, mostly on one or both of the large Townes traps, such as *Nymphalis polychloros*, *Phengaris teleius*, *Pieris napi*, or *Araschnia levana*. Six butterfly species even had a strong bias on trap types, such as *Pieris brassicae or Pararge aegeria* on TowLW, or *Celastrina argiolus* on TowLB. Four species did not show a pronounced difference in catchability among the traps. They are situated on the left side of the graph. Among these species were *Caracharodus alceae*, *Coenonympha pamphilus*, *Hesperia comma* and *Coenonympha arcania*. The first PCA axis captured this species-specific degree of bias on certain trap types. There was a gradient of butterfly catchability indicated in the direction of the first PCA axis. Starting from the most negative values on the first PCA axis, where the catchability of species was almost equal for all trap types, including BarEcl and BarConv (dark, narrow and low roof), the catchability of species in TowLW (white, wide and high roof) increased along the first axis.

Subsequently, we substituted butterfly species with their traits and found that also the traits occurred with different numbers of individuals in the Malaise trap types. Butterflies formed seven clusters that were characterized by trait combinations (K-means clustering) and 86.3% of the variance in the relative number of individuals per trait in the trap types was described by the first two axes of a corresponding PCA (Fig. 4). Every butterfly trait occurred with the highest relative number of individuals in TowLW (see supplementary material Table S7). But for butterflies with traits of cluster 1 ('preference for open habitat', 'egg laying in grass', 'smallest sized', 'partly dark', 'non tree-feeder') catchability was least skewed towards TowLW (38–44% of butterflies with these traits in the white Townes trap). Apart from this, they were caught in almost equal numbers by the remaining four trap types which can mean equal catch efficiencies of different trap shapes (Townes/Bartak) for butterflies with traits of cluster 1. Contrastingly, 59–64% of butterflies with traits of cluster 4 ('large', 'living in the forest', 'laying their eggs on woody plants') occurred in TowLW. At the same time, they have never or rarely occurred in the Bartak traps. Abundance patterns of traits in Cluster 2 ('mate locating in grass', 'never mate locating in grass', 'basking in grass', 'habitat generalist') and 3 ('small sized', 'tree feeder',

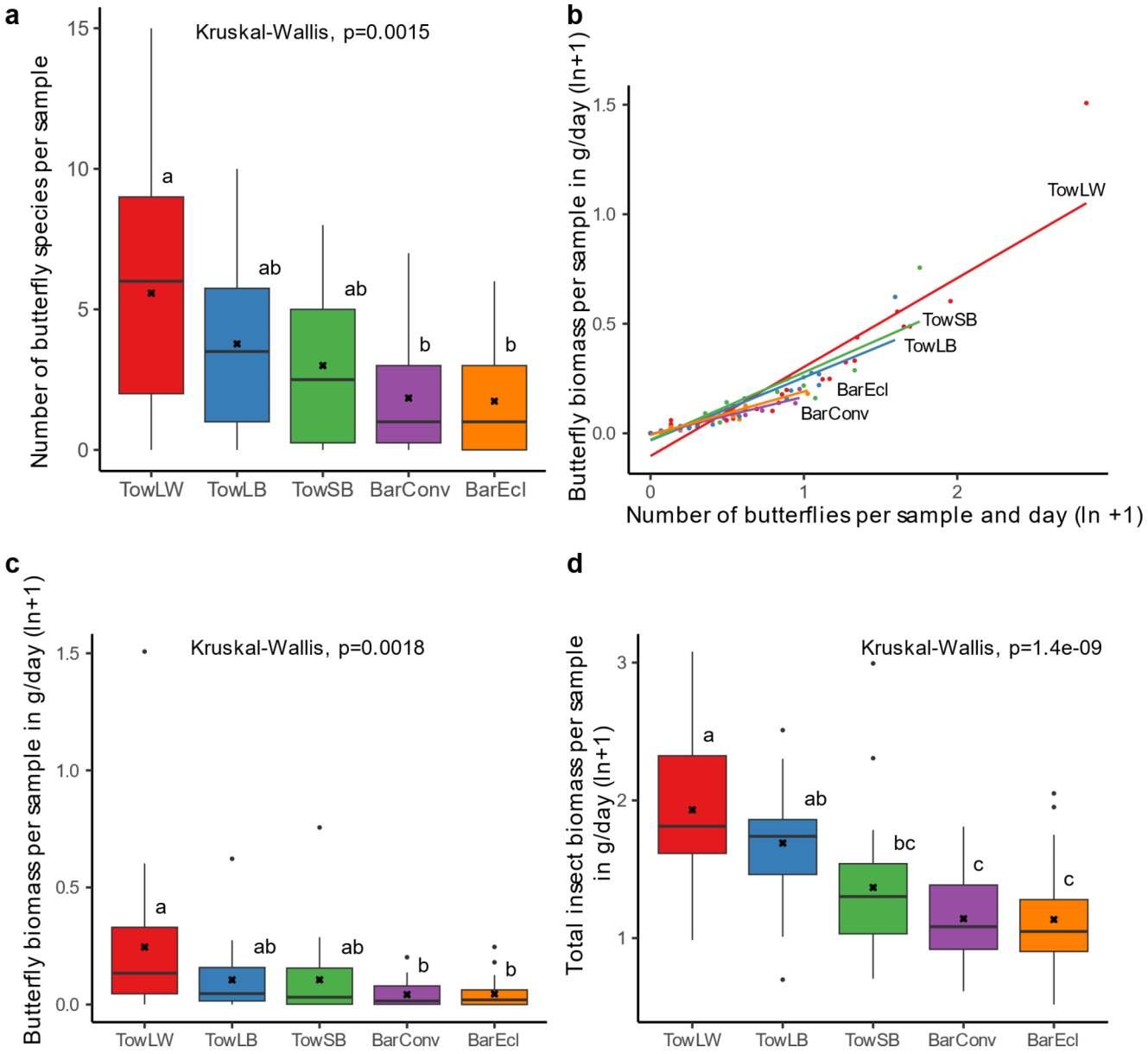

Fig. 2 Malaise trap types and the number of butterfly species caught per sample (**a**), relationship between number of individuals per day and butterfly biomass per day (**b**), butterfly biomass per day (**c**) and the total insect biomass per day (**d**) caught by each trap type. Total insect biomass was extracted from Uhler et al. (2022b). Comparisons of data for each parameter were performed using a Kruskal-Wallis rank sum test followed by a Dunn's test. Significant differences between trap types ($p < 0.05$) are marked with different letters. (TowLW = Large Townes trap with white roof, TowLB = large Townes trap with black roof, TowSB = small Townes trap with black roof (), BarConv = Bartak trap with conventional capture bottle, BarEcl = Bartak trap with eclector bottle

'middle sized', laying eggs on herbs') complete the pattern of a catchability gradient along the first PCA-axis which had already been identified for the species. Again, we saw an increasing catchability of butterflies with TowLW (white, wide and high roof) when having the traits in the positive direction of the first PCA axis. Along this gradient, body sizes and host plant heights also increased.

In parallel to the upward trend in TowLW, we observed a decreasing catchability of butterflies with the Bartak traps (dark, narrow and low roof) when having the traits in the negative direction of the first PCA axis. As the decrease only occurred in the Bartak traps, an influence of roof design on species capture seems possible.

Finally, the catch efficiency of TowLW reached its peak when it came to the capture of pale butterflies (Cluster 5). 67% of pale butterflies were captured by TowLW. In contrast, butterflies with a dark wing colour (Cluster 6) showed a similar catchability pattern as traits of Cluster 1 but

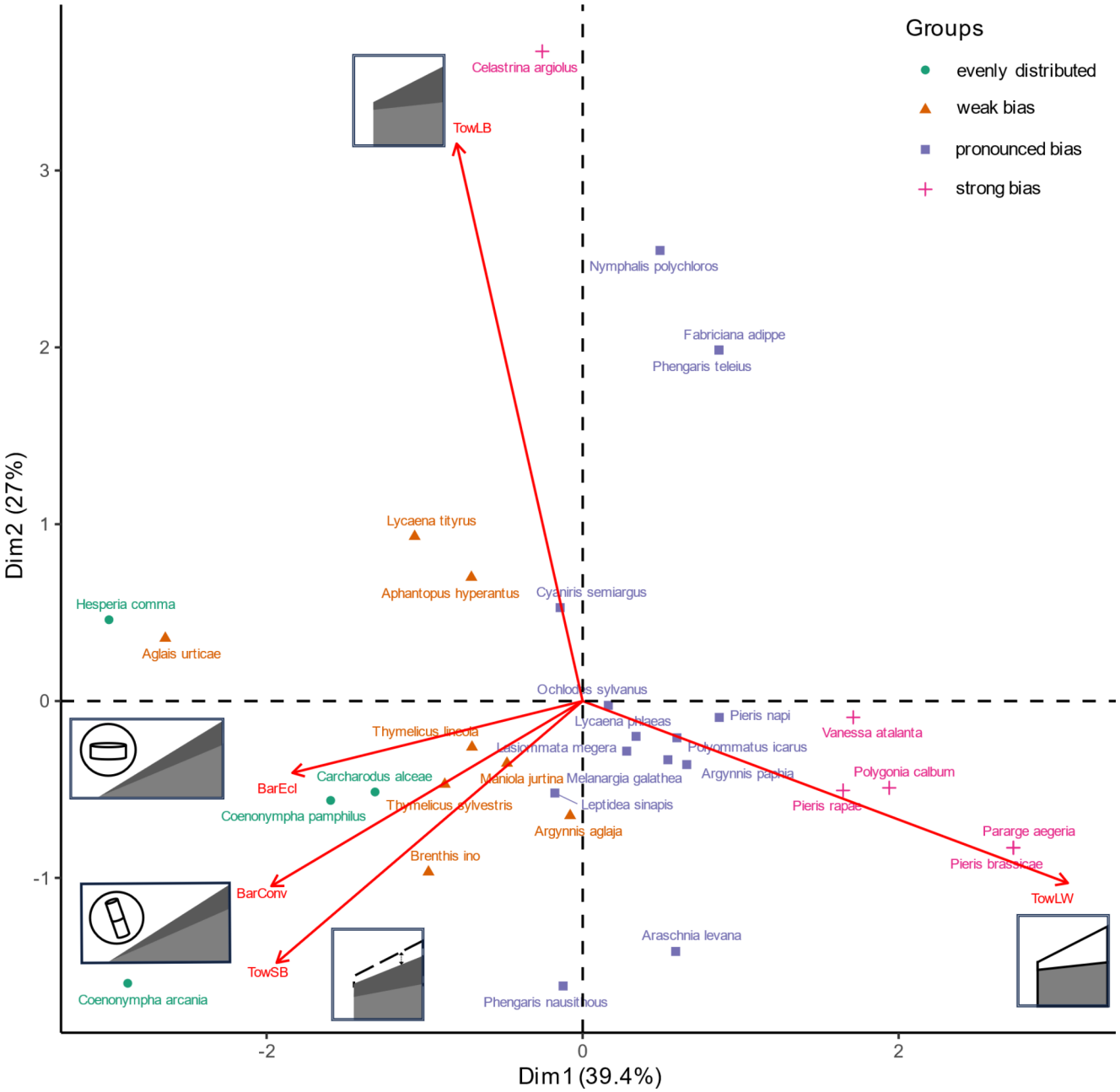

Fig. 3 PCA biplot of butterfly species. The position of the butterfly species relative to each other shows their similarities and differences in terms of capture by the different types of traps (arrows). The shorter the distance of a species to a trap type, the higher its abundance in the trap. The bias of each species on one or more trap types(s) is displayed with different colours. Four species were evenly distributed among trap types and six species had a strong bias on TowLW/TowLB. TowLW = Large Townes trap with white roof, TowLB = large Townes trap with black roof, TowSB = small Townes trap with black roof, BarConv = Bartak trap with conventional capture bottle, BarEcl = Bartak trap with eclector bottle

differed in capture rates from the other trap types. Cluster 7 had an outstanding high abundance in TowSB (30%).

With our GLMM we found that butterfly biomass affected total insect biomass, but the contribution of butterfly biomass to total insect biomass varied among the five different types of Malaise traps (Table 1). This is reflected in the different slopes of the relationship between butterfly biomass and the biomass of the other insects (Fig. 5a) which describe the different selectivity of the trap types for butterflies. Adjusted R^2 for butterflies ranged between < 0.01 in BarConv to 0.25 in TowSB. The intercept indicates the mean catchability of the traps for species other than butterflies. Mean masses of other insects than butterflies varied, between 2.2 g per day for BarConv and 6.6 g per day

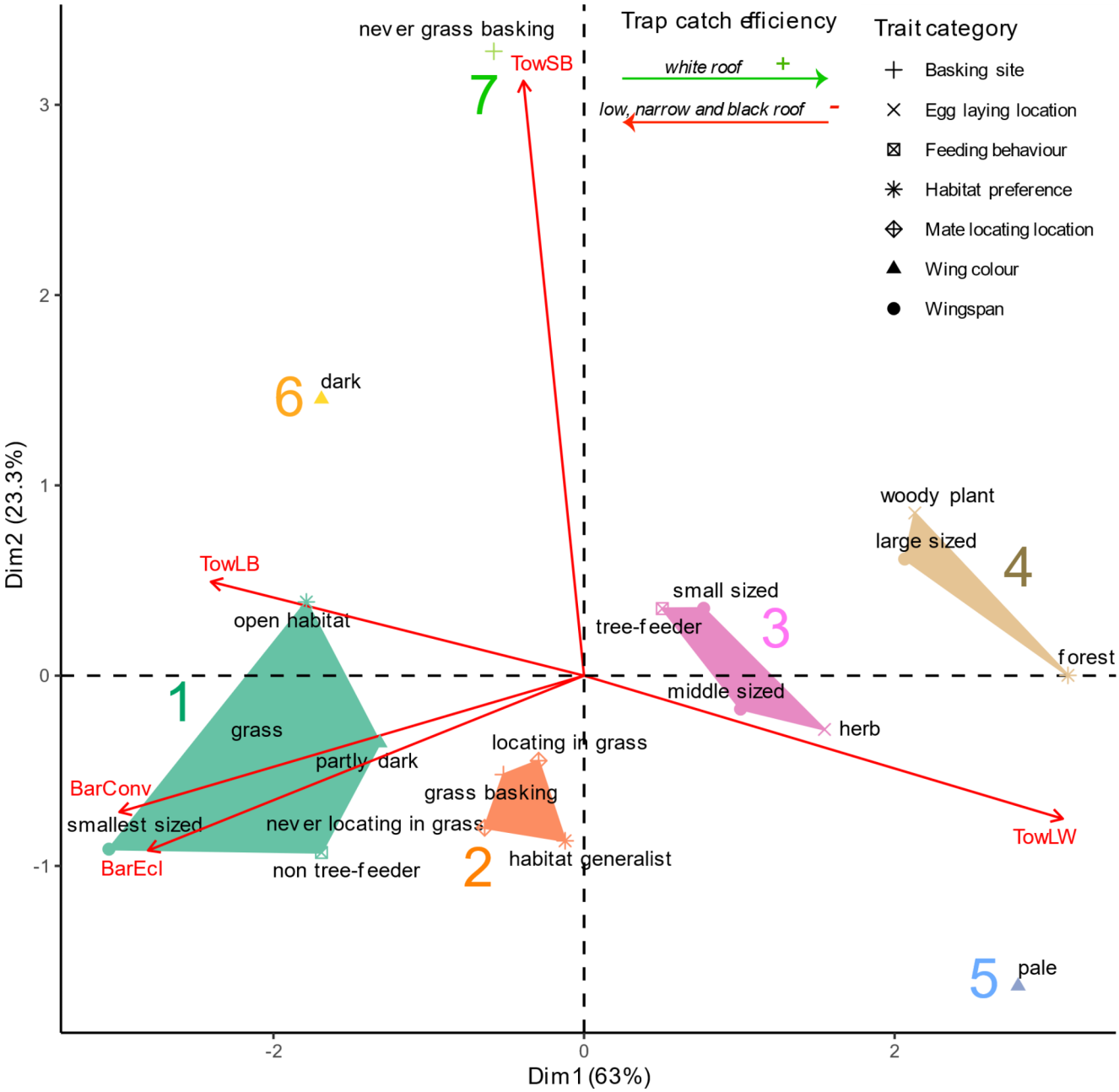

Fig. 4 PCA biplot of butterfly species traits. The position of the butterfly species traits relative to each other shows their similarities and differences regarding the number of individuals per trait captured by the different types of traps (arrows). The shorter the distance of a trait to a trap type, the higher the relative number of individuals with this trait in the trap type. Butterfly traits were grouped into seven clusters and formed a catchability gradient in the direction of the positive first PCA axis, displaying a rising catchability of butterflies with the corresponding traits in the white Townes trap (increasing trap catch efficiency of the white roof). Simultaneously, in the direction of the negative first PCA axis, we observed a negative trend in the catchability of butterflies with the corresponding traits only in the Bartak traps (decreasing trap catch efficiency of the low, narrow and black roof). TowLW = Large Townes trap with white roof, TowLB = large Townes trap with black roof, TowSB = small Townes trap with black roof, BarConv = Bartak trap with conventional capture bottle, BarEcl = Bartak trap with eclector bottle

for TowLW. BarConv had the highest selectivity for butterflies. Here, the increase in biomass of other insects per unit butterfly mass is the lowest. In contrast, BarEcl had a very low selectivity for butterflies. The largest additional mass of other insects is caught per unit of butterfly biomass. Townes traps caught higher biomasses and biomasses of other insects overall. They also achieved the highest butterfly biomasses. Intermediate masses of additional insects were also caught relative to the butterfly biomass in the trap. For the noctuid moths, we also found significant variation

Table 1 Results of the GLMM for total insect biomass per day (Gamma distributed response variable with inverse link function) in relation to butterfly biomass per day, trap type and an interaction between butterfly biomass per day and trap type. The region was set as a random factor. Results of the GLMM for noctuid moth biomass were added in parentheses. Significant p-values are marked with an asterisk

Predictors	Estimate		Std. Error		*P*-value	
(Intercept)	0.185	*(0.176)*	0.052	*(0.054)*	**<0.001***	***(<0.01*)***
Biomass butterflies (*noctuid moths*)	-0.019	*(-0.016)*	0.007	*(0.024)*	**<0.01***	*(0.509)*
Trap type TowLB	0.062	*(0.069)*	0.023	*(0.028)*	**<0.01***	***(<0.05*)***
Trap type TowSB	0.178	*(0.221)*	0.031	*(0.043)*	**<0.001***	***(<0.001*)***
Trap type BarConv	0.278	*(0.294)*	0.046	*(0.052)*	**<0.001***	***(<0.001*)***
Trap type BarEcl	0.326	*(0.308)*	0.045	*(0.054)*	**<0.001***	***(<0.001*)***
Biomass butterflies (*noctuid moths*): Trap type TowLB	-0.096	*(-0.030)*	0.046	*(0.041)*	**<0.05***	*(0.457)*
Biomass butterflies (*noctuid moths*): Trap type TowSB	-0.192	*(-0.266)*	0.034	*(0.073)*	**<0.001***	***(<0.001*)***
Biomass butterflies (*noctuid moths*): Trap type BarConv	-0.468	*(-0.134)*	0.591	*(0.156)*	0.429	*(0.377)*
Biomass butterflies (*noctuid moths*): Trap type BarEcl	-1.081	*(-0.543)*	0.262	*(0.307)*	**<0.001***	*(0.077)*

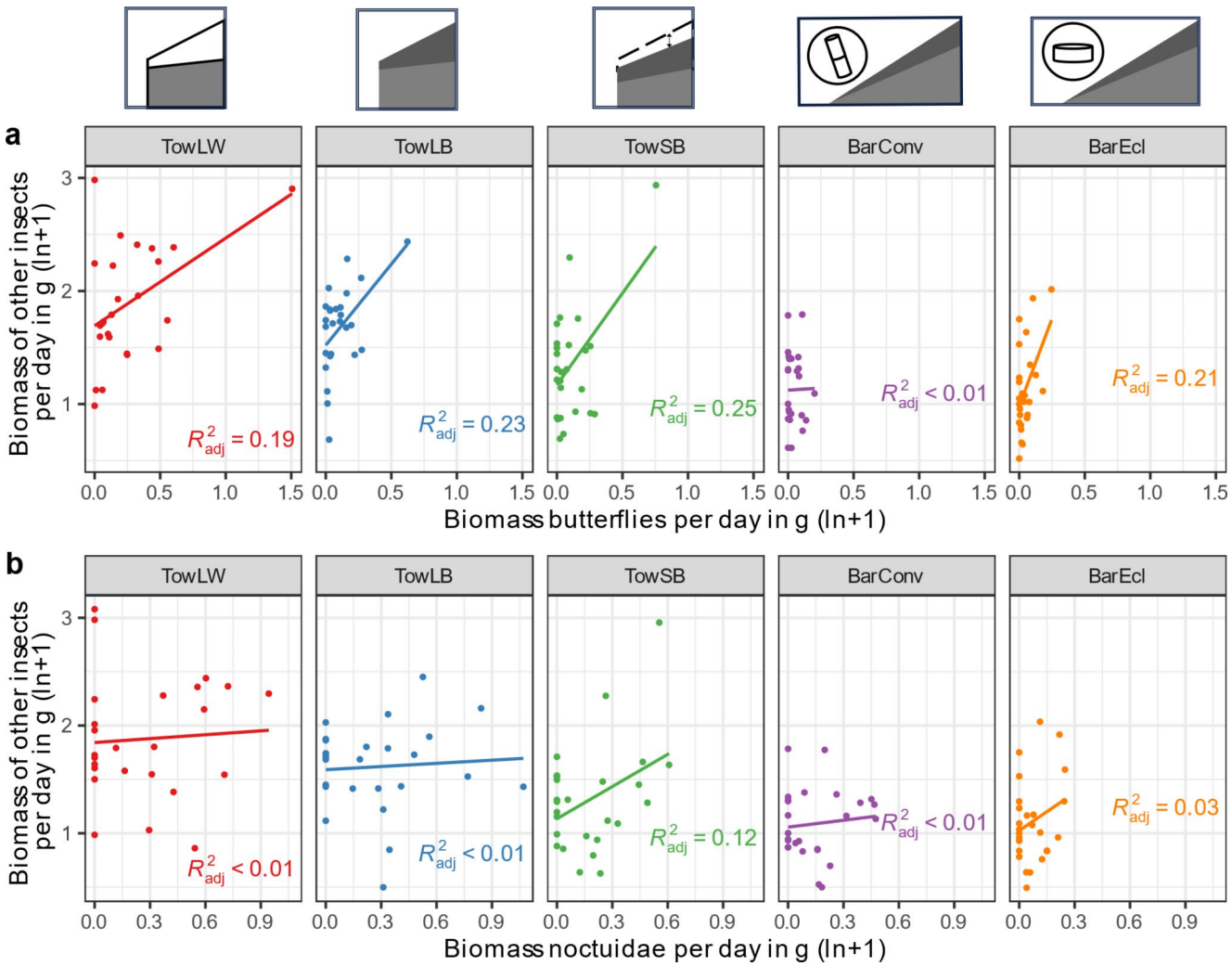

Fig. 5 Logarithmic biomass of other insects per day plotted against logarithmic biomass of butterflies per day (**a**), resp. against logarithmic biomass of noctuid moths per day (**b**), for all five trap types: Large Townes trap with white roof (TowLW), large Townes trap with black roof (TowLB), small Townes trap with black roof (TowSB), Bartak trap with conventional capture bottle (BarConv) and Bartak trap with eclector bottle (BarEcl). For each trap types, linear regression lines and adjusted R^2 were added

between trap types in the contribution of noctuid biomass to total biomass (Table 1). Here, adjusted R^2 varied from < 0.01 in TowLW, TowLB and BarConv to 0.12 in TowSB (Fig. 5b). BarConv also showed the highest selectivity for noctuid moths.

Discussion

Our study revealed marked differences in butterfly species catchability patterns among different Malaise trap types. We suggest the species catchability to be affected by butterfly species traits as butterfly species traits were also represented with different numbers of individuals in the Malaise trap catches. This is likely the result of trap-specific trait catch efficiencies due to different roof colours and trap shapes.

We found white, wide and high roofs, represented by trap type TowLW, to have the highest catch efficiency for all traits in our study, resulting in greatest butterfly species and biomass. White roofs increased catch efficiency, specifically for pale butterflies and forest inhabitants. Traps with dark roofs captured fewer butterfly species and had a lower butterfly biomass.

Between the dark Townes traps and the dark Bartak traps, we identified different catch efficiencies regarding butterfly wingspans, egg-laying locations, and feeding preferences. Townes traps performed better at capturing butterflies with larger wingspans, as well as those having higher egg-laying locations above the ground (woody plants), and having the opportunity to feed on trees, presumably due to a higher capture rate of high-flyers. For low flyers, Townes traps and Bartak traps captured almost the same numbers.

The selectivity for butterflies of Townes traps was intermediate. Among the Bartak traps, the selectivity for butterflies varied, with conventional sampling bottles showing a high, and eclector bottles showing a low selectivity. This trait-dependent efficiency in catching butterflies and butterfly selectivity therefore can affect the butterfly biomasses that are caught with the different trap types. Depending on the trap type, season and habitat, this can have the potential to affect overall insect biomass results.

Effects of species traits on the catchability

Our results imply that the high catch efficiency of the white Townes trap is due to its roof design, which is most suited for the majority of butterfly traits, and consequently, behavioural patterns, in line with the findings of Uhler et al. (2022a) that this trap captures the largest number of butterfly species. Especially, we observed a large share of pale butterflies and forest inhabitants being caught in this trap. We propose that this high capture efficiency for pale and forest butterflies is linked to the white colour and the light permeability of the roof, which a dark roof is lacking. Pale species, which in our study mainly were the Pierids, seemed to be more attracted by the white roof than dark species. Dark butterflies tended to fly more equally into white and black-roofed traps. This may be due to family-specific colour perception abilities and feeding preferences, as the white roof of the trap could be thought to be a batch of white flowers from a distance (Stavenga and Arikawa 2006; van Achterberg 2009). Another explanation could be a family-specific flight behaviour inside the trap. Due to their bright colour and the missing mimicry option, Pierids use rapid flight to reach higher grounds in the escape mode (Syrgley and Chai 1990; Almbro and Kullberg 2009). The white colour of the roof offers a possible path out of the trap where the Pierids can fly to. Darker species, that have the option of mimicry, tend to hide in the vegetation and camouflage themselves (Vallin et al. 2006). Here, the white roof may not cause as strong a bias as it does for Pierids.

The white-roofed trap may also have a high catch efficiency for butterflies living in the forest because it offers bright light conditions that forest butterflies use to visit (Kozel et al. 2021). In the forest, bright tree gaps offer several favourable biotic and abiotic environmental conditions for butterflies. There, they find a larger flower cover and a high number of flowering plant species usable as host plants (Braun-Reichert et al. 2021), a large understorey height diversity for shelter or roosting (Zellweger et al. 2016), and a higher irradiance and temperature (Ritter et al. 2005) for behavioural thermoregulation (Kemp and Krockenberger 2002) and spontaneous movements (Mellanby and Gardiner 1997). The advantage of bright light conditions for the capture of forest species is also indicated by the higher number of forest inhabitants in the Bartak trap with the eclector bottle compared to the Bartak trap with the conventional capture bottle because the eclector bottle was designed to increase light availability due to a clear plastic cover.

Apart from different wing colours and habitat preferences in trap types, we also found differences in the abundance of butterflies with differing wingspans, egg-laying locations and feeding behaviours between trap types. For example, butterflies with a wingspan larger than 60 mm were captured almost exclusively with Townes traps. The smaller the butterflies were, the more often they also appeared in the Bartak traps. In this context, McCravy et al. (2019) reported higher escape rates for larger insects from Malaise traps. Hence, it seems possible that a narrower trap design and a lower coverage of the intercept panel by the roof increases the escape rate of large butterflies.

Townes traps performed better than Bartak traps in the capture of butterflies laying their eggs on woody plants and feeding potentially on trees. Whereas we found Bartak traps

performed almost as well as black Townes traps, capturing species laying their eggs in grass and never feeding on trees. What these traits have in common is that they can influence flight height. As such, the egg-laying location of butterflies is correlated with their flight height (Beccaloni 1997; Popović et al. 2022). Female butterflies of some species spend most of their flight time exploring a certain area for possible host-plants while males are locating them around their hatching place (Beccaloni 1997). Consequently, Bartak traps only lowered their escape rates when it came to the capture of low flyers. Such differences in the trapping of insects which were present at different height levels, have also been found by Uhler et al. (2022a), as they identified a higher number of ground-dwelling taxa in Bartak traps than in Townes traps. The trapping of a target insect group at a height where it is mainly present, e.g. where it has its nesting location, has been found by McCravy et al. (2019) to be beneficial for its catchability. Against this background, it seems possible that Bartak traps can lower their escape rates for low flyers because they provide them with direct contact with the roof and guiding them upwards into the sampling bottles.

When considering flight height, additional impacts of the wingspan should also be taken into account. Large butterflies generally fly above the grass zone avoiding the risk of exposing their wings to a clustered environment as it has been investigated for large bumblebees by Crall et al. (2015). This flight behaviour is also the result of a low manoeuvrability in dense vegetation, which was concluded from field experiments by Rayner (1988). In contrast, butterflies with a very small wingspan (20–30 mm) in our study, were mostly individuals of *Hesperiidae* and *Lycaenidae*, and were among the low flyers in the grass zone as it has been observed by Betts and Wootton (1988) for butterflies with short and broad wings. Here, the cluttered environment has favoured adaptations towards a higher manoeuvrability as wing protection (Le Roy et al. 2019). As a result, Bartak traps could become competitive with Townes traps at trapping smaller butterflies because they targeted them where they are mainly present.

In contrast to traits affecting species catchability, we also identified traits that were supposed not to contribute to differences in species abundance in traps, because they were located along the second PCA axis. These were traits of the categories 'basking site' and 'mate locating location' which may be linked to actions butterflies do not spend much time performing (Popović et al. 2022).

Implications for total catch biomass

Trait-dependent efficiency and selectivity in catching butterflies can affect the butterfly biomass that is caught by the different trap types. In our study, we found significant differences in butterfly biomass between white Townes traps and the Bartak traps. Between trap types of different shape but equal roof colour, namely black Townes traps and dark Bartak traps, we did not observe significant differences in butterfly biomass, which we presume to be closely related to an underrepresentation of large and high-flying species.

This general lack of large species in comparison to other sampling methods is common for Malaise traps (McCravy et al. 2019; Kerner et al. 2024). However, it is possible that differences can be more pronounced between traps of different shapes at other local conditions. For example, if many large species are present because of temporal fluctuations. This also applies to butterfly biomasses of black and white Townes traps which, in our study, were not found to be significantly different. For noctuid moths, we did not find any significant differences in their masses between trap types, which could be due to the mitigation of the effect of the roof colour.

Finally, we found butterfly and noctuid moth biomass to contribute differently to total insect biomass because traps showed a different butterfly selectivity. Especially in habitats and seasons where butterflies and noctuid moths contribute a high share to total insect biomass, differences in butterfly biomass have the potential to affect overall insect biomass results. This can particularly apply to those traps with a high butterfly selectivity.

Conclusion

For practical purposes, we can conclude that in the compilation of studies using different Malaise trap types, different species and trait compositions should always be expected between traps of different roof colours (e.g. dark and white) and trap shapes (e.g. Townes shape and Bartak shape). This can consequently cause differences in butterfly biomass and ultimately affect total insect biomass, depending on the butterfly selectivity of the trap type.

In our Malaise trap study, we used butterflies as a model group because their ecological traits are well known. We are aware that for specific studies on butterflies and noctuid moths, non-lethal methods, such as transect walks and light traps, are a better option than Malaise traps. But we assume that our results can be extended to other insect groups with similar traits, e.g. high flying in bees because of large body size, for which Malaise trap are predominantly used.

We provide a basis for screening insect assemblages for over- and under-represented traits depending on the trap type. The affected trait categories include those which can affect the light sensitivity of insects (e.g. wing colour or habitat preference), their escaping ability (e.g. body size) or their flight height (e.g. body size, egg-laying location,

feeding behaviour). Our results provide essential knowledge for the compilation of data between studies performed with different Malaise trap types and highlight the importance of explicitly stating which Malaise trap variant was used for sampling.

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Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by L.H., S.S., J.U., M.P. and L.M. The first draft of the manuscript was written by L.H. and S.S. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability The data that supports the findings in this study is available at Pangaea (Felden et al. 2023). The butterfly and noctuid moth abundance data can be found under https://doi.org/10.1594/PANGAEA.971783 and the butterfly weight data under https://doi.org/10.1594/PANGAEA.971791. The biomass data of the respective samples was reused from Uhler et al. (2022b).

Declarations

Competing interests The authors declare no competing interests.

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