



Declining abundance of beetles, moths and caddisflies in the Netherlands

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Abstract. 1. Recently, reports of insect declines prompted concerns with respect to the state of insects at a global level. Here, we present the results of longer-term insect monitoring from two locations in the Netherlands: nature development area De Kaaistoep and nature reserves near Wijster.

2. Based on data from insects attracted to light in De Kaaistoep, macro-moths (macro-Lepidoptera), beetles (Coleoptera), and caddisflies (Trichoptera) have declined in the mean number of individuals counted per evening over the period of 1997–2017, with annual rates of decline of 3.8, 5.0 and 9.2%, respectively. Other orders appeared stable [true bugs (Hemiptera: Heteroptera and Auchenorrhyncha) and mayflies (Ephemeroptera)] or had uncertainty in their trend estimate [lacewings (Neuroptera)].

3. Based on 48 pitfall traps near Wijster, ground beetles (Coleoptera: Carabidae) showed a mean annual decline of 4.3% in total numbers over the period of 1985–2016. Nonetheless, declines appeared stronger after 1995.

4. For macro-moths, the mean of the trends of individual species was comparable to the annual trend in total numbers. Trends of individual ground beetle species, however, suggest that abundant species performed worse than rare ones.

5. When translated into biomass estimates, our calculations suggest a reduction in total biomass of approximately 61% for macro-moths as a group and at least 42% for ground beetles, by extrapolation over a period of 27 years. Heavier ground beetles and macro-moths did not decline more strongly than lighter species, suggesting that heavy species did not contribute disproportionately to biomass decline.

6. Our results broadly echo recent reported trends in insect biomass in Germany and elsewhere.

Key words. Beetles, collecting at light, insect declines, macro-moths, pitfall trap, trend analysis.

Introduction

Insects, despite their huge diversity, and despite their importance for ecosystem functioning, are generally much less studied than,

for example, birds and mammals. As a consequence, information on the abundance and trends of insects is largely lacking, and/or is geographically limited, preventing the assessment of their state in the landscape (Habel *et al.*, 2019a). Additionally, large-scale monitoring data exist usually only for species such as butterflies (Van Dyck *et al.*, 2009; van Strien *et al.*, 2019), dragonflies (Termaat *et al.*, 2015; 2019), bees (Biesmeijer *et al.*, 2006; Aguirre-Gutierrez *et al.*, 2016) and moths (Groenendijk & Ellis,

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2011; Habel *et al.*, 2019b), taxonomically limiting the inference that can be made over the state entomofauna in general. Nevertheless, studies on these species largely reveal patterns of decline in abundance over recent decades (Sánchez-Bayo & Wyckhuys, 2019), with reports on insect declines coming from tropics (Lister & Garcia, 2018; Janzen & Hallwachs, 2019), to the arctic (Gillespie *et al.*, 2019). Recently, a large decline in flying insect biomass was reported for German lowland nature reserves (Hallmann *et al.*, 2017; Schuch *et al.*, 2019) prompting concerns with respect to the state of insects at a global level. In response to the findings in Germany, and commissioned by the Dutch ministry of environment and agriculture, Kleijn *et al.* (2018) identified a list of existing data sets potentially suitable to derive trends for insects species in the Netherlands, and to allow for comparison to the German case. Here, we use two long-term data sets (each from a single location or area, using different approaches) covering a wide range of insect families, to provide further insights into trends in insect abundance in the Netherlands, the trends in their biomass, and to examine trend variation along species-specific traits.

Analysis of insect trends over time poses significant challenges. First, it is often hard to differentiate long-term trends from natural cycles (Fewster *et al.*, 2000; Benton *et al.*, 2002), particularly in the absence of prolonged sampling over many years. Secondly, seasonal activity of the insects plays a significant role in the numbers trapped, particularly when species have multiple generations and peaks throughout the year. Thirdly, weather variation, possibly at multiple time spans and with variable time lags, influences the population dynamics and activity of the insects (Johnson, 1969; Jonason *et al.*, 2014; van Wielink, 2017a,b). Hence, sampling characteristics such as timing (both in the season and during the day) and duration of sampling, can play important roles in the numbers caught, and hence trend estimates. If meaningful trends of insect numbers are to be derived, such sampling characteristics need to be accounted for in the analyses.

To contribute to answering the question whether the abundance and biomass of insects is declining in the Netherlands, we report here on insect trends in two longer-term data sets, while correcting for sampling and weather aspects, and assess the relative performance of the various insect orders. For the most well-studied and most species-rich orders, beetles and

macro-moths, we also report trends per species, and we examine trend variation along a number of species traits as a means to pinpoint potential drivers of trends in abundance (e.g. Potocký *et al.*, 2018; Habel *et al.*, 2019c). For instance, these analyses will show whether insect species associated with certain types of host plants or specific habitats decline more than other insect species. On the other hand, if species trends show no relationships to species traits, pressure factors would be suspect that affect all types of insects in the same way. Additionally, based on general weight-length relationships (Sabo *et al.*, 2002; García-Barros, 2015), we attempt to derive estimates of trends in total biomass, in order to compare these to the recently reported trends in flying insect biomass in Germany (Hallmann *et al.*, 2017). Our specific research objectives were

1 to assess the trends in abundance of various insects at the species and order level,

2 to assess the trend in biomass of macro-moths and ground beetles, and

3 to assess how species-trends vary along species-specific trait axes.

Materials and methods

Data were collected at two groups of sites: De Kaaistoep and Wijster. For each site, we describe the sampling protocols, data set and statistical analysis. A summary description of available data is given in Table 1. In addition, we obtained data from two KNMI weather stations (for De Kaaistoep data: weather station Gilze-Rijen, for Wijster data: weather station Eelde, at, respectively, 3.6 and 40 km from trapping locations), from which we extracted relevant parameters for effect analysis on insect numbers, as well as for correcting trends.

Collecting at light in De Kaaistoep

De Kaaistoep is a 330 ha managed natural area consisting of heathland, pine forest and grassland. It was established in 1994 on former arable land. Information about the location and management history can be found in the study by Felix and van Wielink (2008). Insects were attracted by light in combination with a

Table 1. Summary of the data used in the analyses. For each insect order included in this study, we show the number of years, sites and individuals that were used in the present analysis. Data from the Kaaistoep were collected at light, while data from Wijster using pitfall traps.

Order	Family	Location	Sites	Years	Samples	Individuals	Species
Lepidoptera		Kaaistoep	1	21: 1997:2017	497 nights	54 492	477(178)
Coleoptera		Kaaistoep	1	21: 1997:2017	572 nights	257 793	123(76)
Trichoptera		Kaaistoep	1	10: 2006,2009:2017	261 nights	33 540	
Ephemeroptera		Kaaistoep	1	10: 2006,2009:2017	255 nights	9713	
Neuroptera		Kaaistoep	1	10: 2006,2009:2017	258 nights	936	
Hemiptera		Kaaistoep	1	10: 2006,2009:2017	258 nights	49 747	
Coleoptera	Carabidae	Wijster	48	26: 1986:1997,2002:2003,2005:2016	26 years	264 986	156(98)
Coleoptera	Carabidae	Wijster	31	16: 2002:2017	15 672 weeks	99 075	

Separate species trends are performed on a subset of species for which enough data were available (numbers indicated between brackets).

white cloth (Supporting Information Fig. S1) over a period of 3.3 h per trapping night, normally starting around sunset (Fig. 1c). During this sampling period, individuals of the various insect taxa were counted, or were estimated in the case of large numbers. All macro-moths were always counted and identified, while for other groups of insects, between 25 and 100% were collected for identification. Further details of the sampling protocol are given in the study by van Wielink and Spijkers (2013).

Data in the present analysis have been collected during 628 trapping nights between 1997 and 2017, on average 30 evenings per year (10–77). Data were available for the period of 1997–2017 for macro-moths (Lepidoptera), beetles (Coleoptera) and ground beetles (Carabidae), while for caddisflies (Trichoptera), lacewings (Neuroptera), true bugs (Hemiptera-Heteroptera and Hemiptera-Auchenorrhyncha) and mayflies (Ephemeroptera) data were available only for the years 2006 and 2009–2017. Of the large number of Coleoptera, only ground beetles, ladybirds and carrion beetles were identified to species up to 2017, accounting for 48 000 of 239 000 beetle specimens.

As it is known that the environmental conditions (like temperature) during each trapping night influenced the number of insects caught, we aimed to include relevant covariates in our analyses. Information about the timing and duration of sampling were available for 91.2% of the nights ($n = 574$), and lacking more in the first few years of sampling than later on. The number of sampling hours per night varied little among years (Fig. 1a)

but did increase from an average of 3.1 h (1997–2009) to an average of 3.8 h per night after 2010 ($F = 48.98$, d.f. = 572, $P < 0.001$; Fig. 1b). Timing of onset of sampling was roughly at sunset throughout the years, with the exception of the first few years in which sampling started on average up to half an hour after sunset (Fig. 1c,d). The starting time of sampling correlated significantly ($R^2 = 96.6\%$, $df = 514$, $P < 0.001$) with the evaluated sunset moment for the specified location (Meeus, 1991; Bivand & Lewin-Koh, 2015). Additionally, the slope of the linear relationship between the starting and sunset moments did not deviate significantly from one ($F = 0.809$, $P = 0.369$), and the intercept did not deviate from zero ($F = 1.568$, $P = 0.211$).

To analyse trends for each order (or species) k , we modelled the counts in year t and on day d using generalised additive models (GAMs; Wood, 2006) and assuming a negative-binomial distribution (White & Bennetts, 1996) and a log link to the predictors. GAMs were deemed more appropriate than generalised linear models, as insects counts vary considerably throughout the year, often with multiple peaks (i.e. generations), as well as between years (i.e. nonlinear dynamics). We constructed six basic models, differing in how the year covariate is treated (linear, non-linear, and categorical), and if the weather covariates were included or not (Supporting Information Table S1). We considered linear as well as non-linear trends over time, as well as an annual index (the latter for visual assessment). Additionally, in all models, we included a smooth seasonal component

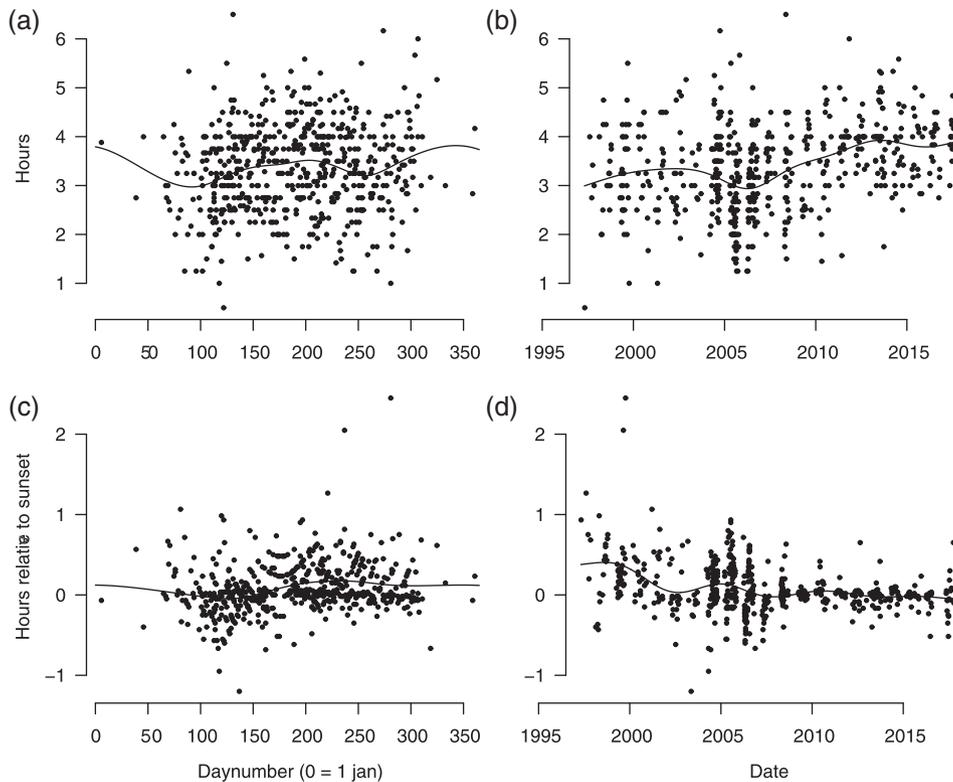


Fig. 1. Sampling characteristics for De Kaaistoep data set. (a) Number of sampling hours per evening plotted against day of the year (1 = 1 January). (b) Number of sampling hours per evening per year. (c) Start of sampling relative to sunset (in hours) versus day of the year. (d) Start of sampling relative to sunset per year.

[γ s(d)] and a quadratic component for sampling duration ($h + h^2$), as we expected non-linear responses to sampling duration. Weather covariates included mean temperature, sum of precipitation, mean relative moisture content and mean wind speed. Additionally, as response variables may have a convex relationship (e.g. optima) to weather variables, we also included quadratic effects. Each weather covariate in the design matrix \mathbf{W} (including the squared values) was standardised to a zero mean and unit variance. The different models were compared by the Akaike's information criterion (AIC) (Burnham & Anderson, 2003), a measure of parsimony that tries to balance the amount of deviance explained and the number of parameters.

Pitfall traps near Wijster

A long-term monitoring program using pitfall traps was started at the Wijster Biological Station (and continued by the Foundation Willem Beijerink Biological Station) in two nature reserves in the province of Drenthe: National Park Dwingelderveld and the fragmented, but increasingly reconnected Hullenzand. In these reserves restoration measures, mainly in the form of topsoil removal and reconnection, were carried out during the early 1990s. The pitfall data have been collected between 1959 and 2016 at in total 48 unique locations (mean = 9, range 4–19 operating locations per year). The locations consisted mainly of heathlands, with some forest sites, a forest edge and an abandoned crop field. At each location, three square pitfall traps (25×25 cm) were installed (Supporting Information Fig. S2): one lethal funnel trap with a 3% formaldehyde solution and two live traps. The traps at each location were spaced 10 m apart. Caught ground beetles (Coleoptera: Carabidae) have been identified at weekly intervals. Further details on the sampling protocol and the area are given in the study by den Boer and van Dijk (1994). Because we are only interested in recent trends in insect abundances, and because sampling protocols were not consistent in the early years, we only used data collected since 1986. We performed two types of analyses: we first used the annual sums per species and location for the period of 1986–2016 (Table 1), and secondly, the weekly sums per species and location that have been fully digitised and checked: 2002–2017.

Annual totals 1986–2016. In total, 7778 records of species-specific counts were used in the present analyses, which amounted to 264 986 individual ground beetles. For 20 records, we used multiple imputation (Onkelinx *et al.*, 2017) to derive more reliable estimates for suspected erroneous counts. This method is based on the correlation structure between years and between other species. Note that in the years 1998–2001, no monitoring took place, and 2004 was omitted because of incomplete catches. We used GAMs to model the annual community abundance and counts per species (based on annual totals) with a negative-binomial distribution and a log link. We treated trap location as a random effect by making use of the random effects as smooth terms (Wood, 2006; 2008). We considered six basic models depending on how the year covariate is treated, and if weather covariates are included or not (Supporting Information Table S2). We considered both linear and nonlinear trends over

time, as well as an annual index (the latter for visual assessments). Weather covariates included mean temperature, sum of precipitation, mean relative moisture content, and mean wind speed, over the spring months in each year (March to May), and separately over the summer months (June to August). Additionally, we also included quadratic effects of each variable. Each weather covariate in \mathbf{W} (including the squared values) was standardised to a zero mean and unit variance.

The number of years each location was sampled varied between 1 and 22, with 19 of the locations only sampled in 1 year and 10 locations only sampled in 2 years. To assess whether our trend estimates were affected by including locations with limited years of sampling, we repeated the analysis by only including locations in our models when the number of years sampled exceeded a particular threshold. This threshold varied between 2 and 10 years, and, for each repetition, we computed the annual trend coefficient from model M1, along with the standard error.

Weekly counts 2002–2017. For the years for which weekly data were available, the catches at weekly intervals were analysed to observe how weather patterns and seasonal variation might account for some of the inter-annual variation in ground beetle abundances. Here too, we used GAMs with a negative binomial error structure, and a log link. We used modelling formulations with a seasonal component (a cubic cyclic spline for all models), a random effect for trap location (for all models), and an inter-annual component that was specified either as a categorical variable, as a linear trend, or as a smooth thin plate covariate. Additionally, we evaluated effects of temperature and precipitation in half of the models, yielding in total six different model formulations (Supporting Information Table S3). Location was included in all models as a random effect.

Biomass estimation

Insect monitoring at De Kaaistoep and Wijster is based on counts of individuals per species or higher taxa, while weighing of insects is not part of the monitoring protocol. Yet, we deemed it interesting to try to compare our abundance trends to recent findings of insect biomass declines in Germany (Hallmann *et al.*, 2017). We therefore tried to translate species-specific counts into total biomass estimates. For that purpose we used known species length measurements and known relationships of length to weight (Sabo *et al.*, 2002; García-Barros, 2015). For the Carabidae in the Wijster data set, we used the minimum and maximum body length as stated in the Dutch ground beetles field guide (Boeken *et al.*, 2002). Per species we averaged the minimum and maximum lengths, and used these averages to estimate mass per specimen (k), using the mass-length relationship determined by Sabo *et al.* (2002) for terrestrial insects:

$$\text{mass}_k = 0.032 \times \text{length}_k^{2.63} \quad (1)$$

where mass is in mg and length in mm.

For the macro-moths at De Kaaistoep site, we used species-specific minimum and maximum lengths of the front wings,

which is the only size measure provided at the website of the Dutch Butterfly Conservation (assessed 11 April 2018). Again we averaged the minimum and maximum lengths (sometimes sex-specific) per species, but now used a Lepidoptera-specific mass-length relationship. García-Barros (2015) measured the mass (mg) and front wing lengths (mm) of 665 specimens. As García-Barros only reported the means and sample sizes per superfamily (his Supporting Information 5), we analysed those summary data in a log-log regression analysis with sample size as the weight of the records. Superfamily-specific residuals (ϵ_k) of this regression analysis were stored. The fitted model was then used to estimate the mass of macro-Lepidoptera species based on its average front wing length and the superfamily it belongs to:

$$\text{mass}_k = \exp(-5.144 + 3.018 \times \log(\text{length}_k) + \epsilon_k) \quad (2)$$

where, for instance, the effect sizes (ϵ_k) of Noctuoidea and Geometroidea were 0.218 and -0.126 , respectively.

In order to calculate the reduction in biomass over the years, we used the sum of individual species weights (B_t) estimated for a particular year t (for ground beetles in the Wijster data set) or day d (for macro-moths in De Kaaistoep data set):

$$B_t = \sum_{k=1}^K B_{k,t} \quad (3)$$

and where $B_{k,t} = Y_{k,t} \times \text{mass}_k$, i.e. numbers counted per species ($Y_{k,t}$) multiplied by their estimated mean mass.

We ran GAMs on the resulting responses, using a Gaussian distribution and log-link relationship to the covariates. For De Kaaistoep data, we used the formulation of model M4 (Supporting Information Table S1) and for the Wijster data model A1 (Supporting Information Table S2).

Trend classification

We classified order- and species-specific trends in abundance and biomass, based on estimates of the annual trends coefficient ρ and on its significance. The trend coefficients represent the annual intrinsic rate of population change, or equivalently, the natural logarithm of the mean annual multiplication factor. Trend coefficients close to zero ($-0.025 < \rho < 0.025$) were interpreted as indicators of stable population trends, while more negative ρ associated with P -values larger than 0.05 were classified as 'uncertain declines'. Declines were labelled 'severe' when significant ρ values were lower than -0.05 . More information on these trend classifications can be found in the Supporting Information Table S4.

Species traits

We examined variation in species mean log annual trend in relation to ecological traits, for macro-moths in De Kaaistoep, as well as ground beetles from Drenthe. For macro-moths, trait data were assembled from existing literature, and include voltinism (five classes: one generation per year, one or two generations, two generations,

two or three generations, and three generation per year; Waring & Townsend, 2015), wintering strategy (four classes: as egg, caterpillar, pupa or adult; Ebert, 2005; Waring & Townsend, 2015), host plant type (six classes: grass, herb, trees and shrubs, trees only, diverse, and other; Waring & Townsend, 2015), host plant specificity (three classes: monophagous, oligophagous and polyphagous; Waring & Townsend, 2015), rarity (five classes: rare to very common, Ellis *et al.*, 2013), and the log of species weight (see the aforementioned explanation). Host plant type class 'other' included several species of heath, and mosses and lichens. Using data from Habel *et al.* (2019c), we also examined the effects of Ellenberg values of the host plants of macro-moths, and major habitat type, on mean annual species trends. This was done for a subset of the species that overlapped between the present study and the one of Habel *et al.* (2019c), and for which trends were estimable ($N = 146$ out of 178 species trend estimates).

For ground beetles in Drenthe, we derived species traits from Turin (2000), while reducing the number of categories for several traits in some variables. We used three categorical trait variables, namely: flight ability [macropterous (i.e. having large wings), brachypterous (i.e. having reduced wings), dimorphic or polymorphic], habitat specialisation [four classes: from stenotopic (i.e. specialised to one or few habitats) to very eurytopic (i.e. habitat generalist)], distribution type (four classes marginal, submarginal, sub central and central), and the log of species weight. Habitat specialisation was condensed from numeric scale (2–10) into the four mentioned classes as follows: 2–4 stenotopic, 5–6 less stenotopic, 7–8 less eurytopic, and 9–10 eurytopic. The original rankings simply resemble the number of types of habitat each species has been found in the Netherlands.

To examine the effects of the traits, we regressed the intrinsic rate of increase to the aforementioned traits using generalised least squares. As we expected greater residual variation in low-density species because of higher demographic stochasticity (i.e. heteroscedasticity), we specified the variance around the mean ($V(y)$) as an exponential function of the log of mean species abundance as:

$$V(y) = \sigma^2 \exp(2 \times \varphi \times \log(y)) \quad (4)$$

where φ is an to be estimated parameter measuring the decline in variance with increasing species abundance. Starting with a global model (all traits as covariates) and using a stepwise deletion of insignificant terms, we derived the most parsimonious models for each group.

Results

Collecting at light at De Kaaistoep

Across insect orders, models including weather variables always prevailed over models without weather variables (Supporting Information Table S5). Across orders, sampling duration was significantly positively related to the number of insects counted. Given the increase in sampling duration from an average of 3.1 h in the period of 1997–2006 to an average

of 3.8 h in 2009–2017 (Fig. 1b), fitted trends over the study period were slightly lower when correcting for sampling duration (Supporting Information Fig. S3). Hence, we derived annual trends while accounting for weather variables and sampling duration (see Supporting Information Table S6 for coefficients).

Trends of the abundance of six insect orders (based on an annual index, a linear and a non-linear trend) are depicted in Fig. 2. Following correction for sampling duration and weather effects, and based on the overall mean (linear) estimates, true bugs (Hemiptera-Heteroptera and Hemiptera-Auchenorrhyncha) appeared to be stable, and lacewings (Neuroptera) appeared to decline but not significantly so, and hence their trend was considered to be uncertain. In contrast, caddisflies (Trichoptera), mayflies (Ephemeroptera), beetles (Coleoptera) and moths (macro-Lepidoptera) showed significant negative coefficients. The linear trends per order are summarised in Table 2. Because apparent declines in Trichoptera and Ephemeroptera might have been dominated by high counts in 2006, we re-analysed these trends while excluding data from 2006. For mayflies, the trend coefficient changed both magnitude and sign ($\rho = 0.010$, $se = 0.058$, P -value = 0.87), and we therefore labelled the trend of this insect order to be stable. For caddisflies, the trend became slightly less negative when the year 2006 was omitted but remained significantly negative ($\rho = -0.070$, $se = 0.033$, P -value = 0.033).

Trends of macro-moth species were variable, with on average a decline of 4% per year (Fig. 3a). The largest group of species (38%) showed a declining trend, while only 5% showed an increase and the remainder of the species had stable or insignificant trends (Fig. 3b). Declines of individual species were positively, but not significantly, related to mean abundance (mean number of individuals per trapping night; t -value = 0.861, P -value = 0.392).

Within the 76 beetle species for which enough data was available to analyse population trends, the average annual decline was estimated to be -0.05 , with 38% of the species showing a significant (and severe) decline, while 12% of the species significantly increased (Figure 3). The species-rich family of ground beetles (Carabidae) dominated these results, with numeric declines (totals within family) of ground beetles declining steeper ($\rho = -0.090$, $se = 0.021$, P -value < 0.001) than those of ladybirds (Coccinellidae, excluding the invasive exotic *Harmonia axyridis*, $\rho = -0.029$, $se = 0.012$, P -value = 0.001), whereas carrion beetles (Silphidae, $n = 4$) were found to significantly increase ($\rho = 0.035$, $se = 0.016$, P -value = 0.003). Within ground beetles, average species declines amounted to 6.8% per year, and although species-specific trends were highly variable, a large proportion of these species showed significantly declining trends (44.1%), and only few (6.8%) showed increases (Supporting Information Figure S4).

Pitfall traps near Wijster

In total, 156 species of ground beetles were found in the pitfall traps. Year totals of specimens over all species of ground beetles showed a declining pattern regardless of the considered model. Although non-linear trends explained year totals significantly better than linear models (AICnl = 3768.26, $df = 35.54$ versus AICl = 3773.63, $df = 33.48$). Models considering weather

variables did not improve model fit, regardless of whether they were measured over spring (March to May) or summer (June to August). Hence, we present trends based on models that omit weather effects. The linear trend coefficient was significantly negative ($\rho = -0.044$, $se = 0.006$, P -value < 0.001, 4% decline per year, Fig. 4). Results of the non-linear trend model however showed that the trend initially increased, followed by a decline starting after 1995 (Fig. 4). The linear annual trend since 1995 showed even steeper declines ($\rho = -0.060$, $se = 0.009$, $P < 0.001$), implying a 6% annual decline since 1995.

Furthermore, the trend estimates were affected by the minimum number of years that a given location was sampled. While the main analysis included all locations, including only locations with more than 2 years of sampling resulted in a slightly more negative trend coefficient of $\rho = -0.051$ ($se = 0.005$), i.e. 5% annual decline rate. Restricting the analysis to the 12 locations with at least four sampling years made the trend even more negative (5.5% annual rate of decline, Supporting Information Figure S5).

Among 127 ground beetle species with sufficient data, the average of the species trends (based on year totals) amounted to a 7% decline per year (Fig. 3a), which is more negative than the trend of the year totals. Most species (42.5%) showed declining (most of which severe declines) trends, while 29.4% of the species showed stable or uncertain trends and 8.5% of species showed significantly positive trends (Fig. 3b).

Trend estimates as obtained from our analysis of the weekly counts of all ground beetles combined (over the years 2002–2017, see Methods) were similar but more negative to that of the year totals over the longer period. In these seasonal analyses, models with weather variables did outperform models without such variables (Supporting Information Table S7). On the contrary, the mean annual trend coefficient did not differ much between these models. Based on the weather-corrected annual trend coefficient, we estimated the annual decline at an average of 7.41% ($\rho = -0.077$, $se = 0.002$, $P < 0.001$) for the period of 2002–2017 (Supporting Information Figure S6).

Trends in estimated insect biomass

For the macro-moths at De Kaaistoep site, our calculations culminated in an estimation of ‘severe decline’ for total biomass ($\rho = -0.036$, $se = 0.006$, $P < 0.001$, i.e. -3.3% , $se = 0.52$ mg/year; Fig. 5a). For the ground beetles near Wijster, we estimated the average decline in total biomass to be 2% ($se = 0.48$) annually (Fig. 5b), which is considerably less than that of numbers per species or total sums of individuals. Nevertheless, considering only the period after 1995, the rate of decline in biomass appeared a lot more severe ($\rho = -0.0414$, $se = 0.006$, $P < 0.001$), implying an on average 4.1% ($se = 0.53$) decline per year.

Species traits

For both macro-moths and ground beetles, accounting for heteroscedasticity provided a significant better fit to the data (log-likelihood ratio of 19.91, $P < 0.0001$, for macro-moths,

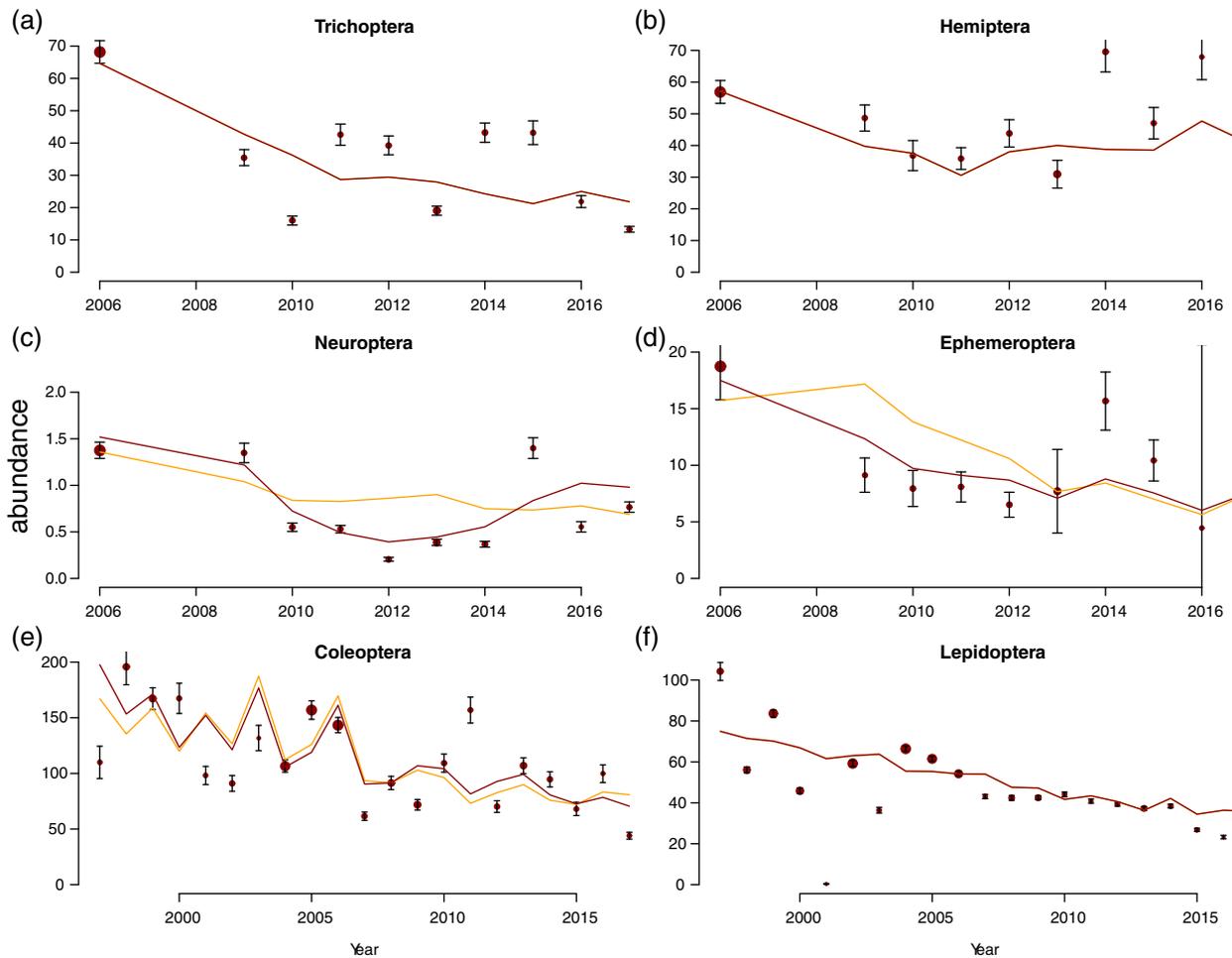


Fig. 2. Trends in numbers counted per evening of six orders of insects at De Kaaistoep. For each order, the annual indices (points, model M3), and estimates of the linear (orange, model M4) and non-linear (blue, model M5) trends are given. Evidence for non-linearity is only apparent in Neuroptera, Ephemeroptera and Coleoptera, while for the remainder of the orders models M4 and M5 are indistinguishable. [Color figure can be viewed at wileyonlinelibrary.com]

and 25.99, $P < 0.0001$, for ground beetles) and hence was retained in all models. Analysis of the trends of macro-moths in relation to traits showed that out of the covariates considered, only host plant type explained a significant amount of variation (Supporting Information Table S8), with species depending on grass, herbs or diverse host plant species declining most (Fig. 6, Supporting Information Table S9). Additional analysis based on a subset of the macro-moth species in relation to Ellenberg values of the host plants (data from Habel *et al.*, 2019c) did not reveal any significant effects of the predictors (Ellenberg values for nitrogen, pH, light, continentality, humidity and temperature; Supporting Information Table S10).

For ground beetles in the Wijster area, lower intrinsic rates were observed among species that are considered in the Netherlands to be in the margin or sub-margin of their distribution, among very stenotopic (i.e. restricted to few types of habitats) or very eurytopic species (i.e. habitat generalists), among lighter species, and among xerophilic (i.e. occurring in dry habitats) species (Fig. 7; Supporting Information Tables S11 and S12).

Discussion

We reported trends of six insect orders collected at light in De Kaaistoep, and one family of beetles in the Wijster region. Macro-moths, caddisflies, beetles and its subset of ground beetles at De Kaaistoep, and ground beetles near Wijster, showed severe declines. Only true bugs and mayflies appeared to be stable, while the negative trend for lacewings was statistically not significant. The majority of macro-moths (macro-Lepidoptera) are attracted to light, as are mayflies (Ephemeroptera) and caddisflies (Trichoptera), and hence are expected to be well represented in the data obtained by collection at light in De Kaaistoep. Similarly, the Wijster pitfall dataset, with 127 of 395 species observed in the Netherlands, can be considered as representative for ground beetles (Coleoptera: Carabidae) species present in the Netherlands.

Amid recent reports of broad insect decline in German nature reserves (Hallmann *et al.*, 2017; Habel & Schmitt, 2018; Homberg *et al.*, 2019; Schuch *et al.*, 2019), concerns with respect to

Table 2. Trend evaluation per insect order. For each order, we provide the annual trend coefficient (log of average annual population growth rate) of model M_4 , along with its standard error between brackets, as well as a translation into the percentage decline per year.

Insect order	Annual trend coefficient (ρ)	% Decline	P-value	Trend evaluation
Lepidoptera	-0.040 (0.006)	3.9	<0.001	Decline
Coleoptera	-0.048 (0.010)	4.7	<0.001	Decline
Trichoptera	-0.096 (0.021)	9.2	<0.001	Severe decline
Ephemeroptera	-0.128 (0.037)	12.0	0.001	Decline (uncertain)
Neuroptera	-0.047 (0.029)	4.6	0.108	Decline (uncertain)
Hemiptera	-0.006 (0.022)	0.6	0.789	Stable

See Supporting Information Table S4 for the scheme of the significance evaluation of the trends. See the main text for a discussion about the uncertainty concerning the Ephemeroptera trend.

the state of Dutch entomofauna have been raised (Kleijn *et al.*, 2018). Previous results from country-wide analyses in moths (Groenendijk & Ellis, 2011) and butterflies (van Swaay *et al.*, 2018) showed a drop in absolute numbers of 37% over 30, and 40% in 25 years, respectively. Our analysis, covering a comparatively wider range of insect species (over 1700 species, i.e. 9%, out of the 19 254 known insect species in the Netherlands), and showing broad declines for most orders investigated, are likely to be indicative to a broader group of insects in these areas, reinforcing the concerns with respect to the state of insects in the Netherlands. Yet, since only two areas are included in this analysis, it is hard to

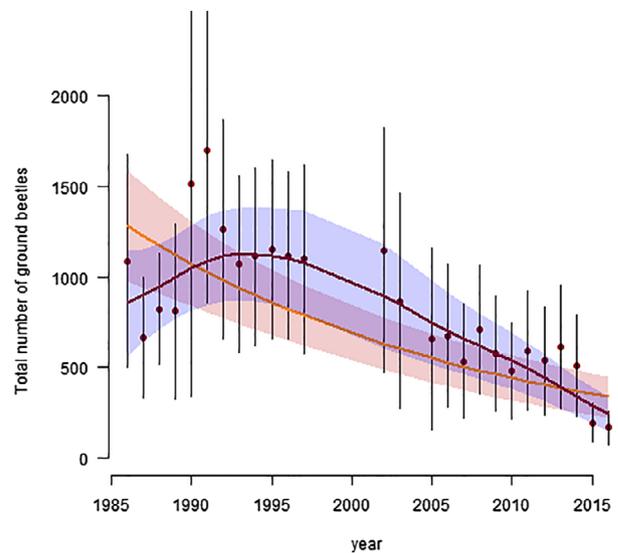


Fig. 4. Trends in total numbers of ground beetles (Coleoptera: Carabidae) in pitfalls near Wijster. [Color figure can be viewed at wileyonlinelibrary.com]

generalise to the national level, and we urge caution with extrapolating conclusions from these results to broader spatial levels.

On average, annual trends of macro-moths were negative (totals: -3.9% , mean species -4%) suggesting a proportionally uniform decline rate across abundance classes of this taxon. Since no relation was found between weight of the species and their annual trend, we conclude that the biomass reduction

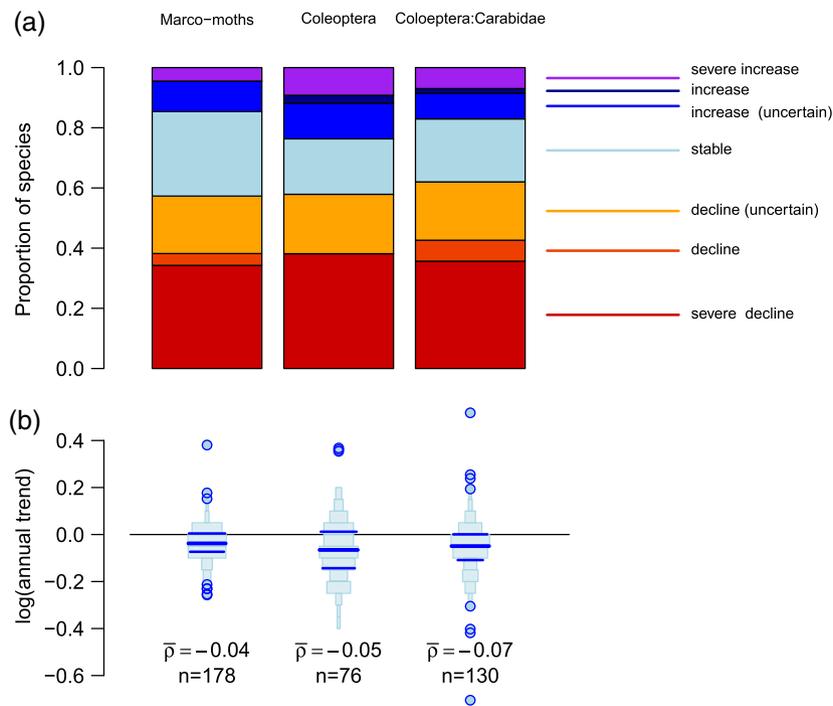


Fig. 3. Log of annual trend coefficient (ρ) of species of macro-moths ($n = 178$) and beetles in De Kaaistoep ($n = 76$) as well as ground beetles in Wijster ($n = 130$). (a) Barplots depicting trend classifications. (b) Distribution of trend coefficients. [Color figure can be viewed at wileyonlinelibrary.com]

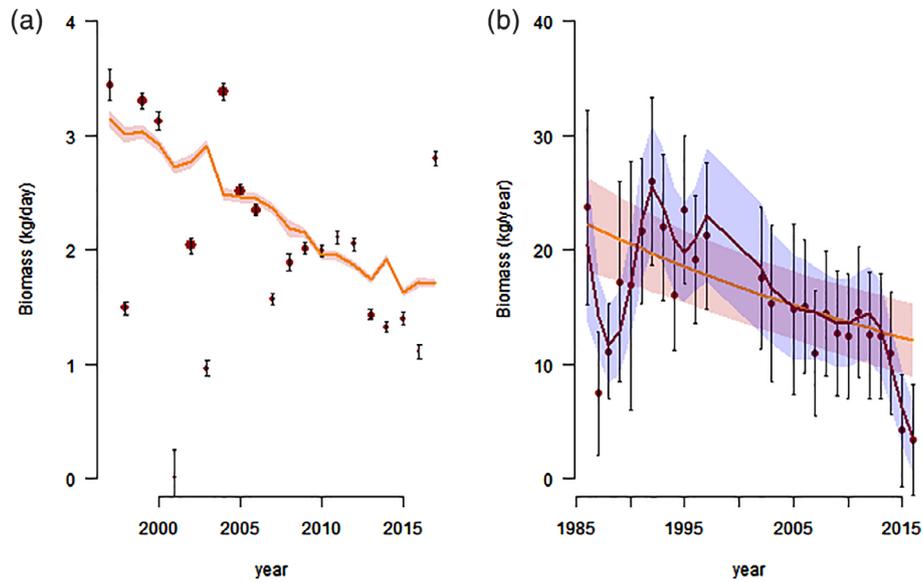


Fig. 5. Biomass trend of (a) macro-moths (Lepidoptera) per trapping night at De Kaaistoep and (b) ground beetles (Coleoptera: Carabidae) per year from pitfalls near Wijster. For each order, the annual indices (points), and estimates of the linear (orange) and non-linear (blue), trends are given. Evidence for non-linearity is only apparent in Ground beetles, while for the remainder of the macro-moths the estimated trends of the two species are indistinguishable. [Color figure can be viewed at wileyonlinelibrary.com]

(−3.3% per year) is shared proportionally among macro-moth species, with declines in abundant species naturally accounting for a larger extent of the biomass decline. Annual decline in total biomass of ground beetles (based on pitfall data), however, was less negative than the average of the individual species trend (totals −6%, mean species trend −7%, biomass −4%). Additionally, following corrections of several traits, a positive effect was found of weight on species trend (Fig. 7c). Here, the less

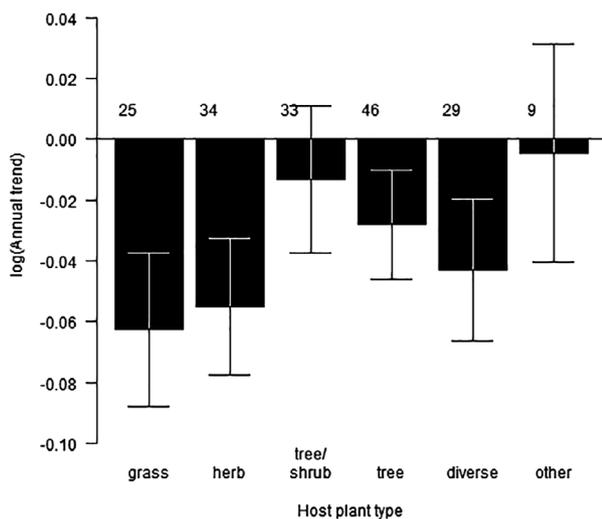


Fig. 6. Mean log annual trend coefficient (ρ , +95% confidence levels) of macro-moth species (in De Kaaistoep) with various types of host plants. The number of macro-moth species are indicated for each host plant category.

abundant and smaller species showed stronger declines than common or larger species, giving rise to a much lower decline rate in biomass as compared to the numerical declines. These results imply that the declines in insect biomass, although indicative to diversity loss, may not always show a one-to-one correspondence to numerical declines (Homburg *et al.*, 2019).

Identifying causes of insect population change was beyond the scope of this study. However, both areas are nature reserves managed with the prime aim to protect and restore biodiversity. In the Wijster region, our data series start a few years prior to 1995, where a peak in numbers (and species) of beetles occurred following restoration of degraded heath. It is possible that, for example, succession from open ground to more closed heath/forest over time may have impacted ground beetle communities. The more negative trends among specialised xerophilic species support this hypothesis. However, lowered trends were also observed among lighter species, and among habitat specialist (i.e. stenotopic) species, implying that succession is not the sole driver of decline here. Similarly, in De Kaaistoep, changes since the 1990s in management of forests and the transformation of the agricultural area into a more natural landscape, together with drying of grassland parcels have possibly affected macro-moth and other insect taxa. Indeed, species depending on grass and herb host plants seemed to be affected more severely in this area. Elsewhere (e.g. Habel *et al.*, 2019c) succession also has been found to be important in shaping moth communities. It has to be noted, however, that due to the attraction by light, species (e.g. moths) are drawn into the study site from a wider area. As such, our results may represent the surrounding environment as well as the local conditions. With the recent notions that biodiversity loss occurs at a landscape scale (Habel & Schmitt, 2018) and that more generalist and abundant species are equally

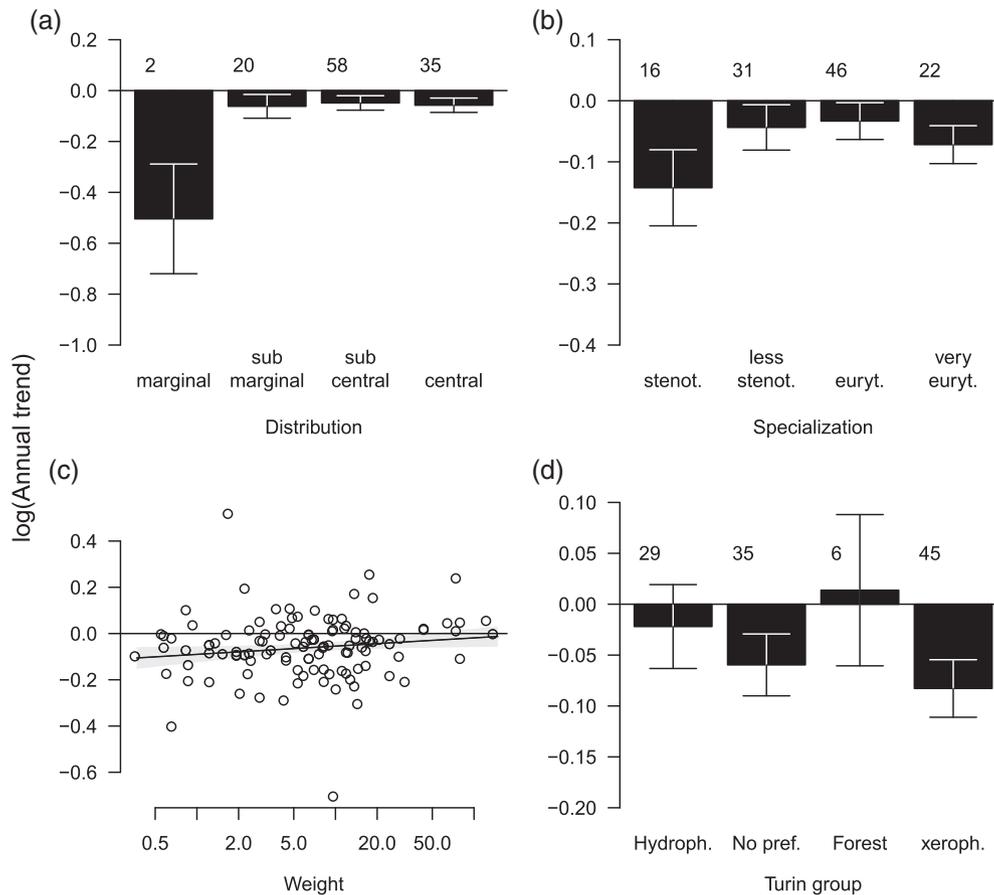


Fig. 7. Mean log annual trend coefficient (ρ , +95% confidence levels) of ground beetle species (in the Wijster region) for different levels of (a) distribution (ranging from species in the Netherlands being in the margin of their distribution to more in the center), (b) specialisation (ranging from stenotopic habitat specialist to eurytopic habitat generalists), (c) weight and (d) Turin (2000) classification depending on preferred habitats [i.e. hydrophilous, no preference, forest, xerophilous (adapted to dry conditions)].

affected as rare species, it may well be that our results regarding macro-moths reflect landscape health, rather than ‘only’ site-specific conditions.

Sometimes a decline or increase can be made very plausible. The decline of Coccinellidae, for example, could be explained by the introduction of the invasive ladybird *Harmonia axyridis*, first noted on the illuminated screen in 2003 and rapidly increasing in the following years (van Wielink, 2017a, b). On the other hand, the increase in carrion-beetles (Silphidae) can be explained by carrion experiments done at approximately 25 m from the light source in the period of 2015, 2016 and 2017. The significant decline in caddisflies (but not mayflies), being aquatic species, is surprising at first sight, because water quality is thought to have improved locally over recent years, with sensitive aquatic species (e.g. larvae of Odonata) showed positive population trends in a stream in De Kaaistoep about 1 km from the collection site (van Wielink & Spijkers, 2012). However, for dragonflies, Termaat and van Strien (2015) report a decline starting around 2008, quite similar to our results. It would require insect and environmental data from multiple sites to tease apart potentially positive effects of

improved water quality and negative effects from other environmental factors (such as eutrophication) and pollutants (including pesticides; Zahrádková *et al.*, 2009; Nakanishi *et al.*, 2018). Additional analyses integrating besides species traits, also habitat and landscape changes (e.g. road traffic, Martin *et al.*, 2018), are likely to increase our understanding of the present declines observed, and help delimit for which part these can be attributed to anthropogenic (e.g. nitrogen deposition and pesticide leaching) or natural (e.g. succession) factors.

In both data sets, the counts of individuals are a reflection of both abundance and activity of species. This implies that the numbers caught cannot be translated into a (relative) measure of abundance directly, but require accounting for effects of seasonality, phenology and weather. Moreover, inter-annual cyclic or erratic patterns in abundance of some species complicates the interpretation of trends, particularly so when shorter-term data underlie the calculations. Here, weather data and the inclusion of seasonality have improved the fit of the models for all orders examined in both areas. For three of the orders in De Kaaistoep, models with an annual index (a categorical covariate) were selected over linear or nonlinear (spline)

models, while second best were usually the nonlinear models. These results show the challenges associated with the erratic temporal behaviour of some insect populations, and the need for more complex models to accommodate sources of variation and bias. Despite our efforts, there is room for improvement in the trend calculations, for example, by incorporating species-specific detection probabilities, for which we currently do not have sufficient information. Hence, we cannot rule out that changes in species-specific detection rates and community composition may be for a small part responsible for the decline rates observed.

Comparison of the presented abundance trends with the German (−76% in biomass) and Puerto Rico (−98% in abundance) results (Hallmann *et al.*, 2017; Lister & Garcia, 2018) remains difficult because insect traps vary widely in which groups of insects are sampled (Russo *et al.*, 2011). The methods used in this study, collecting at light and pitfall traps, both sampled different species and numbers than the malaise traps that were deployed by the Krefeld Entomological Society in Germany, or sweep-netting and sticky-traps as applied in Puerto Rico. Furthermore, in the German study, total biomass of all insects caught in the Malaise traps was analysed, while here we focus on counts of important insect orders. Still, we made an attempt to compare our results with the reported 76% decline in total insect biomass over 27 year (Hallmann *et al.*, 2017). To do so, we estimated total biomass for macro-moths in De Kaaistoep and ground beetles near Wijster based on the assumption that published species-specific sizes and general size-weight relationships would be accurate enough to not affect the biomass estimates in a distorting way. For macro-moths, the biomass reductions amounted to 3.3% per year. Over an extrapolated period of 27 years, this amounted to a reduction of 61%, which is close to (but less than) the reported declines in Germany for total flying insect biomass. Ground beetles of the Wijster data set also showed a negative biomass trend, although at a less strong rate (mean = 2% per year). Over a period of 27 years, this would amount to 42% reduction in total biomass. Additionally, after 1995, the average rate of decline in biomass was more severe (4.1%), which, over a period of 27 years, would amount to 67%. Even higher rates of decline can be found depending on which locations are included (i.e. including only long series of locations results in more negative annual trends, Supporting Information Fig. S5). Given the latter, our results for the ground beetles in the heathlands and forests near Wijster are likely to be conservative. While we lacked the required species-specific information to estimate biomass trends for the other insect orders, the variable trends at the order level (e.g. severe decline in caddisflies, stable in true bugs) suggests that not all insect orders might have contributed equally to the decline in total insect biomass as suggested in the Krefeld study. Note, however, that elsewhere in Germany true bugs did show strong declines (Schuch *et al.*, 2019), suggesting that the present trends of true bugs might not be indicative for large-scale trends. Future research will hopefully disentangle these contributions by various insect groups in a quantitative analysis, which should also shed more light on the factors that are most instrumental in causing insect numbers and biomass to decrease this much.

Conclusions

In Dutch nature reserves, insects, particularly macro-moths, ground beetles and caddisflies, appear to be in considerable decline according to the studied datasets, as are lacewings, albeit with less certainty. Together with recent reports on butterflies (van Swaay *et al.*, 2018) at the national level, the limited information that is available suggests that many insect species in the Netherlands are in decline too (but not all, e.g. Termaat *et al.*, 2015), similar (but a little less negatively) to the trends reported for the German nature areas (Hallmann *et al.*, 2017) or in other regions (Lister & Garcia, 2018, Sánchez-Bayo & Wyckhuys, 2019). As such, we suggest that the declines in insects may be a widespread phenomenon not limited to nature areas in Germany only. The fact that these studies are based on data collected using different approaches strengthens this conclusion. Moreover, with exception of Hemiptera, our results suggest similar rates of decline as reported in a recent literature review study (Sánchez-Bayo & Wyckhuys, 2019).

Standardised networks to monitor the state of insects in the Netherlands are largely absent, or limited to few species groups only. Including a relatively broad spectrum of insect species, this study shows many species being in severe decline, but also few species increasing, and some groups being affected less or not at all. More detailed monitoring and ecological studies are thus required to shed light on the actual causes of decline. Structural funding and facilitation for developing such monitoring networks, possibly using citizen science, is highly required at the moment, as this would provide the information necessary to assess the state of entomofauna in the Netherlands, investigate drivers and to develop conservation guidelines. Further work should concentrate on formulating and testing plausible causes for the declines observed presently.

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Conflict of Interest

All authors declare that they have no conflict of interest.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting Information

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