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More than 75 percent decline over 27 years in total fly insect biomass in protected areas

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Abstract

Global declines in insects have sparked wide interest among scientists, politicians, and the g and abundance is expected to provoke cascading effects on food webs and to jeopardize ec of the extent and underlying causes of this decline is based on the abundance of single spe than changes in insect biomass which is more relevant for ecological functioning. Here, we u measure total insect biomass using Malaise traps, deployed over 27 years in 63 nature prot location-year combinations) to infer on the status and trend of local entomofauna. Our analy 76%, and mid-summer decline of 82% in flying insect biomass over the 27 years of study. W regardless of habitat type, while changes in weather, land use, and habitat characteristics ca yet unrecognized loss of insect biomass must be taken into account in evaluating declines ir insects as a food source, and ecosystem functioning in the European landscape.

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Introduction

Loss of insects is certain to have adverse effects on ecosystem functioning, as insects play including pollination [1, 2], herbivory and detrivory [3, 4], nutrient cycling [4] and providing a such as birds, mammals and amphibians. For example, 80% of wild plants are estimated to while 60% of birds rely on insects as a food source [5]. The ecosystem services provided by $57 billion annually in the USA [6]. Clearly, preserving insect abundance and diversity shoul priority.

Current data suggest an overall pattern of decline in insect diversity and abundance. For exa grassland butterflies are estimated to have declined by 50% in abundance between 1990 ar taxa such as bees [8–14] and moths [15–18] suggest the same trend. Climate change, habit deterioration of habitat quality have been proposed as some of the prime suspects responsil However, the number of studies on insect trends with sufficient replication and spatial covera restricted to certain well-studied taxa. Declines of individual species or taxa (e.g. [7, 26]) ma entomofauna [27]. The total insect biomass would then be a better metric for the status of in ecosystem functioning, but very few studies have monitored insect biomass over an extensi extent total insect biomass has declined, and the relative contribution of each proposed fact highly relevant questions for ecosystem ecology and conservation.

Here, we investigate total aerial insect biomass between 1989 and 2016 across 96 unique lo representative of Western European low-altitude nature protection areas embedded in a hur all years we sampled insects throughout the season (March through October), based on a s Malaise traps. We investigated rate of decline in insect biomass, and examined how factors variables influenced the declines. Knowledge on the state of insect biomass, and it's directic ecology and conservation, but historical data on insect biomass have been lacking. Our stuc and provides information that is vital for the assessment of biodiversity conservation and ec landscapes.

Materials and methods

Data

Biomass data.

Biomass data were collected and archived using a standardized protocol across 63 unique l (resulting in 96 unique location-year combinations) by the Entomological Society Krefeld. Th has been originally designed with the idea of integrating quantitative aspects of insects in th areas, and to construct a long-term archive in order to preserve (identified and not-identified studies. In the present study, we consider the total biomass of flying insects to assess the st

All trap locations were situated in protected areas, but with varying protection status: 37 loca seven locations within designated Nature reserves, nine locations within Protected Landsca measures), six locations within Water Protection Zones, and four locations of protected habi For all location permits have been obtained by the relevant authorities, as listed in the S1 Ap nutrient-poor heathlands, sandy grasslands, and dune habitats provide lower quantities of bi nutrient-rich grasslands, margins and wastelands. As we were interested in whether the dec traps locations were pooled into 3 distinct habitat clusters, namely: nutrient-poor heathlands cluster 1, n = 19 locations, Fig 1A), nutrient-rich grasslands, margins and wasteland (habitat a third habitat cluster that included pioneer and shrub communities (n = 3 locations).

Fig 1. Examples of operating malaise traps in protected areas in western Germany, in habitat cluster 1 methods).

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Most locations (59%, n = 37) were sampled in only one year, 20 locations in two years, five l years, yielding in total 96 unique location-year combinations of measurements of seasonal t not represent longitudinal records at single sites, suitable to derive location specific trends (years is in the present context (protected areas) deemed undesirable, as the sampling proce insect stocks. However, the data do permit an analysis at a higher spatial level, i.e. by treati random samples of the state of entomofauna in protected areas in western Germany.

Malaise traps were deployed through the spring, summer and early autumn. They operated catches were emptied at regular intervals, on average every 11.2 days (sd = 6.3). We collec average of 16 (4–35) successive catches per location-year combination (Table 1). Between invertebrates have been collected and stored, over a total trap exposure period of 16908 da days per location-year combination. Malaise traps are known to collect a much wider diversi compared to suction traps (e.g. [28]) and are therefore considered superior as a method of partial assessments, we can assume that the total number of insects included in 53.54 kg bi individuals.

Year	Number of locations	Number of locations sampled previously	Number of Samples	Mean exposure time	St. Dev exposure ti
1989	8	0	152	146.62	12.81
1990	2	0	82	228.00	34.65
1991	1	0	10	146.00	
1992	4	0	54	118.75	15.50
1993	4	0	38	109.50	58.74
1994	4	0	60	170.75	72.83
1995	2	0	41	144.00	83.34
1997	1	0	20	152.00	
1999	2	0	56	196.00	0.00
2000	2	1	47	174.00	11.31
2001	3	2	81	190.00	0.00
2003	3	1	80	201.00	7.81
2004	2	0	48	200.00	5.66
2005	4	0	70	188.75	30.53
2006	2	0	28	188.00	0.00
2007	2	0	15	197.00	0.00
2008	2	0	24	182.00	0.00
2009	4	0	23	120.50	2.89
2010	2	0	13	85.00	0.00
2011	1	0	4	68.00	
2012	2	0	23	158.50	4.95
2013	8	2	128	175.50	21.71
2014	23	15	348	212.74	11.21
2015	1	1	10	224.00	
2016	7	7	82	190.86	12.56

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Table 1. Overview of malaise-trap samples sizes.

For each year, the number of locations sampled, the number of location re-sampled, total
mean and standard deviation of exposure time at the trap locations (in days) are presente

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The sampling was standardized in terms of trap construction, size and design (identical part sealing, trap orientation in the field as well as slope at the trap location. Hence none of the t aspects. Our trap model was similar to the bi-colored malaise trap model by Henry Townes [and accompanying methods of biomass measurement as designed and applied by the Ento elsewhere [34–36] and in S2 Appendix.

Trap catches were stored in 80% ethanol solution, prior to weighing, and total insect biomas based on a standardized measurement protocol by first subtracting fluid content. In order to species determination, the insects were weighed in an alcohol-wet state. First, the alcohol c stabilized to 80%, while this concentration was controlled with an areometer over a period o biomass per sample with sufficient accuracy and comparability, the measuring process was [34]. For this purpose the insects of a sample were poured onto a stainless steel sieve (10cr sieve is placed slightly obliquely (30 degrees) over a glass vessel. The skew position accele the whole measuring procedure. The drop sequence is observed with a stopwatch. When th 10 seconds for the first time, the weighing process is performed with a laboratory scale. For precision scales and analytical scales from Mettler company were used with an accuracy of calibrated test weights at the beginning of a new weighing series. In a series of 84 weighting this measurement procedure, an average deviation from the mean value of the measureme (unpublished results).

Weather data.

Climate change is a well-known factor responsible for insect declines [15, 18, 21, 37]. To tes observed decline, we included mean daily temperature, precipitation and wind speed in our weather stations [38] located within 100km to the trap locations. We examined temporal tre course of the study period to assess changes in climatic conditions, as a plausible explanati weather variable at the trap locations were obtained by interpolation of each variable from th

We initially considered mean daily air temperature, precipitation, cloud cover, relative air mo sunshine duration. However, only temperature, precipitation and wind speed were retained f significantly correlated with the selected variables [R(temperature, cover) = –43.2%, R(temp R(precipitation, moisture) = –47.3%] and because we wanted to keep the number of covaria calculated the number of frost days and the sum of precipitation in the months November- F We used spatio-temporal geostatistical models [39, 40] to predict daily values for each weat Amongst other methods, the geostatistical approach is considered a superior interpolation m variables to trap locations [41]. Uncertainty in interpolated variables such as wind speed is u

differences. However, as our trap locations are all situated in lowland areas with little altitude
error in our interpolations at trap locations.

We decomposed the daily values of each weather variable into a long-term average trend (b
and a yearly seasonal anomaly component (S2 Fig), modeled using regression splines [42]
stations. The remaining residual daily values of each station were further modeled using a s
For example, temperature T, on given day t, of a given year k at a given trap location s is mo

$$T(t,s,k) = f_k(k) + f_t(t) + r(k,t) + a \times h + C_{s,t}$$

where $f_k(k)$ is the long-term trend over the years (a thin plate regression spline), $f_t(t)$ the mea
penalized cyclic cubic regression spline), $r(k, t)$ the mean residual seasonal component, whi
daily values across selected stations, and a is the linear coefficient for the altitude h effect. T
structure $C_{s,\ t}$, fitted independently to the residuals of each weather variable model, allowed
between daily weather data within and between stations, as well as to interpolate to trap loca
locations was extracted from a digital elevation models at 90m resolution [43].

Land use data.

Land use variables (and changes therein) were derived from aerial photographs [44] taken w
1989–1994, and between 2012–2015), and allowed us to characterize land use composition
changes over time. We distinguished cover of forests, agricultural areas, natural grassland,
location, aerial photographs were manually processed, polygons extracted and categorized,
a radius of 200 meter. Preliminary analysis of the relationship between log biomass and land
locations, indicated that land use elements at 200m radius better predicted insect biomass t
similar to findings elsewhere for wild bees [45]. Land use variables were measured at a coar
cover the temporal span of insect sampling. To link the cover of a given land use variable to
particular year, we interpolated coverage between the two time points to the year of insect s
models with a binomial error distribution, a logit link, and an estimated dispersion parameter
of the two time points are depicted in S3A & S3B Fig.

Habitat data.

Plant inventories were conducted in the immediate surroundings (within 50m) of the trap, in
These data permitted the assessment of plant species richness (numbers of herbs, shrubs a
based on average Ellenberg values [46–48], as well as changes therein over time. Each Elle
nitrogen, pH, light, temperature and moisture) was averaged over all species for each locatio
annual trends in each of the above-mentioned variables in order to uncover potential structu
over time. Species richness was analyzed using mixed-effects generalized linear models [49
location and assuming a Poisson distribution for species richness, and a normal distribution
Although a Poisson distribution fitted tree and shrub species adequately, (residual deviance/
respectively), severe overdispersion was found for herb species richness (residual deviance
coefficients of richness over time between a Poisson mixed effects model and a negative bin
differed in magnitude (Poisson GLMM: –0.034 (se = 0.003), vs NB GLMM –0.027 (se = 0.00
case of herb richness, we believe our trend adequately describes direction of change over ti
richness are depicted in S3C Fig.

Insect biomass model

The temporal resolution of the trap samples (accumulated over several days) is not directly c
distribution of the weather data (daily values). Additionally, variable exposure intervals betwe
variation in trapped biomass between samples, and hence induce heteroscedasticity. Furthe
only be positive on the real line, and we require a model to reflect this property of the data. E
intervals however, log-transforming the response would be inappropriate, because we requi

exponentiation, rather that the exponent of the sum of log-daily biomass values. In order to i weather variables, to account for the variation in time exposure intervals over which biomas to respect the non-negative nature of our data, we modeled the biomass of each catch as th unobserved) latent daily biomass. The mass *m* of each sample *j*, at site *s* in year *k*, is assun sum of the latent expected daily mass ($z_{t,s,k}$), with variance σ_j^2:

$$m_{j,s,k} \sim N(\mu_{j,s,k}, \sigma_j^2)$$

subject to $\mu_{j,s,k} = \sum_{t=\tau_1(j)}^{\tau_2(j)} z_{t,s,k}$ where τ_1 and τ_2 mark the exposure interval (in days) of biomas daily biomass itself is represented by a log normal distribution, in which coefficients for cova variance are all represented on the log scale. In turn, daily biomass is modeled as

$$z_{t,s,k} = e^{y_{t,s,k}}$$

$$y_{t,s,k} = c + log(\lambda)k + \mathbf{X}\beta_x + u_s$$

where *c* is a global intercept, **X** a design matrix of dimensions n×p (number of samples × nu below), β_X the corresponding vector of coefficients that measure the weather, habitat and lar annual population growth rate parameter. The random term (u_S) denotes the location-specifi distributed normally about zero $u_s \sim N(0, \sigma_{site}^2)$. The exponentiation of the right hand side of E positive.

The expected residual variance of each sample σ_j^2, is expressed as the sum of variances of

$$\sigma_j^2 = \sum_{t=\tau_1(j)}^{\tau_2(j)} \sigma_{t,s,k}^2$$

The variances of daily biomass should respect the non-negative nature of the data as well. A able to compare the residual variance with the random effects variance, and this requires th we expressed the variance of the daily biomass as a function of the variance of the logarithr method of moments:

$$\sigma_{t,s,k}^2 = e^{2y_{t,s,k}+v}(e^v - 1)$$

where *v* represents the residual variance of daily log-biomass.

Analysis

We developed a series of models each consisting of a set of explanatory variables that mea local habitat characteristics. Significant explanatory variables in these models were combine reduced to exclude insignificant effects. An overview of which covariates were included in ea

Covariate class	Covariate name	Null model	Basic	Weather	Habitat	Land use Interactions	Land use	Final model
Temporal	Intercept	✓	✓	✓	✓	✓	✓	✓
	Day number	✓	✓	✓	✓	✓	✓	✓
	Day number^2	✓	✓	✓	✓	✓	✓	✓
	Year		✓	✓	✓	✓	✓	✓
Climate	Temperature			✓				✓
	Precipitation			✓				✓
	Wind Speed			✓				
	Frost days			✓				✓
	Winter Precipitation			✓				
Habitat	Herb Species				✓			✓
	Tree Species				✓			✓
	Nitrogen				✓			
	pH				✓			
	Moisture				✓			
	Light				✓			✓
	Ellen. Temperature				✓			✓
	Habitat cluster 2	✓	✓	✓	✓	✓	✓	
	Habitat cluster 3	✓	✓	✓	✓	✓	✓	
Landscape	Arable land					✓	✓	✓
	Grassland					✓	✓	✓
	Forest					✓	✓	✓
	Water					✓	✓	✓
Interactions	Year × Day number		✓	✓	✓	✓	✓	✓
	Year × Day number^2		✓	✓	✓	✓	✓	✓
	Year × Agriculture						✓	✓
	Year × Forest						✓	✓
	Year × Water						✓	
	Year × Grassland						✓	✓
Variance	σ_{res}	✓	✓	✓	✓	✓	✓	✓
	[illegible]	✓	✓	✓	✓	✓	✓	✓

Table 2. Overview of covariates included in each of the seven models.

The year covariate yields the annual trend coefficient.

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Weather effects explored were daily temperature, precipitation and wind speed, as well as tl
precipitation in the preceding winter. Habitat effects explored tree and herb species richness
for nitrogen, pH, light, temperature and moisture, per location-year combination. Land use e
agricultural area, forest, grass, and surface water in a radius of 200m around the plot locatic

Parameter values are obtained by the use of Markov chain Monte Carlo (MCMC) methods b
Sampler [50]) invoked through R [51] and the R2Jags package [52]. JAGS model scripts are
in S1 and S2 Dataset. For each model, we ran 3 parallel chains each consisting of 24000 ite
every 10^{th} value as a way to reduce within chain autocorrelation. We used vague priors for a
for the residual and random effect variance components, and flat normal distributions (with v
parameters. Covariates in **X** were standardized prior to model fitting, with the exception of ye
variables (proportions within 0–1 range).

For all models, we computed the Deviance Information Criterion [53] (DIC) as well as the sq
between observed and mean posterior estimates of biomass on the log scale. Results are g
was assessed by the potential scale reduction factor [54] (commonly $\hat{R}$), that measures the
independent MCM chains (in all models, all parameters attained values below 1.02). For all
distribution of the trend coefficient did not confound any other variable by plotting the relevai
pairwise correlation coefficients.

model	npar	Deviance	DIC	pD	R^2	ΔDIC
Final	23	12082.48	12177.07	94.59	0.67	0.00
Weather	13	12178.84	12261.52	82.68	0.65	84.45
Land use+ Interactions	16	12336.22	12427.16	90.95	0.62	250.09
Habitat	15	12354.95	12445.93	90.98	0.62	268.86
Land use	12	12377.27	12453.23	75.97	0.61	276.16
Basic	8	12390.26	12465.08	74.82	0.61	288.00
Null	5	13230.65	13307.59	76.94	0.39	1130.52

Table 3. Results for 7 models ranked by Deviance Information Criterion (DIC).

For each model, the number of parameters, the Deviance Information Criterion, the effect
calculated R^2 and difference in DIC units between each model and the model with lowest
included in each model.

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Our basic model included habitat cluster (3 levels), a quadratic effect for day number, an an

of biomass change, and the interactions between the annual trend coefficient and the day nu
models each consisting of either weather variables (S1 Table), land use variables (S2 Table)
interactions between the annual rate of change and land use variables seemed plausible, a
these interactions (S3 Table). Finally, all significant variables were combined into our final m
an annual trend coefficient, season (linear and quadratic effect of day number), weather (ter
days), land use (cover of grassland and water, as well as interaction between grassland cov
herb and tree species as well as Ellenberg temperature).

Class	Variable	mean	sd	2.50%	97.50%	P	
Temporal	Intercept	2.460	0.233	1.983	2.891	0.000	***
	log(H)	-0.080	0.007	-0.094	-0.067	0.000	***
	Day number	-0.100	0.028	-0.155	-0.045	0.001	***
	Day number^2	-0.447	0.029	-0.504	-0.390	0.000	***
Weather	Temperature	0.304	0.022	0.263	0.347	0.000	***
	Precipitation	-0.071	0.034	-0.143	-0.009	0.014	*
	Frost days	-0.021	0.024	-0.067	0.025	0.194	
Land use	Habitat Cluster 2	0.420	0.162	0.080	0.729	0.007	**
	Habitat Cluster 3	0.332	0.237	-0.133	0.806	0.076	
	Arable land	-1.063	0.184	-1.420	-0.709	0.000	***
	Forest	-0.522	0.218	-0.947	-0.121	0.007	**
	Grassland	0.818	0.233	0.367	1.265	0.000	***
	Water	-0.327	0.175	-0.659	0.000	0.027	*
Habitat	Herb species	-0.054	0.043	-0.137	0.037	0.119	
	Tree Species	0.104	0.032	0.041	0.167	0.000	***
	Ell. Nitrogen	0.181	0.065	0.051	0.311	0.003	**
	Ell. Light	0.162	0.039	0.088	0.236	0.000	***
	Ell. Temperature	-0.071	0.031	-0.131	-0.011	0.018	**
Interactions	Year × Day number	-0.003	0.001	-0.006	-0.000	0.017	*
	Year × Day number^2	0.010	0.001	0.007	0.013	0.000	***
	Year × Arable land	0.047	0.008	0.031	0.064	0.000	***
	Year × Forest	0.035	0.010	0.016	0.055	0.000	***
	Year × Grassland	-0.059	0.014	-0.086	-0.033	0.000	***
Random effects	σ_{loc}	0.334	0.037	0.270	0.412		
Residual variation	ε	0.870	0.009	0.852	0.888		

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Table 4. Posterior parameter estimates of the final mixed effects model of daily insect biomass.
For each included variable, the corresponding coefficient mean, standard deviation and 9
P-values were calculated empirically based on posterior distributions of coefficients.
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Our estimate of decline is based on our basic model, from which we can derive seasonal es
year. The basic model includes only a temporal (annual and seasonal effects, as well as inte
distinction (additive effects only) as well as a random trap location effect. We here report the
weighted estimate of decline that accounts for the within season differences in biomass decl
decline was estimated by projecting the seasonal biomass (1-April to 30-October) for years
basic model, and then dividing the summed (over the season) biomass of 2016 by the sumn

Using our final model, we assessed the relative contribution (i.e. net effect) of the explanato
both combined and independently. To this aim we projected the seasonal daily biomass for t
kept covariates at their mean values during the early stages of the study period, and seconc
according to the observed mean changes (see S2 and S3 Figs). Difference in the total biom
projections are interpreted as the relative contribution of the explanatory variables to the dec
effects of each covariate were calculated by projecting biomass increase/decline as result o
in each variable separately, and expressing it as percentual change.

Our data provide repetitions across years for only a subset of locations (n = 26 out of 63). A
biomass may confound the estimated trend. To verify that this is not the case, we fitted our b
number and year interaction to avoid overparameterization) to the subset of our data that in
in more than one year. Seasonal profiles of daily biomass values are depicted in S4 Fig. Fin
two (of the three) habitat clusters (for which sufficient data existed; see Biomass Data) sepa
decline between them (S5 Fig).

Results

Following corrections for seasonal variation and habitat cluster (basic model, see Materials a
coefficient of our basic model was significantly negative (annual trend coefficient = −0.063, s
Based on this result, we estimate that a major (up to 81.6% [79.7–83.4%]) decline in mid-su

place since 1989 (Fig 2A). However, biomass loss was more prominent in mid-summer as c
season (Fig 3A), indicating that the highest losses occur when biomass is highest during the
seasonally weighted estimate (covering the period 1-April to 30-October; see methods) resu
decline over a 27 year period. The pattern of decline is very similar across locations that we
suggesting that the estimated temporal decline based on the entire dataset is not confounde
estimation of the annual decline based on 26 locations that have been sampled in more thar
rate of decline (76.2%[73.9–78.3%]).

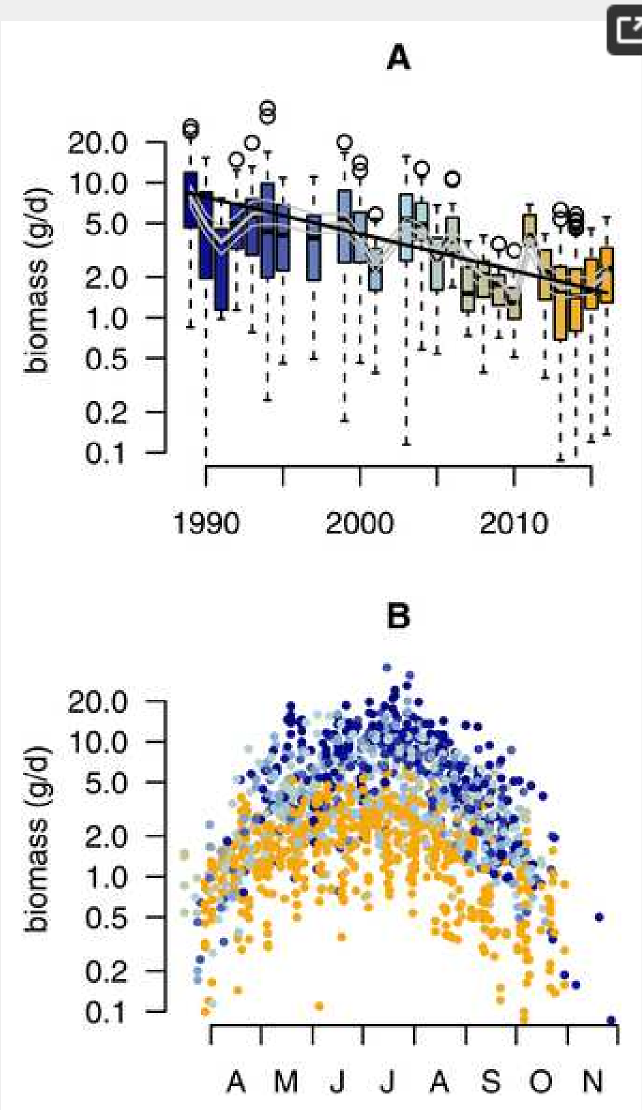

Fig 2. Temporal distribution of insect biomass.

(A) Boxplots depict the distribution of insect biomass (gram per day) pooled over all traps
1503). Based on our final model, the grey line depicts the fitted mean (+95% posterior cre
weather, landscape and habitat effects. The black line depicts the mean estimated trend a
(B) Seasonal distribution of insect biomass showing that highest insect biomass catches
declines. Color gradient in both panels range from 1989 (blue) to 2016 (orange).
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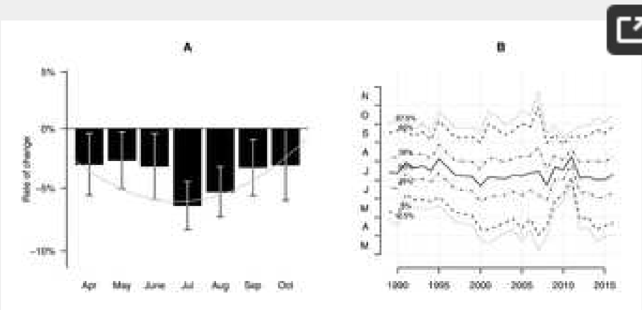

Fig 3. Seasonal decline and phenology.

(A) Seasonal decline of mean daily insect biomass as estimated by independent month s bars), and our basic mixed effects model with interaction between annual rate of change number in season. (B), Seasonal phenology of insect biomass (seasonal quantiles of bio locations revealing substantial annual variation in peak biomass (solid line) but no directi changes have occurred with respect to temporal distribution of insect biomass.

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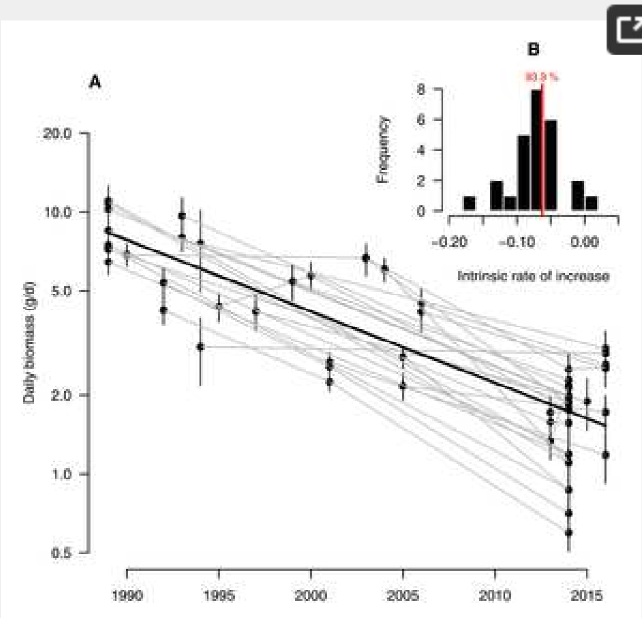

Fig 4. Temporal distribution of insect biomass at selected locations.

(A) Daily biomass (mean ±1 se) across 26 locations sampled in multiple years (see S4 Fi Distribution of mean annual rate of decline as estimated based on plot specific log-linear –0.053, sd = 0.002, i.e. 5.2% annual decline).

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Insect biomass was positively related to temperature and negatively to precipitation (S1 Tab revealed no effect of either number of frost days, or winter precipitation, on the biomass in th model fit improved as compared to our basic model (R^2 = 65.4%, Table 3), explaining within biomass, but not the overall decline (log(λ) = –0.058, sd = 0.002). Over the course of the stu occurred in the means of the weather variables (S2 Fig), most notably an increase by 0.5°C m/sec in mean wind speed. Yet, these changes either do not have an effect on insect bioma expected to positively affected insect biomass (e.g. increased temperature). Furthermore, a earlier in the season could have resulted in lower biomass in the mid-season (Fig 3A), but th none of the seasonal distribution quantiles in biomass showed any temporal trend (Fig 3B).

There was substantial variation in trapped insect biomass between habitat clusters (see Mat grasslands, margins and wasteland containing 43% more insect biomass than nutrient-poor dunes. Yet, the annual rate of decline was similar, suggesting that the decline is not specific further characterize trap locations, we used past (1989–1994) and present (2012–2015) aer cover within 200m around the trap locations. On average, cover of arable land decreased, c grassland and surface water did not change much in extent over the last three decades (S3 alone did not lead to a substantial improvement of the model fit (R^2 = 61.3%, Table 3), nor d ($\log(\lambda)$ = –0.064, sd = 0.002). While presence of surface water appeared to significantly lowe variables were significantly related to biomass. However, including interactions between the variables increased the model fit slightly (Table 3), and revealed significant interactions for a water (S2 Table). These interactions, which were retained in our final model (Table 4), revea coverage of grassland was higher, while lower declines where forest and arable land covera

We hypothesized that successional changes in plant community [55] or changes in environn affected the local insect biomass, and hence explain the decline. Plant species inventories tl vicinity of the traps and in the same season of trapping, revealed that species richness of tre significantly over the course of the study period (S3 Fig). Including species richness in our b and log number of herb species, revealed significant positive and negative effects respective the annual trend coefficient (S3 Table), explaining some variation between locations rather tl Moreover, and contrary to expectation, trends in herb species richness were weakly negativ biomass, when compared on per plot basis for plots sampled more than once. Ellenberg val indicator for the environmental conditions such as pH, nitrogen, and moisture [46, 47]. Arour (across all locations) were stable over time, with changes in the order of less than 2% over t these variables to our basic model revealed a significant positive effect of nitrogen and light, Ellenberg temperature on insect biomass, explaining a major part of the variation between tl values did not affect the insect biomass trend coefficient ($\log(\lambda)$ = –0.059, sd = 0.003, S3 Ta model fit (R^2 = 61.9%, Table 3). All habitat variables were considered in our final model (Tab moisture.

Our final model, based on including all significant variables from previous models, revealed to our basic model ($\log(\lambda)$ = –0.081, sd = 0.006, Table 4), suggesting that temporal developr variables counteracted biomass decline to some degree, leading to an even more negative marginal net effect of changes in each covariate over time (see Analysis), showed a positive temporal developments in arable land, herb species richness, and Ellenberg Nitrogen, while tree species richness and forest coverage (Fig 5). For example, the negative effect of arable combination with a decrease in coverage of arable land (S3 Fig), have resulted in a net posi Projections of our final model, while fixing the coefficient for the temporal annual trend $\log(\lambda)$ have remained stable, or even increased by approximately 8% (mean rate = 1.075, 0.849–1 period.

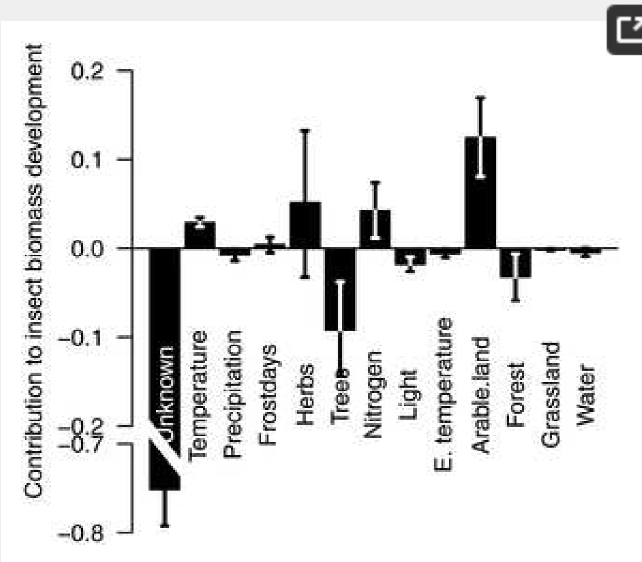

Fig 5. Marginal effects of temporal changes in considered covariates on insect biomass.
Each bar represents the rate of change in total insect biomass, as the combined effect of the temporal development of each covariate independently (S2 and S3 Figs).
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Discussion

Our results document a dramatic decline in average airborne insect biomass of 76% (up to 8
protected nature areas in Germany. This considerably exceeds the estimated decline of 58%
vertebrates over a 42-year period to 2012 [56, 57]. Our results demonstrate that recently rep
butterflies [7, 25–27, 58], wild bees [8–14] and moths [15–18], are in parallel with a severe lo
suggesting that it is not only the vulnerable species, but the flying insect community as a wh
last few decades. The estimated decline is considerably more severe than the only compara
biomass elsewhere [28]. In that study, 12.2m high suction traps were deployed at four locati
1973–2002, and showed a biomass decline at one of the four sites only. However, the samp
between the two studies. Suction traps mainly target high-flying insects, and in that study th
flies belonging to the Bibionidae family. Contrary, malaise traps as used in the present study
surface (up to 1 meter), with a much wider diversity of taxa. Future investigations should loo
among insect species, and how species trends contribute to the biomass decline.

Although the present dataset spans a relatively large number of years (27) and sites (63), th
years of seasonal distributions at the same locations) was lower (n = 26). We are however c
decline in total biomass resembles the true rate of decline, and is not an artifact of site selec
an annual rate of decline) outperformed the null-model (without an annual rate of decline; ΔI
the same time, between-plot variation (i.s. σ_{site}) and residual variation (v) decreased by 44.3
incorporating an annual rate of decline into the models. Secondly, using only data from sites
in at least two years, we estimated a rate of decline similar to using the full dataset (Fig 4), v
congruent across locations (S4 Fig). Taken together, there does not seem to be evidence th
this dataset forms a confounding factor to the estimated temporal trend, and conclude that c
representative for lowland protected areas in west Germany.

In light of previously suggested driving mechanisms, our analysis renders two of the prime s
climate change [15, 18, 21, 37], as unlikely explanatory factors for this major decline in aeria
protected areas. Habitat change was evaluated in terms of changes in plant species compos
locations, and in plant species characteristics (Ellenberg values). Land use changes was ev
changes in aerial photographs, and not for example changes in management regimes. Give

about 80%, much stronger relationships would have been expected if changes in habitat an
with the somewhat crude parameters that were at our disposal.

The decline in insect biomass, being evident throughout the growing season, and irrespecti
configuration, suggests large-scale factors must be involved. While some temporal changes
have taken place, these either were not of influence (e.g. wind speed), or changed in a man
biomass (e.g temperature). However, we have not exhaustively analysed the full range of cli
impact insect biomass. For example prolonged droughts, or lack of sunshine especially in lo
effect on insect biomass [59–62]. Agricultural intensification [17, 20] (e.g. pesticide usage, y
fertilizers and frequency of agronomic measures) that we could not incorporate in our analys
reserves in which the traps were placed are of limited size in this typical fragmented West-E
locations (94%) are enclosed by agricultural fields. Part of the explanation could therefore b
insect sources) are affected and drained by the agricultural fields in the broader surrounding
ecological traps) [1, 63–65]. Increased agricultural intensification may have aggravated this
protected areas over the last few decades. Whatever the causal factors responsible for the
devastating effect on total insect biomass than has been appreciated previously.

The widespread insect biomass decline is alarming, ever more so as all traps were placed i
preserve ecosystem functions and biodiversity. While the gradual decline of rare insect spec
time (e.g. specialized butterflies [9, 66]), our results illustrate an ongoing and rapid decline i
in space and time. Agricultural intensification, including the disappearance of field margins a
been associated with an overall decline of biodiversity in plants, insects, birds and other spe
67]. The major and hitherto unrecognized loss of insect biomass that we report here for prot
this discussion, because it must have cascading effects across trophic levels and numerous
urgent need to uncover the causes of this decline, its geographical extent, and to understan
ecosystems and ecosystem services.

Supporting information

S1 Appendix. Malaise trap permissions.

https://doi.org/10.1371/journal.pone.0185809.s001
(PDF)

S2 Appendix. Malaise traps.

https://doi.org/10.1371/journal.pone.0185809.s002
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S1 Code.

https://doi.org/10.1371/journal.pone.0185809.s003
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S1 Dataset.

https://doi.org/10.1371/journal.pone.0185809.s004
(CSV)

S2 Dataset.

https://doi.org/10.1371/journal.pone.0185809.s005
(CSV)

S1 Fig. Map of study area.

Insect trap locations (yellow points) in Nordrhein-Westfalen (n = 57), Rheinland-Pfalz (n = 1)
weather stations (crosses) used in the present analysis.
https://doi.org/10.1371/journal.pone.0185809.s006
(TIFF)

S2 Fig. Temporal variation in weather variables.

Annual means (A-C), daily means (D-F), and mean daily residual values (G-I) of temperatur
respectively. In all panels, black lines depict data while blue and red lines represent long ter
variables, respectively.
https://doi.org/10.1371/journal.pone.0185809.s007
(PDF)

S3 Fig. Land use and plant species richness changes.

Mean land use in 1989–1994 (A) and 2012–2014 (B), based on aerial photograph analysis a
of arable land and an increase in forested area over the past 25 years. (C) Changes in plant
shrubs (red) and trees (blue). Annual means as well as mean trends are depicted in the corr
based on generalized linear mixed effects models with a Poisson error distribution and a ran
zero values for tree and shrub species not depicted.
https://doi.org/10.1371/journal.pone.0185809.s008
(PDF)

S4 Fig. Seasonal profiles of daily biomass across 26 locations.

For each location, different colors represent different years, with time color-coded from gree
represents day number (January 1 = 0).
https://doi.org/10.1371/journal.pone.0185809.s009
(PDF)

S5 Fig. Daily biomass of insects over time for two habitat clusters.

Boxplots depict the distribution of insect biomass pooled over all traps and catches in each y
heathland, sandy grassland, and dunes (A), and in nutrient-rich grasslands, margins and wa
mean (+95% posterior credible intervals), while the black lines the mean estimated trend. Es
7.5%(6.6–8.4) for habitat cluster 1, as compared to 5.2% (4.8–5.5) habitat cluster 2. Models
location. Color gradient in all panels range from 1989 (blue) to 2016 (orange).
https://doi.org/10.1371/journal.pone.0185809.s010
(PDF)

S1 Table. Posterior parameter estimates of the mixed effects model including weather variables.

For each included variable, the corresponding coefficient posterior mean, standard deviation
P-values are calculated empirically based on posterior distributions of coefficients.
https://doi.org/10.1371/journal.pone.0185809.s011
(PDF)

S2 Table. Posterior parameter estimates of the mixed effects model including land use variables and inte

For each included variable, the corresponding coefficient posterior mean, standard deviation
P-values are calculated empirically based on posterior distributions of coefficients.

https://doi.org/10.1371/journal.pone.0185809.s012
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S3 Table. Posterior parameter estimates of the mixed effects model including habitat variables.

For each included variable, the corresponding coefficient posterior mean, standard deviatior
P-values are calculated empirically based on posterior distributions of coefficients.
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(PDF)

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