# Is less simply less? A comparison of abundance and biomass losses in auchenorrhynchan grassland communities and their different impacts on trait composition and taxonomical diversity

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ABSTRACT

Declines in insect biomass and individual numbers have been demonstrated in many parts of the world, including central European dry grasslands. It is, howver, unclear if biomass data or individual numbers are superior as measures of change in species composition, and in trait composition of insect communities. We revisited a former study of ours demonstrating severe losses in abundance of planthoppers and leafhoppers in Central European grasslands since the 1960s. We performed a series of univariate, multivariate and trait-based tests to investigate the relationship between biodiversity change and environment, and compared the results for number-weighted and biomass-weighted community data.

While both individual numbers and biomass declined strongly over time, no changes in species diversity (Jost's D) were observed irrespective of the measure used for weighting. Surprisingly, metrics for trait diversity tended to increase over time in both the number-weighted and biomass-weighted data. For both measures, community composition changed strongly over time for species and trait data, and was also associated with landscape structure and mean annual precipitation. Of the tested traits, we only found associations between an early phenology and time, and a temporal increase of species over-wintering in a nymphal stage, but again there was no major difference between the measure used for weighting.

Our study shows that declining assemblage size (regardless of the measure used) does not necessarily translate in concomitant changes in functional diversity or trait diversity. From a methodological perspective, no clear evidence emerged for either biomass or individual number as measure of assemblage size being more sensitive to environmental change. This implies that conversion of widely used data of individual numbers to biomass values is unlikely to bring much additional insights. With respect to the general scarcity of quantitative data on insect communities, the focus should be on using whatever data is available.

## 1. Introduction

There is increasing evidence for worldwide declines of terrestrial insect individual numbers and biomass (van Klink et al., 2020), and a recent report for German landscapes which comprises the time span of 2008–2017 found biomass declines of 67 % for grasslands and 41 % for forests (Seibold et al., 2019). Here, we revisit data from an earlier long-term investigation (Schuch et al., 2012) on changes in insect richness and abundance in dry grasslands of Central Europe. We previously showed that individual numbers of planthoppers and leafhoppers (Hemiptera: Auchenorrhyncha, hereafter 'leafhoppers' for brevity) had declined by >40 %, and their biomass had declined by ca. 55 % (Schuch et al., 2019) between the 1960′s and the period 2008–2010. This implies that a major loss of insect abundance had probably already taken place before most recent monitoring schemes started. Along with these abundance declines, we found a strong turnover of species, in line with major reviews showing a prevalence of species turnover worldwide (Dornelas et al., 2014, Hillebrand et al., 2017). Thus, there are not only

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**Table 1**
Selected traits for Auchenorrhyncha (data from Nickel 2003). Variable type was abbreviated as I for interval, O for ordinal, and N for nominal.

| Trait variable | Abbreviation | Explanation | Type | Notes |
|---|---|---|---|---|
| Body length, min | Lmin | Minimal body length within a species, from the frontal tip of the vertex to the dorsal tip of the forewing (in mm) | I | separate for sexes |
| Body length, max | Lmax | Maximal body length within a species, from the frontal tip of the vertex to the caudal tip of the forewing (in mm) | I | separate for sexes |
| Body length, mean | Lmean | Mean body length as average of minimum and maximum body length of males and females | I | separate for sexes |
| Body weight | Weight | Dry weight calculated from mean body length | I | |
| Diet width | Hostrange | Degree of host plant specialisation | O | monophagous 1st and 2nd degree; oligophagous 1st and 2nd degree; polyphagous |
| Type of diet | Plantnom | Plant family the species feeds on | N | e.g. Poaceae, Rosaceae, … |
| Dormancy | Overwinter | Developmental stage in which species overwinters | N | egg, larvae, imago |
| Voltinism | Genyear | Generations per year: below one, to up to three | O | 1, 1-2, 2+ |
| Utilized substrates | Resource | Utilization of different types of food sources; the type is largely combined with phylogenetic affiliations | O | phloem, xylem, mesophyll |
| Habitat preference | Habpref | Habitat type in which species mainly occurs | N | dry, dry to wet, wet, dry/wet/disturbed, on wood |
| Dispersal capability | Wings | Wing length | O | long dispersal = macropterous; semi long dispersal = subbrachypterous; short dispersal = brachypterous |
| Phenology – start | Phenostart | Start of phenological season: time first adults appear | I | month of year |
| Phenology – end | Phenoend | End of phenological season: time adults start to disappear | I | month of year |
| Phenology – length | Phenotot | Timespan in which the adults of a species occur during the year | I | duration in months |

quantitative, but also qualitative changes in these communities. However, it remains unclear if these changes in individual numbers, biomass and species composition were associated with changes in trait composition, which might be expected since the functional traits of species should be related to the environment. Environmental changes with respect to land-use and climate have been pronounced in Central Europe over this period (Oliveira et al., 2016, Habel et al., 2019).

Community wide changes in functional traits are commonly measured by community-weighted mean trait composition (CWM), by measuring the multivariate trait variation (functional diversity metrics), or by matching traits to environmental conditions (4th corner analysis). When calculating metrics of taxonomical or trait diversity and composition, the species can be weighted by either the number of individuals observed, or by their combined biomass. Studies on the trait composition of insect communities have traditionally relied on number-weighted measures (e.g. van Klink et al., 2019), whereas studies on plants rely on various abundance proxies including biomass (Grime 1998, Pérez-Harguindeguy et al., 2013). However, the discussion about the importance of insect biomass has received a lot of attention since it was reported in 2017 that 76 % of flying insect biomass had been lost from Western German nature reserves (Hallmann et al., 2017), and recently, researchers have started converting data of individual numbers of insects to biomass (e.g. Macgregor et al., 2019, Schuch et al., 2019, Seibold et al., 2019). This focus agrees with general considerations on ecosystem functioning, i.e. the biomass-ratio-hypothesis (Grime, 1998, Sonkoly et al., 2019). However, it remains unclear if biomass changes or changes in individual numbers are more informative about biodiversity changes in terms of functional trait composition.

There are arguments in favour of and against the use of biomass when studying trait composition. On the one hand, many ecosystem functions and (dis)services depend on the number of individuals performing a certain function. For example, most insectivores can only consume one individual organism at a time, but the ratio between effort to find prey and the energy it provides depends on the size of the organism consumed. In this case, it is more important which kind of prey can be found in sufficient quantities than how much biomass is present in a given habitat. Another example relates to insects as vectors, not only of pollen but also of diseases, and here it is the number of individuals rather than the biomass that largely determines the efficiency as a vector. On the other hand, biomass is more informative regarding the amount of energy that is transferred between trophic levels, i.e. from plants to herbivores to predators, and ecosystem functioning is usually measured in biomass (Grime 1998, Brun et al., 2022). This illustrates that different measures of assemblage size might be of use depending on the problem under question.

Here, we investigate the methodological and ecological sides of declines in insect biomass and number of individuals. From a methodological perspective, we use our long-term dataset to explore whether biomass-weighted biodiversity metrics provide additional or better information on taxonomic and trait biodiversity change over traditional number-based weighting. From an ecological perspective, the general decline in individual numbers and biomass reported previously (Schuch et al., 2012, Schuch et al., 2019) should result in a decline in trait diversity (hypothesis 1). We expect strong changes in both species and trait composition at the community level, and these to be related to changes in climate and landscape composition (hypothesis 2). We also expect to find associations between (changes in) landscape structure, climate, and selected traits of the insect community (hypothesis 3).

We take an exploratory approach to study trait diversity changes of leafhoppers based on biomass and individual numbers, and compare the effect sizes of both measures on different indices of trait diversity and trait composition. We used morphological and ecological traits (Table 1) to compare the trait composition in the 1960s and the 2010s, and relate this to the landscape and climatic changes that occurred over this period.

## 2. Methods

### 2.1. Study sites and sampling

A total of 26 dry grasslands in eastern Germany were sampled between 1963 and 1966 (Schiemenz 1969) and again from 2008 to 2010 (S1). The investigated plots reflect different types of dry grassland vegetation that are spread all over Eastern Germany (detailed information on the study area in Schuch et al., 2012). The methods and sampling seasons from the earlier decade were repeated as well as was possible for the more recent decade: 200 strokes with a Ø 30 cm sweep net at each sampling occasion (Schiemenz 1969). For each decade, the results of the catches (200 strokes per plot) of a spring, summer, and autumn visit were summed up. Thus, the overall sampling frequency for each plot per decade was three, comprising species abundance data of 600 strokes. Hereafter, 1964 to 1966 refers to historical and 2008 to 2010 refers to recent decade. The data set was not fully balanced across both sampling decades (Table S1a).

All auchenorrhynchan individuals were collected, later identified to species level (except for nymphs), and identified in the laboratory using a digital stereo microscope following Biedermann and Niedringhaus (2004). Scientific nomenclature follows Nickel et al. (2016). Females of some genera could not be identified to species level (e.g. *Anaceratagallia*, *Jassargus*, *Psammotettix*). If present, we assigned them to congeneric males, otherwise we identified them at the genus level. In cases of more than one species of a genus, we assumed the proportions of females to correspond to the proportions of males.

### 2.2. Body length, body mass and other traits

The average body lengths for males and females are known for all planthoppers and leafhoppers of Central Europe (Biedermann & Niedringhaus 2004), and are surprisingly stable irrespective of species and sex. This allows obtaining data on average body length for each species from literature. We assumed that females and males occur in a ratio of approximately 1:1. For *Zyginidia scutellaris*, which was particularly common in the 2010s with almost 14,000 specimens caught, we determined a gender ratio of 1.058:1.000. To obtain the approximate biomass
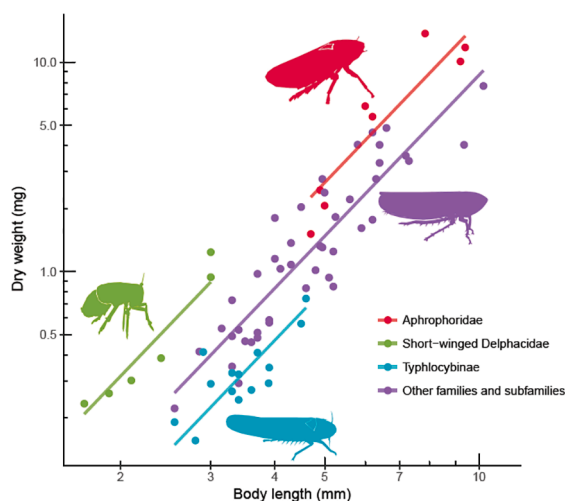


**Fig. 1.** Relation of body length (*s*) and dry weight of leafhoppers and planthoppers. Slopes were identical for the four groups distinguished at s = 2.55678, yet intercepts differed. The main regression model for most families and subfamilies was ln(dry weight) = −3.72698 + ln(mean body length) × s. Three groups differ with respect to body shape, for Aphrophoridae applies: ln(dry weight) = −3.13787 + ln(mean body length) × s; for Typhlocybinae applies: ln(dry weight) = −4.29938 + ln(mean body length) × s; and for brachypterous Delphacidae applies: ln(dry weight) = −2.92340 + ln(mean body length) × s (Schuch et al., 2019).

(dry weight in mg) of each auchenorrhynchan species, we used a regression model (Fig. 1), based on its body length and taxonomic group.

To calculate the dry body biomass based on body length, we fitted a regression model to 72 individuals of at least 56 species from 6 families and 11 subfamilies of Auchenorrhyncha from the private collection of R. van Klink. The individuals were dried in a standardized procedure for 24 h at 60 °C and then weighed (to the nearest three decimal places in mg). The full body length (including the wings, as this is the metric available in the literature) was measured using a stereo microscope with measurement ocular. We used a regression model with $\log_e$-transformed body-length and subfamily (only for the Delphacidae we additionally distinguished between brachypterous and macropterous individuals, as both are common, but differ in total body length) as explanatory variables for $\log_e$-transformed body-weight. We selected the most parsimonious model by a backward selection procedure: we sequentially set the group with the highest p-value equal to the reference level (Deltocephalinae, the most common group in the dataset), until all remaining p-values were <0.05. This model selection procedure resulted in four general groups with differing intercepts: Aphrophoridae (frog hoppers), Cicadellidae: Typhlocybinae, short-winged Delphacidae (planthoppers), and 'typical' Auchenorrhyncha: Cicadellidae: Deltocephalinae, Idiocerinae, Agallinae, Cicadellinae, Aphrodinae, Dictyopharidae, Membracidae, Cixiidae, long-winged Delphacidae. The final models had an explanatory power of $r^2_{adj} = 0.90$. It should be noted that many of the merged (sub)families have few species in Central Europe, and with sufficient data their length-weight relations may differ from those of the Deltocephalinae.

We also compiled other traits from Nickel (2003) and Biedermann and Niedringhaus (2004). We obtained information (Table 1) on dormancy (as egg, nymph or adult), voltinism (1 or 2 generations per year), dispersal capability (brachypterous, subbrachypterous or macropterous), degree of host plant specialisation (diet width: monophagous 1st and 2nd degree, oligophagous 1st and 2nd degree or polyphagous), feeding resource (phloem-, xylem- or mesophyll-suckers), phenology (first month of adult activity and last month of adult activity) for every species. Additionally, every species was assigned to its host plant family/families (i.e. Poaceae, Cyperaceae, Juncaceae, Fabaceae, Asteraceae, Rosaceae, Fagaceae and Betulaceae, and/or rest).

### 2.3. Environmental drivers

With respect to potential drivers of biodiversity change, we evaluated changes in land cover, and compared aerial photographs from the 1960s and from 2008. Cover classes for scrub (including forest), grasslands, cropland, and settlements were expressed as a percentage (in 5 % intervals) for circular buffers within a radius of 200 m around the centre of the sampling plots (using a 50 × 50 m$^2$ grid as visual aid, for details see tables in S1 and Schuch et al., 2011). Historical and recent images were additionally overlaid to double check these estimations. All historical photographs were retrieved from the Bundesarchiv Berlin. As a second potential and independent driver, we obtained data for mean annual temperature (MAT) and mean annual precipitation (MAP) from CHELSA (Karger et al., 2017, were we used the CRUTS subset available for both decades). Temperatures increased uniformly over time, while trends in precipitation differed between sites (Fig. S2).

### 2.4. Statistical analysis

We calculated biodiversity metrics weighted by (i) the number of individuals and (ii) body biomass, except for species richness and functional richness, which are both not weighted by abundances. For taxonomical diversity, we used species richness, abundance/weight (no. of individuals, total biomass), Jost's true species number s($=e^{Shannon}$) and Shannon evenness. We calculated the following trait diversity metrics, again both by numbers and by biomass: Rao's quadratic entropy (RaoQ), functional evenness, functional dispersion and functional

richness using the FD package (Laliberté and Shipley 2009).

To test for changes over time and the effects of climate (hypothesis 1), we used linear mixed models (when appropriate, data were log-transformed) with plot as a random factor. We assessed correlation structures among predictors and selected a predictor for each major group to keep overall complexity of analyses within limits. We started with model simplification using decade (proxy for time, correlated with increasing shrub cover and temperature), % grass cover (proxy for landscape structure) and precipitation (proxy for climate, as temperatures could not be separated from the temporal trend). Models were simplified via ANOVA-based comparison; significances reported refer to the parsimonious models. We used graphical methods to check for model quality. Because of multiple testing, we corrected raw p-values by false discovery rate (FDR) for 8 tests per group.

To assess trends in community composition (hypothesis 2) we used taxonomic compositional data and also calculated community weighted means of traits (CWM) using package FD; for nominal traits and ordinal traits total weight of all individuals in a given group or level was extracted. Similarities in taxonomical composition were visualized using DCA ordination; for analysis in trait space CWM values of all traits were subjected to centred and standardized PCA. Continuous environmental predictors were fitted *post-hoc* on the ordinations and only displayed if (raw) p < 0.05 (499 permutations). Probability values were subsequently also corrected for multiple testing (FDR). Differences between decades were tested with permutation-based Manova, as dissimilarity measure we used Bray-Curtis for species data and Euclidean for trait CWM (variables scaled to zero mean - unit variance), respectively.

Tests of hypothesis 3 were based on fourth-corner analysis for associations between species traits. We selected those traits that were shown as potentially responsive by the PCA on CWM values and the *post-hoc* fitted environmental drivers. We tested significance of responses with permutation using the most conservative Model 6 (library ade4). Probability values were adjusted for multiple testing using false

discovery rate (FDR). The trait-environment combinations that showed significant associations were plotted individually.

## 3. Results

### 3.1. Changes in trait and taxonomical diversity

The mixed models for all univariate biodiversity metrics consistently showed landscape configuration (percentage grasslands in the surroundings of the site) and precipitation to be non-significant explanatory variables, while decade was significant in several models. In line with our previously published results (on a slightly different data set), we found that the number of individuals declined by 52 % (median 625 -> 325, Fig. 2b; lm, $p_{Numbers}$ = 0.010), and total community biomass declined by 59 % (median weight 527 mg -> 215 mg, $p_{Biomass}$ < 0.001), while the number of species showed no change (Fig. 2a, ns). Shannon evenness and Jost's D, when weighted by numbers of individuals, showed a (non-significant) tendency to decline, while this was even less apparent when weighting by biomass (Fig. 2c and d vs g and h). The differences in diversity and evenness between number-weighted and biomass-weighted data are presumably due to the strong increase of *Zyginidia scutellaris*, which was completely absent in the 1960s but very common in the 2010s. It is a very light species, thus contributing many individuals, but relatively little biomass to the community.

Measures of trait diversity revealed additional information. Rao's Q increased over time irrespective of whether the metrics were weighted by number of individuals or biomass (Fig. 3a, e; $p_N$ = 0.006, $p_B$ = 0.017), and functional dispersion showed a similar trend (Fig. 3c, g; $p_N$ = 0.010, $p_B$ = 0.017). Changes in functional evenness were not pronounced in either data set (Fig b, f; ns) yet slightly more obvious in biomass data. Functional richness showed no differences (Fig. 3d, h; ns).
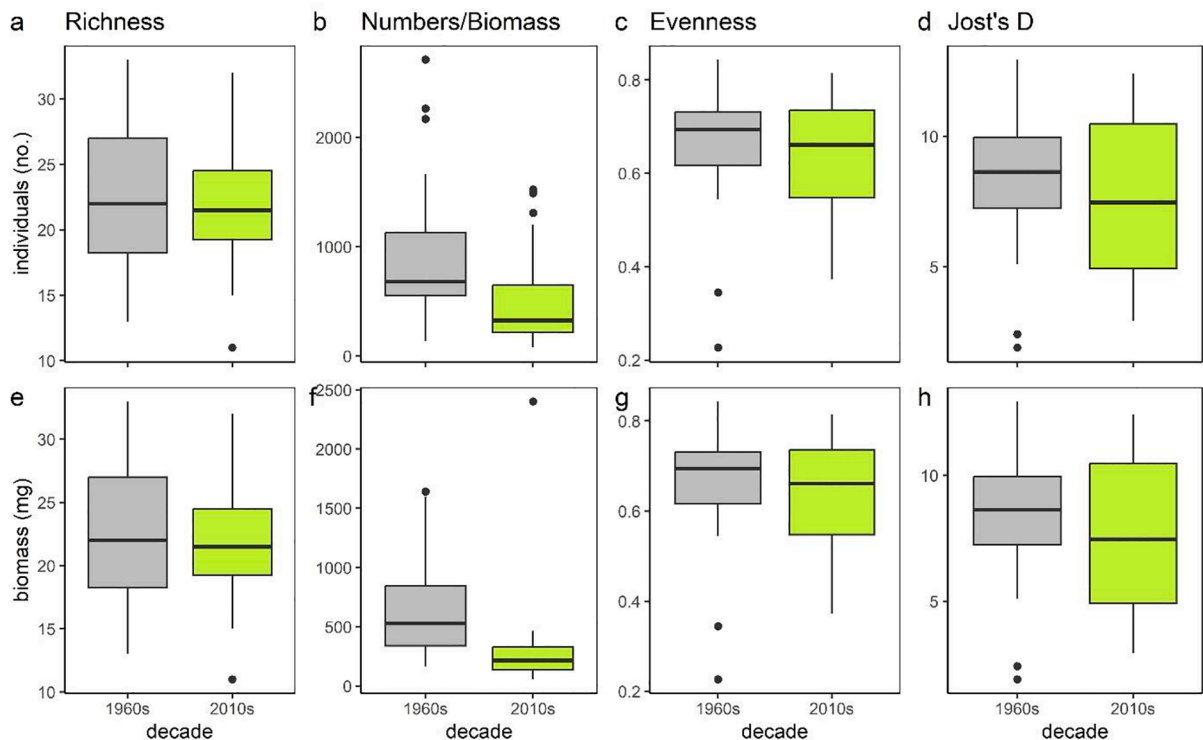


**Fig. 2.** Patterns in taxonomical diversity over time, the first row refers to the individual-number-weighted data, the second row to those on biomass; a, e) plot level richness (non-significant); b, f) abundance in terms of individual numbers or total biomass in mg ($p_{Numbers}$ = 0.0103, $p_{Biomass}$ = 0.0007, log-transformed data); e, g) Shannon-based evenness (both ns), d, g) Jost's true species numbers (both ns). Significances are based on log-transformed data, p-values were FDR corrected for 8 comparisons.

**Fig. 3.** Measures of trait diversity, upper row for data on no. of individuals, lower row for biomass data. A, e) Rao's Q ($p_{Numbers}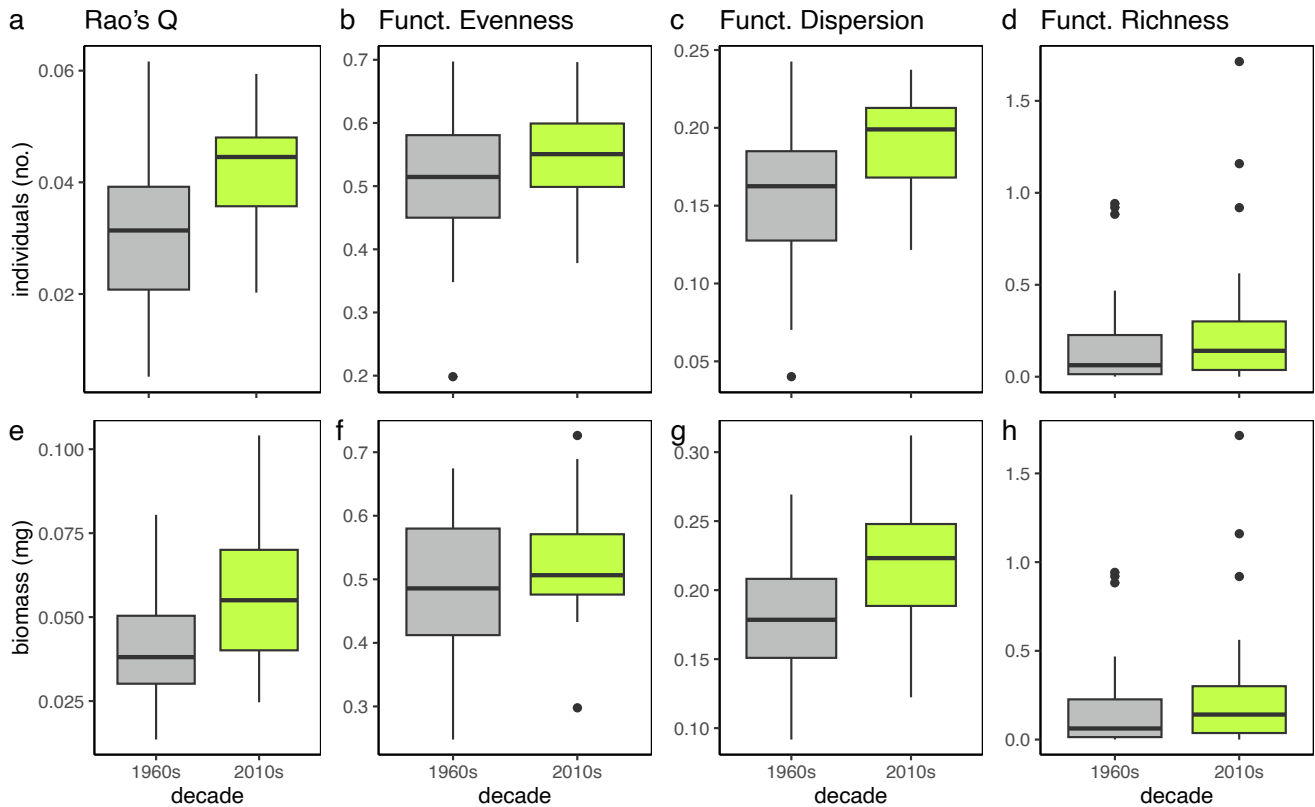$ = 0.0060, $p_{Biomass}$ = 0.0171, log-transformed); b, f) functional evenness (both ns); c, g) functional dispersion ($p_{Numbers}$ = 0.0095, $p_{Biomass}$ = 0.0171); d, h) functional richness (both ns., log-transformed). P-values were FDR-corrected for 8 comparisons.

### 3.2. Changes in community composition

In line with hypothesis 2, we found strong shifts in species composition: the DCA ordination based on individual numbers separated plots from different decades clearly along axis 1. Patterns in the weight-based DCA were, however, less clear (Fig. 4b). Permutation-based Manova showed a significant but in terms of explained variation, modest, effect of decade in both data sets (Bray-Curtis similarity, $r^2_{Numbers}$ = 0.09, $p_{Numbers}$ = 0.002; $r^2_{Numbers}$ = 0.08, $p_{Biomass}$ = 0.002, FDR-corrected for n = 2).

Environmental predictors also changed over time (Fig. S2), with mean annual temperature increasing, mean annual precipitation decreasing, cover of shrubs increasing and cover of grassland showing no temporal trend. *Post hoc* fitting of potential predictors on DCA axes (Table 2a) showed that for both data sets, % grassland cover in surroundings and mean annual precipitation were main predictors associated with species composition.

Changes over time were also apparent in trait composition (Table 2, Table S3). For PCA of number-weighted trait means, plots from different decades were clearly separated in trait space, while the pattern again was less clear for biomass-weighted trait means (Fig. 4c, d). Permutation-based Manova (Euclidean distance of standardized CWMs) revealed a significant effect of decade in number-weighted data, and a weaker yet still significant effect in the biomass data (Euclidean distance based on standardized data, $r^2_{Numbers}$ = 0.09, $p_{Numbers}$ = 0.002; $r^2_{Biomass}$ = 0.04, $p_{Biomass}$ = 0.008, p-values FDR corrected for n = 2). Among the environmental predictors tested (Table 2b), mean annual temperature and mean annual precipitation were associated with PCA axes in both cases, while % grassland in surroundings (and % shrub cover) was only significant for biomass data.

### 3.3. Responses in individual traits

In addressing hypothesis 3, we tested responses of individual traits against relevant predictors according to Table 2b and loadings in Tab S3 using fourthcorner analysis, corrected by false discovery rate (FDR) for multiple comparisons. For the number-weighted data, dormancy was associated with decade, while mean start of phenological season was associated with decade and temperature (Table 3a). There also was a weak tendency (p < 0.1) for an association between resource use and temperature. For the biomass data, only the start of phenological season and decade were significantly associated at p < 0.05, while associations between decade and overwintering mode, as well as between start of phenological season were mere tendencies (p < 0.1). All tests were, however, relatively conservative: Fourthcorner model 6 returns significance only if two permutation tests have been passed, and the correction for multiple comparisons becomes increasingly strict with more response and predictor variables (compare raw p values in Table 3). This implies that retained associations are ecologically meaningful, but also that there may be other, weaker, associations that remained undetected.

The main effects in number-weighted data were that the species overwintering as egg declined in abundance over time, while species overwintering as nymphs tended to increase (Fig. 5a). The numbers of species with an early start of maturity increased, resulting in an earlier mean start of phenological season for the whole community. This is also seen in the correlation between mean annual temperature and phenological activity (Fig. 5b, c). In the more recent decade, start of phenology showed a large variance and stronger response to temperature. Biomass data showed qualitatively similar trends; yet the magnitude was lower (Fig. 5d-f).
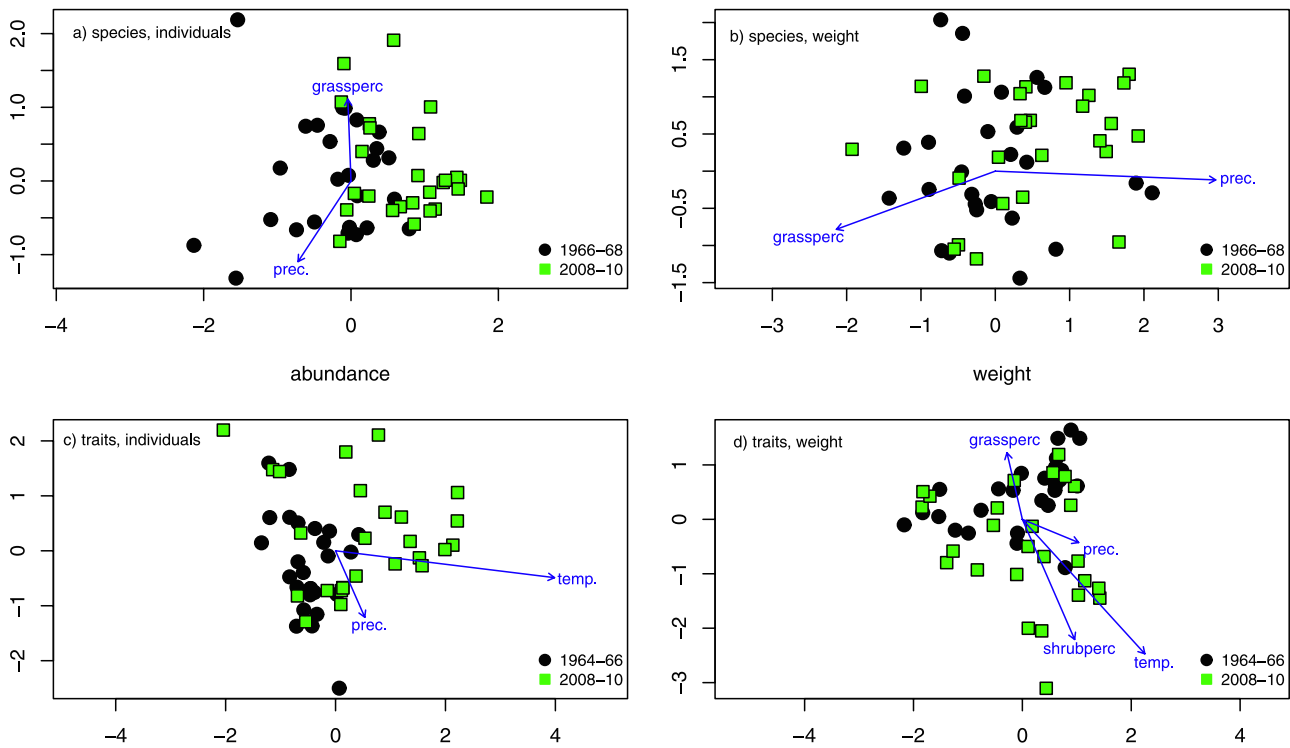
**Fig. 4.** Pattern in community composition, right panel weighted by individual numbers (a, c), left panel weighted by biomass (b, d). DCA ordinations on community composition with detrending by segments and downweighting of rare species: a) species composition for number-weighted data (axis 1 eigenvalues/length of gradient 0.62/4.0; axis 2 0.49/3.5), similar to analysis in Schuch et al. (2012); b) species composition for biomass data (axis 1 0.66/4.0; axis 2 0.49/3.5). PCA ordinations on trait composition (data centred and standardized): c) community weighted means for individual numbers (Eigenvalue/explained variance axis 1 11.3/ 25.4 %; axis 2 6.3/13.6 %); d) community weighted means for biomass data (axis 1 10.5/22.8 %; axis 2 6.6/14.3 %). Environmental predictor variables were fitted *post-hoc* on the ordination plots, shown are those which were significant at $p_{raw} < 0.05$ (1000 permutations). Grassperc/shrubperc = percentage of grassland cover/ shrub cover in the surrounding landscape; temp = mean annual temperature of all plots per year; prec = mean annual precipitation of all plots per year.

**Table 2**
Results of *post hoc* correlation of potential environmental predictors with ordination axes. a) Fit with axes of species composition; b) fit with axes of trait composition. Overall $r^2$-values were assessed by 499 permutations, we report raw p values and after FDR correction (p: (*) < 0.1; *<0.05, **<0.01; ***p < 0.005).

| | Number-weighted | | | | | | Biomass-weighted | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | DCA1 | DCA 2 | DCA3 | $r^2$ | $p_{raw}$ | $p_{adj}$ | DCA1 | DCA2 | DCA3 | $r^2$ | $p_{raw}$ | $p_{adj}$ |
| a) Taxonomic composition | | | | | | | | | | | | |
| % shrub cover | 0.52 | −0.84 | 0.16 | 0.18 | 0.140 | | 0.71 | 0.68 | −0.17 | 0.20 | 0.112 | |
| % grassland | −0.04 | 0.98 | −0.20 | 0.41 | 0.004 | *** | −0.94 | −0.34 | −0.01 | 0.38 | 0.005 | * |
| Mean annual precipitation | −0.55 | −0.83 | 0.11 | 0.56 | 0.002 | ** | 1.00 | −0.04 | −0.04 | 0.65 | 0.001 | ** |
| Mean annual temperature | 0.76 | −0.48 | −0.44 | 0.20 | 0.106 | | 0.59 | 0.77 | 0.23 | 0.22 | 0.070 | |
| b) Trait composition | | | | | | | | | | | | |
| | PC1 | PC2 | PC3 | r2 | $p_{raw}$ | $p_{adj}$ | PC1 | PC2 | PC3 | r2 | $p_{raw}$ | $p_{adj}$ |
| % shrub cover | 0.77 | 0.31 | 0.56 | 0.11 | 0.120 | | 0.36 | −0.82 | −0.44 | 0.20 | 0.010 | * |
| % grassland | −0.52 | 0.06 | −0.85 | 0.12 | 0.111 | | −0.09 | 0.40 | 0.91 | 0.27 | 0.003 | ** |
| Mean annual precipitation | 0.19 | −0.43 | 0.88 | 0.16 | 0.036 | ** | 0.27 | −0.11 | −0.96 | 0.41 | 0.001 | *** |
| Mean annual temperature | 0.93 | −0.11 | 0.36 | 0.39 | 0.001 | (*) | 0.66 | −0.73 | −0.16 | 0.33 | 0.002 | *** |

## 4. Discussion

The aim of this reassessment of our data (Schuch et al., 2012) was to investigate changes in trait composition of Auchenorrhyncha communities of Eastern German dry grasslands over six decades, and to test whether different results would be obtained when measuring assemblage size by individual numbers rather than by biomass. In line with our previous results, we found strong declines in abundance and biomass, but, by contrast, we found an increase in trait diversity, countering hypothesis 1. The changes in species composition could be related to percentage grasslands in the surrounding area and precipitation, whereas trait composition was related to temperature and precipitation, supporting hypothesis 2. In line with hypothesis 3 on individual traits, phenological start of the community was related to temperature and decade, showing that species with an early phenology and species that overwinter as nymphs have become (relatively) more common. Table 4 summarises the results for data weighted by individuals or biomass, which were overall mostly congruent. This suggests that for our leafhopper community these measures are largely interchangeable.

**Table 3**
Summary of fourthcorner analysis for selected traits and main predictors. The rows list the individual pairs of predictor/response tested. The columns describe tested direction of the trends (test), the test statistic (stat) and its observed values (obs), plus raw and FDR-corrected p-values; the latter both for a) abundance-weighted and b) biomass data.

| predictor/response | test | stat | a) abundance Obs | sd obs | $p_{raw}$ | $p_{corr}$ | | b) biomass obs | sd obs | $p_{raw}$ | $p_{corr}$ | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| decade/dormancy | greater | χ2 | 10114.9 | 3.3 | 0.003 | 0.043 | * | 10114.9 | 3.1 | 0.003 | 0.054 | (*) |
| %grass/dormancy | greater | F | 417.9 | −0.2 | 0.438 | 0.717 | | 417.9 | −0.2 | 0.440 | 0.719 | |
| prec./dormancy | greater | F | 484.7 | −0.5 | 0.589 | 0.829 | | 484.7 | −0.5 | 0.577 | 0.826 | |
| temp./dormancy | greater | F | 2398.1 | 1.7 | 0.091 | 0.466 | | 2398.1 | 1.6 | 0.096 | 0.495 | |
| decade/voltinism | greater | χ2 | 6331.4 | 1.8 | 0.064 | 0.419 | | 6331.4 | 1.9 | 0.060 | 0.410 | |
| % grass/voltinism | greater | F | 90.4 | −0.9 | 0.841 | 0.891 | | 90.4 | −0.9 | 0.847 | 0.897 | |
| prec./voltinism | greater | F | 1017.5 | 0.1 | 0.341 | 0.679 | | 1017.5 | 0.1 | 0.346 | 0.695 | |
| temp./voltinism | greater | F | 1031.9 | 0.0 | 0.408 | 0.699 | | 1031.9 | 0.0 | 0.404 | 0.719 | |
| decade/diet_type | greater | χ2 | 7086.1 | 2.0 | 0.070 | 0.419 | | 7086.1 | 2.0 | 0.068 | 0.410 | |
| % grass/resource | greater | F | 623.3 | 0.3 | 0.257 | 0.679 | | 623.3 | 0.3 | 0.256 | 0.695 | |
| prec./resource | greater | F | 949.1 | 0.2 | 0.299 | 0.679 | | 949.1 | 0.2 | 0.294 | 0.695 | |
| temp./resource | greater | F | 3001.6 | 2.3 | 0.047 | 0.419 | (*) | 3001.6 | 2.3 | 0.048 | 0.410 | |
| decade/diet_type | greater | χ2 | 546.1 | −1.3 | 0.996 | 0.996 | | 546.1 | −1.3 | 0.995 | 0.995 | |
| % grass/diet_type | greater | F | 190.9 | −0.6 | 0.674 | 0.829 | | 190.9 | −0.6 | 0.648 | 0.826 | |
| prec./diet_type | greater | F | 255.0 | −0.7 | 0.731 | 0.829 | | 255.0 | −0.7 | 0.707 | 0.826 | |
| temp./diet_type | greater | F | 68.9 | −1.2 | 0.954 | 0.981 | | 68.9 | −1.2 | 0.953 | 0.980 | |
| decade/dispersal | greater | χ2 | 3297.1 | −0.1 | 0.474 | 0.743 | | 3297.1 | −0.1 | 0.479 | 0.750 | |
| % grass/dispersal | greater | F | 228.9 | −0.7 | 0.717 | 0.829 | | 228.9 | −0.7 | 0.722 | 0.826 | |
| prec./dispersal | greater | F | 1079.0 | 0.2 | 0.317 | 0.679 | | 1079.0 | 0.2 | 0.317 | 0.695 | |
| temp./dispersal | greater | F | 1613.5 | 1.1 | 0.163 | 0.679 | | 1613.5 | 1.1 | 0.169 | 0.695 | |
| decade/length_mean | greater | F | 185.1 | −0.6 | 0.737 | 0.829 | | 185.1 | −0.6 | 0.734 | 0.826 | |
| % grass/length_mean | two-sided | r | 0.1 | 0.7 | 0.530 | 0.795 | | 0.1 | 0.6 | 0.553 | 0.826 | |
| prec./length_mean | two-sided | r | −0.1 | −0.9 | 0.402 | 0.699 | | −0.1 | −0.8 | 0.428 | 0.719 | |
| temp./length_mean | two-sided | r | −0.2 | −1.2 | 0.230 | 0.679 | | −0.2 | −1.2 | 0.234 | 0.695 | |
| decade/dryweight | greater | F | 127.2 | −0.5 | 0.723 | 0.829 | | 127.2 | −0.5 | 0.721 | 0.826 | |
| % grass/dryweight | two-sided | r | 0.1 | 1.0 | 0.330 | 0.679 | | 0.1 | 0.9 | 0.348 | 0.695 | |
| prec./dryweight | two-sided | r | −0.1 | −0.9 | 0.358 | 0.679 | | −0.1 | −0.9 | 0.382 | 0.719 | |
| temp./dryweight | two-sided | r | −0.2 | −1.2 | 0.205 | 0.679 | | −0.2 | −1.2 | 0.207 | 0.695 | |
| decade/habpref | greater | χ2 | 6042.4 | 0.7 | 0.232 | 0.679 | | 6042.4 | 0.7 | 0.249 | 0.695 | |
| % grass/habpref | greater | F | 327.6 | −0.5 | 0.602 | 0.829 | | 327.6 | −0.5 | 0.613 | 0.826 | |
| prec./habpref | greater | F | 297.5 | −0.9 | 0.826 | 0.891 | | 297.5 | −0.9 | 0.840 | 0.897 | |
| temp./habpref | greater | F | 1382.7 | 1.0 | 0.173 | 0.679 | | 1382.7 | 1.0 | 0.179 | 0.695 | |
| decade/pheno_start | greater | F | 11487.5 | 4.7 | 0.004 | 0.043 | * | 11487.5 | 4.5 | 0.005 | 0.058 | (*) |
| % grass/pheno_start | two-sided | r | 0.1 | 1.1 | 0.285 | 0.679 | | 0.1 | 1.1 | 0.291 | 0.695 | |
| prec./pheno_start | two-sided | r | 0.1 | 0.4 | 0.697 | 0.829 | | 0.1 | 0.4 | 0.695 | 0.826 | |
| temp./pheno_start | two-sided | r | −0.4 | −2.8 | 0.001 | 0.043 | * | −0.4 | −2.8 | 0.001 | 0.029 | * |

## 4.1. Methodological perspective: Comparison of data on individual numbers and biomass

Interest in the biomass of terrestrial insects has soared since it was reported that insect biomass has declined by 75 % in western German nature reserves since 1990 (Hallmann et al., 2017). In our data on Auchenorrhyncha in dry grasslands, we could confirm that trends in biomass and number of individuals are often similar (also see van Klink et al., 2020). In our case, the total percentage of dry weight losses from historic to recent decade exceeds the total losses in individual numbers by 10 % (54 % vs 44 %). This is not as obvious as it seems because a decline in numbers of individuals with low body mass may be compensated by increases in larger individuals. This is potentially relevant for cases, where the exact species composition of the samples analysed is unknown (e. g. in Shortall et al., 2009, Hallmann et al., 2017).

In the present case, however, strong declines did not translate into declines in species richness, countering the theoretical expectation that a decline in biomass or number of individuals will lead to a decline in species numbers (Hallmann et al., 2021). Instead, our data suggest that the formerly most abundant species have experienced the biggest losses, whereas rarer species either remained present at low densities, or were replaced by other rare species. This agrees with Vereecken et al. (2021), who showed that bee individual numbers and biomass patterns rarely show the same pattern as species richness and other biodiversity metrics.

With respect to the use of biomass or individual numbers in trait-based analyses, we found some modest differences between the results of the two measures: the relations between trait composition and land cover were only significant for biomass, and the relation between trait composition and climate was stronger for biomass (Table 4). In all, our results still suggest that both biomass and individual numbers are appropriate for use in trait-based analyses of insect communities, and we have found no strong reasons to prefer one measure of assemblage size over the other.

## 4.2. Responses in trait composition and diversity

We found significant changes in our Auchenorrhyncha community over the 40-year research period. We confirmed our earlier findings of strong declines in total number of individuals (−44 %; Schuch et al., 2012) and community biomass (−54 %; Schuch et al., 2019) but did not detect declines in the number of species. Changes in species composition were, however, apparent over time, with changes in trait space tending to be less pronounced than in taxonomical space.

Trait diversity in terms of biomass weighted Rao's Q and the conceptually related functional dispersion (Laliberté and Legendre, 2010) increased significantly over time (Fig. 3). This implies that more recent samples tended to be more widely dispersed in traits space. The lack of change in functional richness based on presence-absence data demonstrate that neglecting measures of individual abundance, in this case dry weight, may fail to capture changes in community composition, be it in taxonomical or in trait space. For functional evenness we did not find significant evidence for a change (Fig. 3), possibly reflecting that dominant dry grassland specialists declined, and less dominant dry grassland specialists which had disappeared in period 2 being displaced by generalist species (like *Zyginidia scutellaris*). This results in a
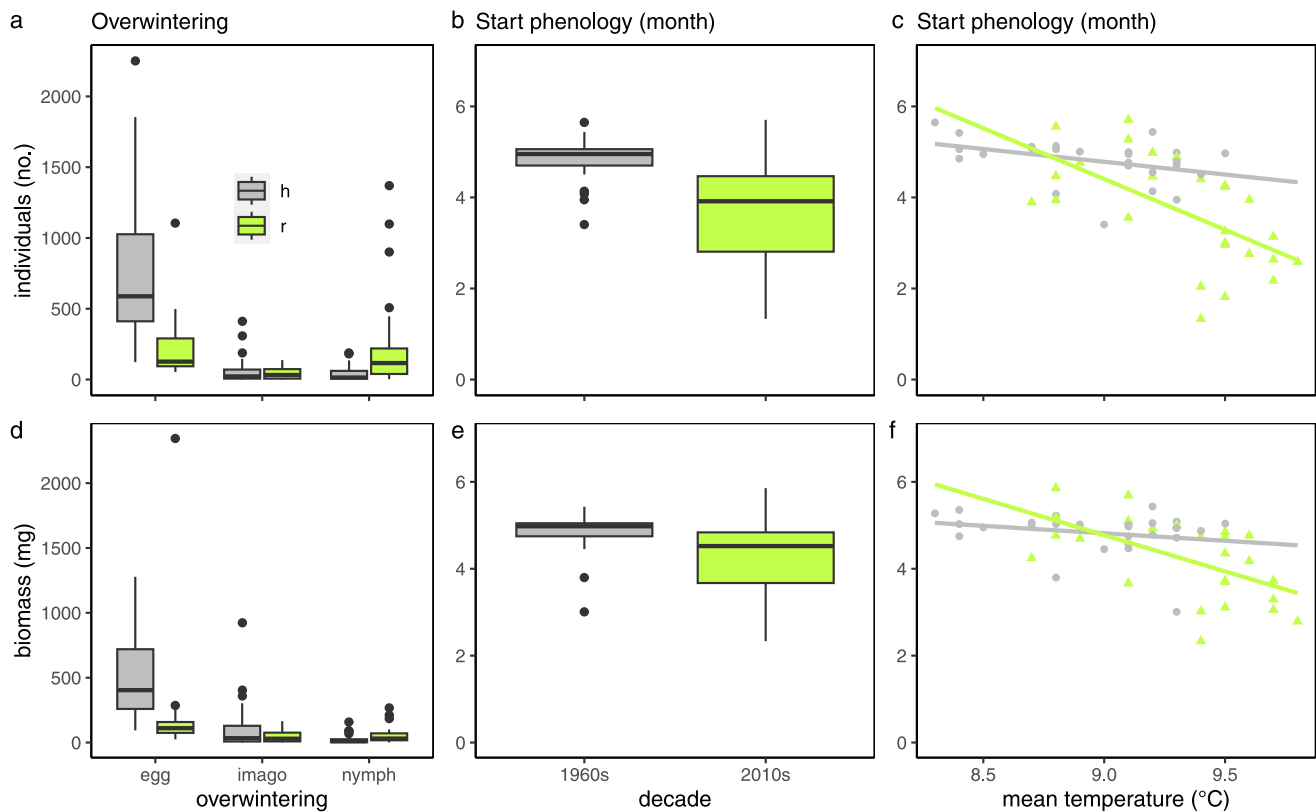
**Fig. 5.** Patterns in responsive traits according to Table 3. Upper row refers to data of individual numbers, lower row to biomass data (the latter given only for completeness although non-significant according to Table 3).

**Table 4**
Summary of results across the main response variables and predictor groups, worked out for both datasets weighted by individual numbers and biomass respectively. Abbreviations: ↓↑ - significant increase/ decrease; (*) - p < 0.1; * - p < 0.05, ** - p < 0.01, *** - p < 0.001, ns - non-significant or non-relevant according to model simplification.

| | | Predictors | Number-weighted | Biomass weighted | Test used | Refering to |
|---|---|---|---|---|---|---|
| Abundance | | Decade (associated with temperature) | ↓* | ↓*** | GLM | Fig. 2 |
| | | Landscape configuration | Ns | ns | GLM | Text |
| | | Precipitation | Ns | ns | GLM | Text |
| Diversity | Taxonomic | Decade | Ns | ns | GLM | Fig. 2 |
| | | Landscape configuration | ns | ns | GLM | Text |
| | | Precipitation | ns | ns | GLM | Text |
| | Trait | Decade | ↑** | ↑* | GLM | Fig. 3 |
| | | Landscape configuration | ns | ns | GLM | Text |
| | | Precipitation | ns | ns | GLM | Text |
| Composition | Taxonomic | Decade | ** | ** | DCA | Fig. 4, text |
| | | Landscape configuration | *** | * | Post hoc | Table 2 |
| | | Precipitation | ** | ** | Post hoc | Table 2 |
| | Trait | Decade | ** | ** | Post hoc | Fig. 4, text |
| | | Landscape configuration | ns | ** | Post hoc | Table 2 |
| | | Precipitation | ** | *** | Post hoc | Table 2 |
| Traits | | Decade | * | (*) | 4th corner | Table 3 |
| | | Landscape configuration | ns | ns | 4th corner | Table 3 |
| | | Precipitation | ns | ns | 4th corner | Table 3 |

somewhat less specialized but similarly even auchenorrhynchan community.

If anything, we found an increase in metrics of trait diversity over time, which is contrary to our expectation of a decline in trait diversity. This implies that species with new trait combinations have colonized our sites, thereby enriching the community in terms of traits. However, since

we did not detect a change in species richness, a similar number of species must have disappeared, with less unique trait combinations. A species that was completely absent in the 1960's, but that was dominant in the 2000's is *Zyginidia scutellaris*. This small species is a grassland generalist that overwinters as adult. Other species that colonized the sites were tree-associated species, such as *Thamnotettix dilutior*, probably

responding to the increase in shrub cover over time (S2). This is consistent with the general changes in vegetation structure of Europeans dry grasslands (Diekmann et al., 2019).

The fourth-corner analysis revealed a relation between over-wintering stage and time, where species that overwinter as nymphs have increased over time, and species overwintering in the egg-stage have declined. This may have several reasons: First, most auchenorrhynchan species that occur in grasslands hibernate as eggs, whereas many species that overwinter as nymphs prefer habitats with some shrubs and trees to overwinter on. In line with this, species with this habitat preference increased in abundance and were more commonly detected in the recent decade. We had found a similar trend in Orthopterans, studied on the same sites (Schuch et al., 2011) supporting the idea of successional changes. Secondly, winter warming has a positive effect on species hibernating as nymphs or adults, and their increase may be related to more suitable climatic conditions during winter. Conrad et al.(2004) found similar patterns in moth communities (decreasing egg hibernation and increasing adult hibernation) and also assumed milder winters to be responsible for this. We found that the start of community phenology tended to become earlier from historical to recent decades, which was associated with rising temperatures. An earlier onset of activity is one of the most commonly observed responses to global warming, although most research has been done on within-species phenological shifts (Parmesan 2006). It must be noted, however, that the traits of over-wintering stage and phenological start are associated, since nymph overwinterers can become active early in the season, as they don't have to hatch anymore.

Predictors that showed no clear temporal trend were also associated to trait- and taxonomic composition. Precipitation and landscape-wide grassland cover were associated with both trait and species composition. This is consistent with previous studies, where the regional percentage of grassland cover was an important predictor of grassland Auchenorrhyncha communities (Rösch et al., 2013, Helbing et al., 2017). Responses of Auchenorrhyncha communities to mean precipitation are less obviously explained, but may simply reflect differences in plant communities, that directly depend on precipitation resulting in an apparent association between climate and insects. Effects of weather on insect communities are commonplace, and this is also confirmed by e.g. long-term studies on insect communities of dry grasslands in Germany (Skarbek et al., 2021), even though our study focused on mean values and thus long-term trends.

We found no significant changes in space or time on dispersal capability, diet width or voltinism. This is surprising, because at least dispersal capability seems to be one of the major traits to indicate disturbance in auchenorrhynchan communities (Simons et al., 2016).

We did not test for changes of species with respect to red list status because it is not a trait in the strict sense. Fig. S4 shows that species considered strongly threatened today or extinct were already rare in the historical data, while abundances in 'near threatened' and especially 'least concern', i.e. not considered threatened, tended to decline. This supports the assumption that we are of losing 'the common and the widespread' (Gaston and Fuller, 2007) of a given habitat type rather than species classified as threatened.

Overall, the observed patterns give strong support for an important role of climate change, with earlier springs, longer summers and milder winters promoting species with earlier phenological activity. Still, temperature trends are modified by effects of succession, precipitation patterns and land use in the wider landscape.

## 5. Conclusions

From a practical perspective, our study confirms that abundance data collected for individual species reveal more different patterns than summary values such as richness or total biomass as they allow for a differentiated view on community composition. Our data do, however, not provide evidence that either collecting individual numbers or

species biomass is generally superior, and, thus, that the conversion of individual-based data into biomass is unlikely to yield many new insights. In our view, the focus should be on employing whatever data are available, especially since historical data on insect abundance rarely go back more than a few decades, often giving few options with respect to abundance measures investigated.

Ecological implications of our study are at least partly surprising. Despite the severe losses in individuals and those even stronger in biomass, we did not find strong decreases in taxonomical or trait diversity. Additionally, we detected only limited trends when we analysed selected traits. Dormancy and phenological dynamics were the only traits that showed detectable trends over decades. This implies that succession and climate change may be the main factors which influenced trait composition during the last 45 years at least in the investigated dry grasslands. This provokes a simple question: have auchenorrhynchan communities been (largely) resilient with respect to functional traits in spite of severe losses? In other words, is less simply less, at least if it comes to trait composition? Obviously, answers depend on the traits selected, and on the perspectives taken, with thermodynamics and food chain approaches being likely to yield different conclusions. Still, it remains to be tested, if the dramatic losses in insect abundance have already led to disappearance of rather than a mere reduction of certain ecological functions.

## 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.

## Data availability

Data will be made available on request.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.109743.

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